ORIGINAL PAPER

Temperature effects on vital rates of different life stages and implications for population growth of Baltic sprat

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Abstract Baltic sprat (*Sprattus sprattus balticus* S.) is a key species in the pelagic ecosystem of the Baltic Sea. Most stocks of small pelagic species are characterized by natural, fishery-independent fluctuations, which make it difficult to predict stock development. Baltic sprat recruitment is highly variable, which can partly be related to climate-driven variability in hydrographic conditions. Results from experimental studies and field observations demonstrate that a number of important life history traits of sprat are affected by temperature, especially the survival and growth of early life stages. Projected climate-driven warming may impact important processes affecting various life stages of sprat, from survival and development during the egg and larval phases to the reproductive output of adults. This study presents a stage-based matrix model approach to simulate sprat population dynamics in relation to different climate change scenarios. Data obtained from experimental studies and field observations were used to estimate and incorporate stage-specific growth and survival rates into the model. Model-based estimates of population growth rate were affected most by changes in the transition probability of the feeding larval stage at all temperatures ($+0$, $+2$, $+4$, $+6$ °C). The maximum increase in population growth rate was expected when ambient temperature was elevated by 4 °C. Coupling our stage-based model and more complex, biophysical individual-based models may reveal the processes driving these expected climate-driven changes in Baltic Sea sprat population dynamics.

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Introduction

Sprat (*Sprattus sprattus* L.) is a small planktivorous marine pelagic clupeoid species with a wide latitudinal distribution in shelf areas of the Northeast Atlantic and is a key trophodynamic player in the Baltic pelagic ecosystem (MacKenzie and Köster 2004; Peck et al. in press). On the one hand, sprat serves as main prey item for Baltic cod (*Gadus morhua*) (Rudstam et al. 1994) while, on the other hand, it is the most abundant planktivorous fish species in the Baltic Sea. Predation pressure by sprat on ichthyoplankton can not only affect the recruitment of Baltic cod but also plays an important role in regulating its own populations through cannibalism (Köster and Möllmann 2000). It also can exert top–down control on zooplankton in both near and offshore areas of the Baltic Sea (Möllmann et al. 2004).

Baltic sprat recruitment is highly variable, which can be partly explained by changes in atmospheric forcing and environmental conditions (Köster et al. 2003; MacKenzie and Köster 2004; Baumann et al. 2006a, b; Dickmann et al. 2007; Peck et al. in press). Among abiotic factors, ambient temperature plays a central role in pacing metabolism and growth, especially in the Baltic where sprat is located at its northernmost limit of distribution (Muus et al. 1999). Several important life history parameters of sprat are

directly affected by temperature. For instance, rates of development and survival of early life stages (Petereit et al. 2008; Peck et al. in press) and the maturation and batch fecundity of adult sprat (Petrova 1960; Haslob 2011; Haslob et al. 2011) depend upon temperature. During ontogeny, different sprat life stages encounter pronounced differences in ambient temperature due to stage-specific differences in vertical distribution in the highly stratified Baltic Sea (Fig. 1a; Nissling et al. 2003; Voss et al. 2007; Baumann et al. 2008) and seasonal timing of peak occurrence (Peck et al. in press). In addition to these intra-annual differences in temperature, a long-term warming trend has been observed in response to global climate change. For example, temperatures in the surface (MacKenzie and Schiedek 2007) and in the deep water layers (MacKenzie and Köster 2004) have increased within the last three decades and are projected to continue to increase during the twenty-first century (Meier 2006). A future warming scenario, as predicted by the IPCC (2007), is likely to affect all depth strata in the Baltic, and hence all life stages of sprat, since the turnover rate of the entire water body in the deep basins of the Baltic is comparatively high (Meier 2005). In addition, increased precipitation within the Baltic watershed in combination with less frequent inflow events of more saline North Sea water is predicted to lower salinities (Meier 2006), which will in turn affect the vertical distribution of and hence ambient temperature experienced by sprat early life stages (Petereit et al. 2009).

For the earliest life stages of sprat, eggs, and yolk-sac larvae, the direct effect of temperature on survival has been examined in laboratory experiments (Nissling 2004; Petereit et al. 2008). In general, survival is low at temperatures colder than 4 °C and warmer than 17 °C (Peck et al. in press). Thermal windows of species contain regions of optimal and suboptimal growth (Pörtner and Farrell 2008;

Pörtner and Peck 2010). In terms of the total, tolerable range of temperatures, sprat eggs and larvae in the Baltic Sea often experience ambient temperatures that are suboptimally cold and that are expected to reduce the rates of growth. Reduced growth rate can indirectly act to decrease survival via increases in inter- and intra-species competition, losses due to predation, and the potential for more severe mismatch situations with prey. Up to the optimal temperature, warmer temperatures are expected to increase the probability of survival and the chances of successful development through successive life stages. Observational data summarized by Peck et al. (in press) indicated that the optimum temperature increases as sprat develops from early larvae through the juvenile period but that feeding larvae have the narrowest range in suitable temperatures. In the adult stage, temperature may play a key role in population dynamics by affecting the reproductive potential of the stock, either by directly affecting growth physiology and egg production or indirectly by impacting prey availability, growth potential, and thus egg production.

Despite knowledge on individual life stages, the relative impacts of temperature-driven processes on sprat recruitment are still poorly understood. One step toward understanding key processes is to identify how critical life stages are affected by key environmental factors. However, in the case of sprat, where all life stages may respond somewhat differently to climate-driven warming, investigating the cumulative effects is most desired. A promising approach to address such differential effects is a stage-based population modeling (Leslie 1945; Lefkovitch 1965), a popular method used to explore life cycle dynamics in other small pelagic fishes (e.g., Rosenberg and Doyle 1986; Butler et al. 1993; Pertierra et al. 1997; Mantzouni et al. 2007). This approach accounts for changes in the vital rates of each specific life stage and thus enables the identification
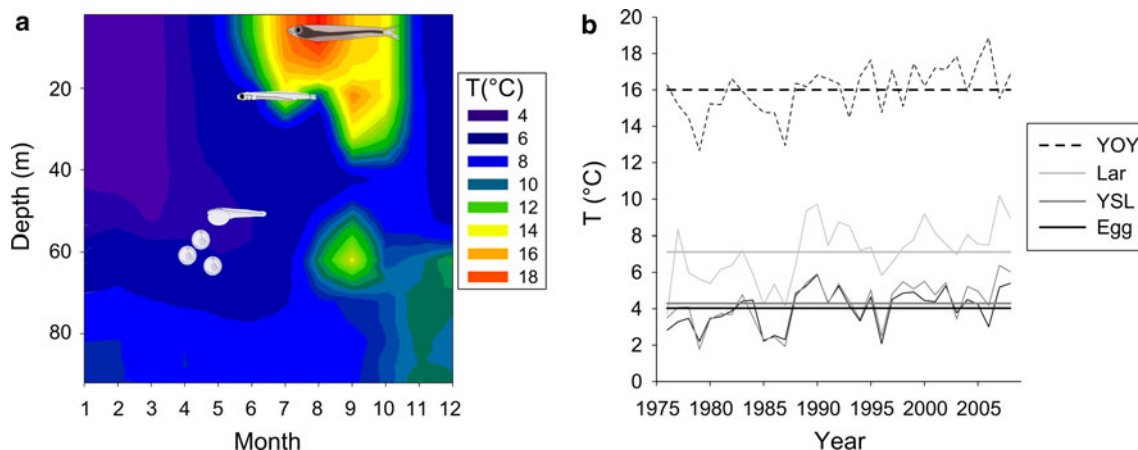

Fig. 1 Typical seasonal temperature distribution in the Bornholm Basin with conceptual distribution pattern of specific sprat life stages (a). Life stage-specific ambient temperature development over the

past 30 years in the Bornholm Basin (b) and ambient mean temperatures (*dashed lines*). *YSL* yolk-sac larvae, *Lar* feeding larvae, and *YOY* young of the year sprat

of the most critical life stages in terms of population response to environmental forcing (Caswell 2001).

In the present study, we introduce the first application of a stage-based matrix model for sprat. For this approach, a Lefkovitch matrix (Lefkovitch 1965) was used, which is an elegant and straightforward computational setup accounting not only for survival rates but also for the probability of growth and development from one life stage to the next. To test the impact of climate-driven warming on the population dynamics of Baltic sprat, we parameterized response functions of sprat vital rates in relation to temperature. We applied published or derived temperature-dependent functions of development, mortality, and reproduction to investigate the impact of different, predicted temperature scenarios (IPCC 2007) on the transition and survival probabilities of the different stages and the resulting response of the population growth rate.

Materials and methods

Life table matrix approach

The life table matrix describes the transition of a population from time t to time $t + 1$ in terms of (i) the probability of surviving and staying in stage i, (ii) the probability of surviving and growing into stage $i + 1$, and (iii) the reproductive rate per stage and unit time. To construct such a model, three important stage-specific life history traits have to be known: (i) the duration of a specific life stage, (ii) the stage-specific mortality or probability of survival, and (iii) the stage-specific reproduction output. We used a Lefkovitch matrix ($\mathbf{A}$) to describe the transition of a population from time t to time $t + 1$ in terms of vital rates of each life stage (Caswell 2001):

$$\mathbf{A}n_t = n_{t+1} \tag{1}$$

where n_t is a vector describing the population at each stage time t and $\mathbf{A}$ is the transition matrix:

$$\mathbf{A} = \begin{pmatrix} P_1 & m_2 & \cdot & \cdot & \cdot & m_q \\ G_1 & P_2 & 0 & \cdot & 0 & 0 \\ 0 & G_2 & P_3 & 0 & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & & G_q - 1 & P_q \end{pmatrix} \tag{2}$$

where P_i is the probability of surviving and staying in stage i, G_i is the probability of surviving and growing into the next stage, and m_i is the maternity per fish per unit time (d); $i = 1,\dots,q$.

The calculation of P_i and G_i follows Butler et al. (1993) and Caswell (2001). The dominant eigenvalue λ of the transition matrix indicates whether the population is growing ($\lambda > 1$), is stable ($\lambda = 1$), or is declining ($\lambda < 1$). The

Table 1 Summary of the six life stages used in the matrix model, the long-term mean ambient temperature (°C) experienced by the respective stages, functions used to describe stage-specific development time D (d) or growth LG (mm d^{-1}), and mortality z in relation to ambient temperature (T) with references to data sources from which these functions were derived. In adult fishes (age1 and 2+), stage duration is constant and corresponds to age

Life stage	Mean ambient temperature (°C)	Growth/development model	Ref	D_{base}	Mortality model	Ref	Z_{base}
Egg (until hatch)	4.03	D_{egg} (d) $= 19.0949 \times e^{(-0.1163 \times T)}$	[1]	11.95	$Z_{egg} = 0.5607 \times e^{(-0.4994 \times T)} + 0.0121 \times T - 0.0582$	[2]	0.065
Yolk-sac larvae (3–5 mm SL)	4.29	D_{ysl} (d) $= 30.71 \times e^{(-0.12 \times T)}$	[2]	18.35	$Z_{ysl} = 0.002 \times e^{(01622 \times T)}$; for T > 6 °C $Z_{ysl} = \frac{0.7841}{1+e^{(\frac{-T - 33206}{-0.7324})}}$; for T < 6 °C	[2]	0.165
Feeding larvae (5–40 mm SL)	7.12	LG_{lar} (mm d^{-1}) $= -0.0023 \times T^2 + 0.0545 \times T + 0.022$	[3]	119.27	$Z_{lar} = 0.045$**	[5]	0.04
Young of the Year (40–90 mm SL)	16.00	LG_{yoy} (mm d^{-1}) $= -0.0024 \times T^2 + 0.0964 \times T - 0.1562$	[4]	64.78	$Z_{yoy} = 0.012$	[6]	0.012
Age 1	4.13*	D_{age1} (d) $= 365$		365	$Z_{age1} = 0.0017$	[6]	0.0017
Age 2+	4.13*	D_{age2} + (d) $= 2190$		2,190	$Z_{age1} = 0.0011$	[6]	0.0011

References: derived from data published by [1] Petereit et al. (2008), [2] Nissling 2004, [3] Clemmesen et al. (2011), [4] Peck et al. subm., [5] Haslob unpubl., [6] MSVPA, ICES (2006)

* Ambient temperature calculated for adult stages is mean winter temperature for the whole water column (quarter 1)

** Daily mortality of feeding larvae was tuned to obtain a stable population as base model run. Duration (D_{base}) and daily mortality (Z_{base}) for the base model run without temperature change

Fig. 2 Conceptual stage-based population model for Baltic sprat. P_i = survival probability, G_i = transition probability, EP_i = reproductive output in produced eggs per individual. *YSL* yolk-sac larvae, *Lar* larvae, *YOY* young of the year sprat, *Age 1* one year old sprat, and *Age 2+* two year old sprat and older
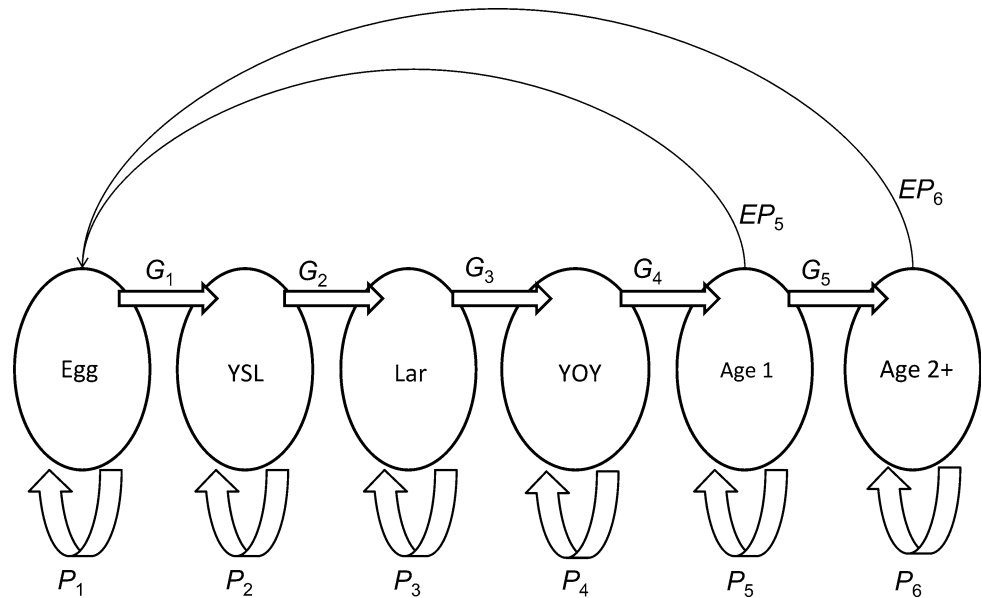
intrinsic growth rate r is given by the natural logarithm of λ. Growth and survival probabilities and thus population growth rate were calculated on a daily basis. To yield annual population growth, λ^{365} was calculated and used to compare effect sizes of different life history trait simulations. The eigenvalues of the population transition matrix were computed using the software "poptools" (Hood 2008).

For the Baltic sprat population matrix, six life stages were defined: eggs, yolk-sac larvae, feeding larvae, young of the year (YOY), adult 1, and adult 2 (Table 1; Fig. 2). The size ranges of the early life stages (yolk-sac larvae to young of the year) follow observed values from the literature (Nissling 2004; Baumann et al. 2008; Petereit et al. 2008; Peck et al. in press). Two adult stages were defined: 1-year-olds in which a highly variable portion can be mature in any year (ICES 2002) and specimens of 2 years and older that are generally all mature. The sizes of the adult stages were obtained from age length keys developed from fishery surveys within the Bornholm Basin (Haslob 2011).

Parameterization of vital rates

To build a model that can provide estimates on how temperature affects population growth rate, temperature-dependent functions of the matrix input parameters were developed. In the case of eggs and yolk-sac larvae, temperature-dependent daily mortality and growth rates were derived from the literature data (Table 1).

For feeding larvae, the effect of temperature on growth rate (mm day^{-1}) was derived from observed RNA/DNA data of field caught Baltic sprat larvae (dataset presented in Clemmesen et al. 2011). Based upon RNA/DNA values of individual larvae and in situ temperature (upper 30 m), weight-specific growth rates (d^{-1}) were calculated using the model

published by Buckley et al. (2008) and converted to length growth (mm d^{-1}) using the weight and length of the individual larvae at catch and the allometric length–weight relationship published in Peck et al. (2005). A dome-shaped polynomial regression ($r^2 = 0.81$, optimum growth at 11.9 °C, Table 1) was fitted to mean length growth data in relation to in situ temperature (nearest °C). Stage duration D_{lar} (d) was then estimated assuming constant growth (mm d^{-1}) by dividing the size interval (35 mm) by the growth rate.

The effect of temperature on the mortality of feeding sprat larvae has not been examined in controlled laboratory studies. Thus, mortality rates were estimated from ichthyoplankton surveys conducted in the Bornholm Basin from 2000 to 2008 (Table 1) by converting abundance-at-length to abundance-at-age using the temperature-dependent growth model. Mortality rates were then obtained by fitting exponential decay models through the abundance data. Since no temperature dependence was observed, a mean value for all years was used, which was subsequently tuned to yield a stable start population ($\lambda = 1$) for the simulations facing no change in ambient temperature.

Temperature-dependent growth of YOY sprat was derived from experimentally obtained temperature-dependent RNA–DNA ratios (Peck et al. in press) and converted to weight-specific growth rate using a linear relationship (Peck, unpubl data). The corresponding increase in length was estimated from published length–weight relationships of different size classes of sprat (Peck et al. 2005), and its relationship to temperature was best described with a quadratic function (Table 1). YOY stage duration D_{yoy} (d) was then estimated assuming constant growth (mm d^{-1}) by dividing the size interval (50 mm) by the growth rate. Mortality rates for YOY sprat were estimated from data provided by a multi-species virtual population analysis

(MSVPA, ICES 2006). For this purpose, the exponential decline in abundance of age 0 (4th quarter) to age 1 (1st quarter of following year) was estimated each year from 1974 to 2005. Since no temperature dependency was detected, a mean value was calculated and used for the subsequent matrix modeling.

The effect of temperature on growth rates of adult sprat is unknown and, consequently, the stage duration of the two adult stages was kept constant. As the first adult stage corresponds to age group one fish and the second adult stage contains fish from 2 to 7 years in age, the durations for these two stages were set to 365 and 2,190 d, respectively (Table 1). Adult life stage mortality was derived from MSVPA data as in the case of YOY fish. For the first adult stage, mortality rates of age 1 fish were used and for the second adult stage, the mean mortality of fish age 2 and older was estimated. The fecundity per fish was estimated by using length-dependent models of sex ratio (i.e., proportion mature females), daily spawning fraction (i.e., proportion females with hydrated oocytes), and batch fecundity. Among these reproductive parameters, the length at first maturation and the batch fecundity were affected by ambient temperature (Table 2). The spawning period was assumed to last 60 d, a mean time series value, when at least half of the population was observed to be in spawning condition (Haslob unpubl). The total annual egg production per fish within this period was then divided by 365 to yield average daily egg production per fish in the model. A possible effect of ambient temperature on the overall duration of spawning season and its interaction with batch fecundity are unknown and were thus not considered.

In order to get a baseline for the population model, ambient temperatures for specific life stages were calculated. Hydrographic data were obtained from the ICES oceanographic data base for the years 1976–2008 (http://ocean.ices.dk). Observations on the seasonal occurrence and vertical distribution of the early life stages were used to calculate the mean ambient temperatures for the stage-specific depth strata (Nissling et al. 2003; Voss et al. 2007;

Baumann et al. 2006a, b). For the adult stages, mean ambient winter temperature (entire water column) was calculated since proportion mature sprat and batch fecundity are affected by this temperature. Then, all stage-specific ambient temperatures were increased by 2, 4, and 6 °C to mimic different climate change scenarios predicted by the IPCC (2007). The effect of specific life stages on population response was investigated by (i) simulating changes in mortality rates and growth rates of feeding larvae and YOY juveniles, and (ii) elasticity and sensitivity analyses (Crouse et al. 1987; Caswell 2001).

Results

Specific sprat life stages have been observed within a wide range of temperatures (Fig. 1). Sprat eggs and yolk-sac larvae are located at depths having the coldest ambient temperatures, whereas feeding larvae occur in upper water layers during the second quarter. The warmest temperatures are experienced by YOY sprat during the third quarter of the year in surface water layers. An increasing trend in ambient temperatures during the last 30 years can be seen in all depth layers (Fig. 1b).

The base transition matrix for the population facing no temperature change is displayed in Table 3. At cold temperatures, daily mortality rates (and transition probabilities)

Table 3 Population matrix for Baltic sprat based on stage-specific vital rates for ambient temperatures

| Egg	YSL	Larvae	YOY	Age 1	Age 2+
0.8832	0	0	0	0.9873	45.0948
0.0534	0.8403	0	0	0	0
0	0.0078	0.9561	0	0	0
0	0	0.0002	0.9778	0	0
0	0	0	0.0101	0.9963	0
0	0	0	0	0.0020	0.9988

Stage abbreviations as in Fig. 2

Table 2 Models used to estimate the daily fecundity per fish with data sources and references

Parameter	Model	
Sex ratio (PF_L) as proportion of females per length class L (cm)	$PF_L = 0.35 + \dfrac{0.65}{1 + e - \left(\frac{L - 13.38}{0.67}\right)}$	[1]
Proportion mature (P_m) as function of length class L (cm). Parameter L_{50} dependent on ambient winter T (°C)	$P_m = \dfrac{0.99}{1 + e - \left(\frac{L - L_{50}}{0.61}\right)}$	[1]
L_{50} in relation to ambient winter temperature T (°C)	$L_{50} = 12.34 - 0.66 \times T$	[1]
Spawning interval (SI_L) per length class L (cm) in days	$SI_L = \left(\dfrac{0.28}{1 + e\left(\frac{-1 \times (L - 10.23)}{0.70}\right)}\right)^{-1}$	[2]
Batch fecundity (BF) in relation to fish length class L (cm) and ambient winter temperature T (°C)	$BF = 359.54 \times L \times e^{\left(-0.5\left(\frac{\ln\left(\frac{T}{6.97}\right)}{1.46}\right)\right)^2} - 2753.16$	[3]

References: [1] survey data Bornholm Basin 1999–2009 (Haslob 2011), [2] derived from data published in Haslob (2011) [3] Haslob et al. (2011)

Fig. 3 Daily mortality rates z (*circles*) and transition probabilities G_i (*triangles*) in relation to ambient temperature for sprat eggs (**a**) and sprat yolk-sac larvae (**b**)
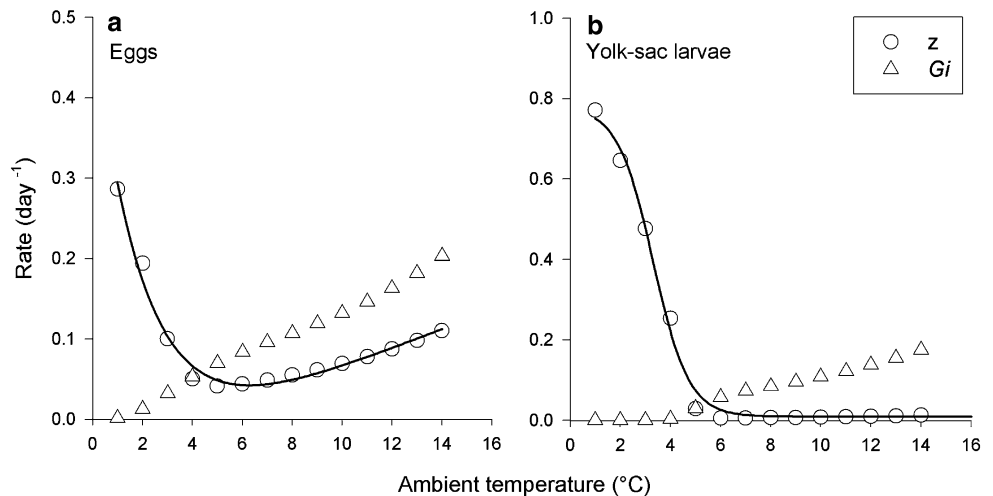
for sprat eggs and yolk-sac larvae were estimated to be high (low) and increased (decreased) with increasing temperature (Fig. 3a, b). Yolk-sac larvae seem to be more sensitive to extremely low temperatures compared to eggs, but exhibit lower mortality rates in warmer temperatures. Daily mortality rates for eggs reached a minimum at 5 °C and increased beyond this temperature due to decreased stage durations. The transition probability, that is, to survive and to grow into the next stage, increases linearly with temperature. Due to the extremely high daily mortalities of yolk-sac larvae at low temperatures in combination with relatively long stage durations, the transition probability was virtually 0 (zero) until 5 °C. Beyond this value, the transition probability increases also linearly with temperature. Similar to the egg stage, the daily mortality rates of yolk-sac larvae increase again with increasing ambient temperature due to the decrease in stage duration. This increase is very subtle within the range of investigated temperatures. However, at temperatures warmer than 6 °C, an exponential growth function was employed to more accurately estimate the daily mortality for yolk-sac larvae.

The length growth rate of feeding larvae in relation to temperature was best described by an optimum curve (Table 1) with a maximum at 11.8 °C. A similar optimum function was found for YOY sprat (Table 1) that suggested a maximum growth rate (mm day^{-1}) at 20.1 °C, a value which can be reached in Baltic surface waters in late summer.

The mean (±SD) mortality rate of feeding larvae estimated from field data was 0.16 (±0.07) d^{-1}, covering a range between 0.05 and 0.34 d^{-1}. Inputting the mean daily mortality to the transition matrix resulted in a negative population growth rate ($r = -0.44$, Fig. 5a). A stable population in the base model run was obtained by tuning this mortality term to 0.04 d^{-1}, a value slightly lower than the lowest observed mortality rate from field data.
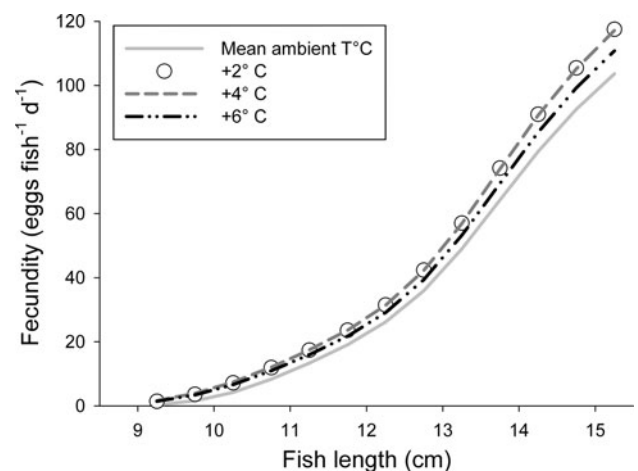

Fig. 4 Modeled length class–specific daily fecundity per fish in relation to changes in temperature

Simulations revealed that the direct influence of temperature on length-specific fecundity per fish was rather low (Fig. 4). Fecundity was predicted to increase with a 2 and 4 °C increase but was predicted to decline with a 6 °C increase (Table 1). Both sensitivity and elasticity of λ to reproduction were always lower than to the survival and transition probabilities of all stages.

Simulations of changes in feeding larvae mortality resulted in pronounced effects on λ. An increase of ambient temperature by 2 and 4 °C resulted in a positive λ in cases where the mortality was reduced by at least 60 % (Fig. 5a). When increasing the ambient temperature by 6 °C, the population growth rate started to decline. As expected, a reduction in the estimated daily mortality rates of YOY sprat also resulted in higher values of λ (Fig. 5b), but the increase was less than when temperature-dependent changes in feeding larval mortality were tested. A slight increase in ambient temperature results in an increase in λ since the population was initiated at a steady state

Fig. 5 Simulated effects of changes in larval mortality (**a**), young-of-the-year mortality (**b**), larval growth rate (**c**), and YOY growth rate (**d**) on the model population growth rate r. Changes in respective parameters are given in percent
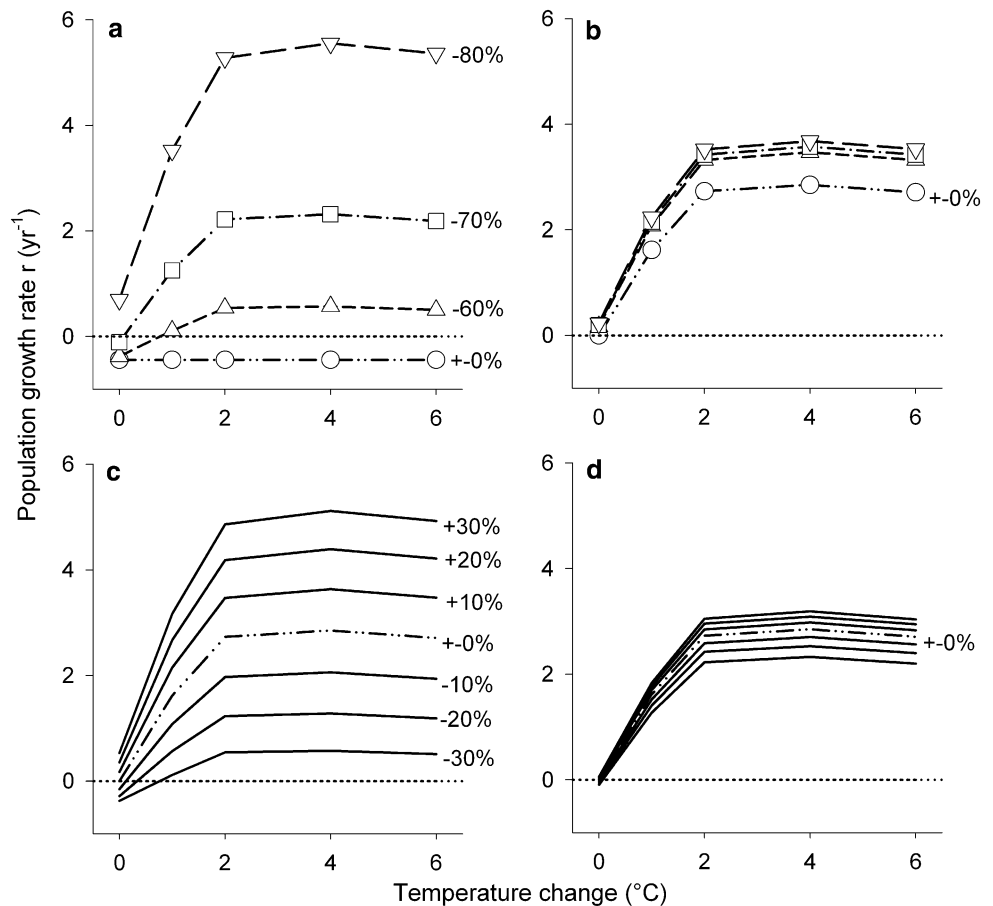
(Fig. 5b). Without reducing the mortality, an increase of 2 °C in ambient temperature results in a 270 % increase in λ. In contrast to the case of feeding larvae, a drastic (80 %) reduction in mortality did not result in a proportional increase in λ. A further increase of ambient temperature only caused a slight increase in λ and a 6 °C increase caused a decline (Fig. 5b). The simulations on reduced mortality of feeding larvae and YOY indicated a higher sensitivity of λ to larval mortality than to YOY mortality.

Similar results were obtained by simulating changes in the growth rate of feeding larvae and YOY sprat. While λ was quite sensitive to changes in larval growth rate (Fig. 5c), the impact of changes in YOY growth rate to λ was relatively small (Fig. 5d). In both cases, increasing ambient temperatures resulted in a pronounced increase in λ, being highest after a 4 °C increase and declining after a 6 °C increase. The overall range in population growth rate due to changes in fish growth rate and temperature is higher in the case of feeding larvae.

To a certain extent, the results from the simulations were confirmed by the sensitivity analysis. The sensitivity of λ in relation to the survival probability P_i denotes the same picture as the elasticity, or the proportional sensitivity, of λ (Fig. 6a, b). At the steady state ambient

temperature scenario, the survival probabilities of the two adult stages have the greatest impact on population growth, especially that of the second adult stage. When elevating the ambient temperature, the importance of the second adult stage decreases and approximates to that of the first adult stage, which slightly increased. The sensitivity of λ to all other stages also increases but only to a minor extent. The elasticity values of λ in relation to the transition probability G_i were similar and low compared to P_i for most of the stages, although values for the first adult stage were lowest (Fig. 6c). Similar to the elasticity values of P_i, the values of G_i increased slightly with increasing temperatures. A completely different picture was revealed by the absolute sensitivity values of λ in relation to G_i. Here, the values for the feeding larvae vastly exceeded the values of the other stages (Fig. 6d). An increase in temperature by 2 °C resulted in a steep increase in the sensitivity values of feeding larvae and a slight increase in those of the first adult stage, indicating that the transition probability of feeding larvae stage has the greatest impact on the population dynamics, followed by that of the first adult stage. A further increase in temperature does not result in pronounced changes in sensitivities.

Fig. 6 Temperature-dependent elasticity (**a**, **c**) and sensitivity (**b**, **d**) of λ in relation to the survival probability (P_i) and the transition probability (G_i). Note the different scaling on the y-axis. Stage abbreviations as in Fig. 2

Discussion

The results of the present study indicate that a warming scenario for the Baltic Sea will likely increase the population growth rate (r) of Baltic sprat, with a maximum increase in r predicted with 4 °C warming of the long-term ambient mean temperature. This amount of warming is well within the range of warming projected by climate models for the Baltic Sea within the twenty-first century (Meier 2006). At a simulated higher temperature change of 6 °C, population growth rate started to decline, although population growth remained far above a steady state. This rapid population growth rate is probably due to the functional form of the optimum growth curves describing the effects of temperature on feeding larvae and YOY juveniles, which were incorporated into the model. Different thermal windows supporting growth of larvae versus YOY juveniles are justified based upon differences in the seasonal timing and spatial/vertical distribution of these two early life stages of Baltic sprat. For example, feeding larvae are often retained within the deep Baltic basins, which serve as sprat spawning habitats, during their occurrence from March to July. These larvae must be able to grow

efficiently at relatively cold, springtime water temperatures (given sufficient prey availability). On the other hand, juveniles are often found schooling in shallow (and often coastal) waters during summer, which are among the warmest Baltic Sea habitats. This shift to increased optimum temperature from larvae to juveniles has also been observed in other species (Schiemer et al. 2003; Pörtner and Peck 2010). However, some uncertainty remains in the temperature-dependent growth function for feeding larvae because only field-based growth data were available and it is impossible to separate the effects of temperature and prey availability on field growth rates.

The simulation of changes in mortality and growth rate among the different warming scenarios as well as the sensitivity of λ to the transition probability demonstrated that the modeled sprat population was heavily affected by changes occurring during the feeding larvae stage. The importance of early larvae is in line with some of the oldest hypotheses suggesting a strong link between the strength of fish recruitment and survival of early life stages (Hjort 1914; Cushing 1990). On the other hand, the elasticity analyses revealed that the survival probability of the adult stage had the largest impact on the modeled population

growth rate. However, the pronounced higher elasticity and sensitivity values of P_i for the adult stages are likely due to the relatively long and fixed stage duration of the two adult stages compared to the shorter durations of the other life stages in the model. Thus, the high elasticity values for the adult stages will lead to the very low elasticity values for the transition probability of all other stages, as the sum of the proportional sensitivity always equals one, making it impossible to detect differences in the elasticity values. The sensitivity analysis of the transition probability revealed the highest impact of the feeding larval stage on population growth rate. Model simulations suggested that changes in the rates of larval mortality and growth had a considerable impact on the population growth rate. However, a drastic (70 %) reduction in the mean larval mortality rate was needed to obtain a stable population with a growth rate of zero ($\lambda = 1$).

The rapid response of small pelagic, zooplanktivorous fishes such as sprat to climate-driven changes in marine systems has often been attributed, in part, to fluctuations in reproductive rates and/or spawning durations (Tsuruta 1992; Zenitani and Kimura 1997). Batch fecundity and proportion mature at length were temperature-dependent in the model. However, the impact of the reproductive output with increasing temperatures on population growth was low compared to changes in larval mortality or larval growth rates. This is due to the used batch fecundity model that has the optimum temperature at approximately 7 °C which is well in the range of the modeled scenarios. Given that mean ambient winter temperature during spawning was 4.13 °C, an increase of 4 °C is expected to exceed the optimum temperature for egg production.

Projected warming of the Baltic Sea is expected to result in more favorable conditions for sprat recruitment in the region, one of the coldest (highest latitude) areas supporting sprat populations in European waters (Peck et al. in press). Many life history traits of Baltic sprat such as survival and recruitment have been positively related to increases in temperature (MacKenzie and Köster 2004; Nissling 2004). The lack of higher latitude sprat populations suggests that YOY juveniles in the Baltic are exposed to cold winter conditions that, in some years, are close to the thresholds for survival. Temperature-dependent, overwinter YOY mortality is a strong factor limiting the latitudinal distribution of many marine fishes (Conover 1992; Sogard 1997; Hales and Able 2001). To the best of our knowledge, no estimates of overwintering survival exist for Baltic sprat except for some indications of overwinter mortality due to changes in maturity-at-length (Haslob 2011). Not only survival and maturation of juvenile (age 1) fishes, but also the growth, condition, and egg production of mature adults may be affected by unfavorable winter conditions. It has to be noted that a

synchronous warming of all water layers as simulated in this study is probably not a realistic scenario. It is more likely that changes in water circulation and vertical mixing will profoundly affect stratification dynamics and oxygen supply to the deep basins, which may also affect survival and growth of sprat early life stages (Petereit et al. 2009; Voss et al. 2011). Besides warming, a number of other physical processes will be impacted by climate changes that have been correlated with sprat survival. For example, climate change may affect the direction and strength of atmospheric wind forcing that will affect wind-driven surface currents and turbulence. These factors may affect the degree of retention of early life stages in the deep basins (Baumann et al. 2006a, b) or turbulence-mediated feeding success (Voss et al. 2008), both of which have been correlated with year-class success in Baltic sprat.

The matrix model presented in this study was constructed to identify how warming would likely affect the vital rates of different life stages and subsequent population growth rates of Baltic Sea sprat. Many of the parameters required to run the stage-based model were available from previous studies and could be expressed as functions of temperature, e.g., egg and yolk-sac larval stage durations (Nissling 2004; Petereit et al. 2008), growth rates of feeding larvae and YOY juveniles (Peck et al. in press; Clemmesen unpubl data), size-at-maturity, and batch fecundity (Haslob 2011; Haslob et al. 2011). For eggs and yolk-sac larvae, the results of laboratory studies examining direct effects of temperature on mortality were utilized. Since these estimates did not include predation or other sources of mortality acting in the field, it was surprising that the population growth rate was negative based upon initial observed parameter estimates. This suggests that observed feeding larvae mortalities and/or field-based (VPA) mortality of juveniles and adults were overestimated.

The stage-based matrix model approach utilized in this study is able to identify critical life stages but not the underlying processes. However, our efforts to parameterize this model revealed important gaps in knowledge concerning how temperature affects mortality (in feeding larvae, YOY, and adults) and growth (in adults) of Baltic sprat. Furthermore, due to the indeterminate spawning strategy of sprat, some assumptions on spawning frequency and duration were necessary in order to calculate daily egg production by the two adult stages. These appear to be important target areas for future studies investigating temperature effects on life history traits of Baltic sprat. Constructing a similar model that includes direct (physiological) and indirect (predation) sources of mortality would be worthwhile. Such a model could identify uncertainties in other parameters (growth, mortality, and reproduction) that might yield more stable values of λ.

A second line of fruitful research would be to compare and/or combine the outputs of relatively simple, stage-based models and more complex, individual-based models (IBMs) (Peck and Hufnagl 2012) that include the effects of foraging on growth and survival. A number of biophysical IBMs have been formulated for the early life stages (eggs and larvae) of clupeid species such as herring (*Clupea harengus*) and sprat that include physiological-based foraging and growth subroutines (Daewel et al. 2008; Hufnagl and Peck 2011; Peck and Hufnagl 2012). An IBM applied to sprat larvae in the Baltic Sea suggested a causal relationship between observed, decadal changes in diel foraging (vertical migration) behavior of larvae and depth-specific changes in the abundance of zooplankton in larval nursery areas (Hinrichsen et al. 2010). During the YOY juvenile phase, sprat in starving condition has been found in coastal waters of the southwest Baltic (Baumann et al. 2007). That study demonstrated that those larvae collected in August had lower (food-limited) growth rates compared to juveniles collected in late November. Furthermore, tight food web coupling between sprat and zooplankton is suggested by the presence of trophic cascades in the Baltic Sea ecosystem (Möllmann et al. 2008) and density-dependent changes in the condition of zooplanktivorous fish competing for limited prey resources (Casini et al. 2011). All of these studies suggest that prey dynamics (indirect effects of climate) need to be included in models that hope to explore the effects of projected warming of the Baltic Sea on sprat population dynamics. Although more complex, physiological-based models exist that simulate the whole life cycle of small, zooplanktivorous fishes as well as the dynamics of their prey fields (e.g., Megrey et al. 2007), these models are difficult to parameterize (Travers et al. 2007). A hybrid model that combines an early life stage IBM with a stage-based matrix model for juveniles and adults could be more easily constructed and used to test hypotheses regarding the importance of climate-driven physical and biological processes to sprat population dynamics in the Baltic Sea.

Our stage-based approach to understanding the effects of warming on sprat populations dynamics does not allow for species interactions and changes in temperature may also result in a number of indirect (trophodynamic) effects such as shifts in predator–prey overlap (Pörtner and Peck 2010). Apart from the links between sprat and their prey, increasing water temperature may also affect other aspects of the food web that alter the productivity of sprat populations. For example, in the last decade, the European anchovy (*Engraulis encrasicolus*) has (re-)immigrated to the Baltic Sea (Draganik and Wyszynski 2004; Raab et al. 2011) and is expected to compete with sprat for prey when the two species overlap. Recent warming has also been associated with an increase in invasive species in the Baltic

region (Ojaveer et al. 2011). An example of this is the relatively recent increase in *Mnemiopsis leidyi*, a ctenophore that will compete with ichthyoplankton for zooplankton prey resources and that can pose a direct predation threat for pelagic fish eggs and larvae (Haslob et al. 2007; Schaber et al. 2011).

Given the complexity of possible temperature-dependent drivers of Baltic sprat survival (Voss et al. 2007), our current approach can be seen as a first step toward projecting climate-driven changes in this region's sprat population. We have identified a number of potential, critical life stages, where intermediate (+4 °C) climate-driven warming might act to initially increase population growth rate. When taking into account all sources of mortality, larger amounts of warming (+6 °C) were expected to pose limits to population growth rate. More importantly, we have identified the aspects of the thermal ecology of Baltic sprat that require future studies such as the potential importance of YOY overwinter survival and feedback loops between temperature, prey, and sprat reproduction.

References

Baumann H, Hinrichsen HH, Voss R, Stepputtis D, Grygiel W, Clausen LW, Temming A (2006a) Linking growth to environmental histories in central Baltic young of the year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. Fish Oceanogr 15:465–476

Baumann H, Hinrichsen HH, Möllmann C, Köster FW, Malzahn AM, Temming A (2006b) Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Can J Fish Aquat Sci 63:2191–2201

Baumann H, Peck MA, Götze H-E, Temming A (2007) Starving early juvenile sprat *Sprattus sprattus* (L.) in western Baltic coastal waters: evidence from combined field and laboratory observations in August and September 2003. J Fish Biol 70:853–866

Baumann H, Voss R, Hinrichsen HH, Mohrholz V, Schmidt JO, Temming A (2008) Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fish Res 91:1–14

Buckley LJ, Caldarone EM, Clemmesen C (2008) Multi-species larval fish growth model based on temperature and fluorometrically derived RNA/DNA ratios: results from a meta-analysis. Mar Ecol Prog Ser 371:221–232

Butler JL, Smith PE, Lo NCH (1993) The effect of natural variability of life-history parameters on anchovy and sardine population growth. CalCOFI Rep 34:104–111

Casini M, Kornilovs G, Cardinale M, Möllmann C, Grygiel W, Jonsson P, Raid T, Flinkman J, Feldman V (2011) Spatial and temporal density dependence regulates the condition of central

Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. Pop Ecol. doi:10.1007/s10144-011-0269-2

Caswell H (2001) Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer, Sunderland

Clemmesen C, Caldarone EM, Voss R, Hinrichsen HH (2011) Effects of photoperiod and temperature on recent growth rates of sprat larvae in the Baltic Sea. ICES CM 2011 H:18.

Conover DO (1992) Seasonality and the scheduling of life history at different latitudes. J Fish Biol 41(sB): 161–178

Crouse DT, Crowder LB, Caswell H (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293

Daewel U, Peck MA, Kühn W, St. John MA, Alekseeva I, Schrum C (2008) Coupling ecosystem and individual-based models to simulate the influence of climate variability on potential growth and survival of larval sprat in the North Sea. Fish Oceanogr 17:333–351

Dickmann M, Möllmann C, Voss R (2007) Feeding ecology of central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival. Mar Ecol Prog Ser 342:277–289

Draganik B, Wyszynski M (2004) The European anchovy (*Engraulis encrasicolus* [L.]) in the Baltic Sea. Bull Sea Fish Inst 162:53–58

Hales L Jr, Able K (2001) Winter mortality, growth, and behavior of young-of-the-year of four coastal fishes in New Jersey (USA) waters. Mar Biol 139:45–54

Haslob H (2011) Reproductive ecology of Baltic sprat and its application in stock assessment. University of Kiel, Germany, Dissertation 133 pp

Haslob H, Clemmesen C, Schaber M, Hinrichsen HH, Schmidt JO, Voss R, Kraus G, Köster FW (2007) Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Mar Ecol Prog Ser 349:303–306

Haslob H, Tomkiewicz J, Hinrichsen HH, Kraus G (2011) Spatial and interannual variability in Baltic sprat batch fecundity. Fish Res 110:289–297

Hinrichsen H-H, Peck MA, Schmidt J, Huwer B, Voss R (2010) Decadal changes in the diel vertical migration behavior of Baltic sprat larvae: causes and consequences. Limnol Oceanogr 55:1484–1498

Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions 20:1–228

Hood GM (2008) PopTools version 3.0.6. Available on the internet. http://www.cse.csiro.au/poptools

Hufnagl M, Peck MA (2011) Physiological-based modelling of larval Atlantic herring (*Clupea harengus*) foraging and growth: Insights on climate-driven life history scheduling. ICES J Mar Sci 68(6):1170–1188

ICES (2006) Report of the Study Group on Multispecies Assessment in the Baltic (SGMAB). ICES CM 2006 BCC:07

IPCC (International Panel on Climate Change) (2007) Climate Change 2007: The Physical Science Basis. IPCC, Geneva

Köster FW, Möllmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES J Mar Sci 57:310–323

Köster FW, Hinrichsen HH, Schnack D, St John MA, Mackenzie BR, Tomkiewicz J, Möllmann C, Kraus G, Plikshs M, Makarchouk A (2003) Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci Mar 67: 129–154

Lefkovitch LP (1965) The study of population growth in organisms grouped by stages. Biometrics 21:1–18

Leslie PH (1945) On the use of matrices in certain population mathematics. Biometrika 33:183–212

MacKenzie BR, Köster FW (2004) Fish production and climate: sprat in the Baltic Sea. Ecology 85:784–794

MacKenzie BR, Schiedek D (2007) Daily ocean monitoring since the 1860s shows record warming of northern European seas. Glob Change Biol 13:1335–1347

Mantzouni I, Somarakis S, Moutopoulos DK, Kallianiotis A, Koutsikopoulos C (2007) Periodic, spatially structured matrix model for the study of anchovy (*Engraulis encrasicolus*) population dynamics in N Aegean Sea (E. Mediterranean). Ecol Model 208:367–377

Megrey B, Rose K, Klumb R, Hay D, Werner F, Eslinger D, Smith S (2007) A bioenergeticsbased population dynamics model of Pacific herring (*Clupea harengus pallasi*) coupled to a lower trophic level nutrient-phytoplankton-zooplankton model: description, calibration and sensitivity analysis. Ecol Model 202:144–164

Meier HEM (2005) Modeling the age of Baltic Seawater masses: quantification and steady state sensitivity experiments. J Geophys Res 110:C02006

Meier HEM (2006) Baltic Sea climate in the late 21st century: a dynamical downscaling approach using two global models and two emission scenarios. Clim Dyn 27:39–68

Möllmann C, Kornilovs G, Fetter M, Köster FW (2004) Feeding ecology of central Baltic Sea herring and sprat. J Fish Biol 65:1563–1581

Möllmann C, Müller-Karulis B, Kornilovs G, St John MA (2008) Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. ICES J Mar Sci 65(3):302–310

Muus BJ, Nielsen JG, Dahlstrøm P, Nyström BO (1999) Sea fish. Wiley-Blackwell, UK 340 pp

Nissling A (2004) Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea–implications for stock development. Hydrobiologia 514:115–123

Nissling A, Müller A, Hinrichsen HH (2003) Specific gravity and vertical distribution of sprat eggs in the Baltic Sea. J Fish Biol 63:280–299

Ojaveer H, Kotta J, Põllumäe A, Põllupüü M, Jaanus A, Vetemaa M (2011) Alien species in a brackish water temperate ecosystem: annual-scale dynamics in response to environmental variability. Environ Res 111:933–942

Peck MA, Hufnagl M (2012) Can IBMs explain why most larvae die in the sea? model scenarios and sensitivity analyses reveal research needs. J Mar Sys 93:77–93

Peck MA, Clemmesen C, Herrmann J-P (2005) Ontogenic changes in the allometric scaling of the mass and length relationship in *Sprattus sprattus*. J Fish Biol 66:882–887

Peck MA, Baumann H, Bernreuther M, Clemmesen C, Herrmann JP, Haslob H, Huwer B, Kanstinger P, Köster FW, Petereit C, Temming A, Voss R (in press) The ecophysiology of *Sprattus sprattus* in the Baltic and North Seas. Progress in Oceanography

Pertierra JP, Lleonart J, Lo NCH (1997) Application of a stage-specific matrix model and length-cohort based analysis to assess the anchovy fishery in Catalan coastal waters (NW Mediterranean Sea). Fish Res 30:127–137

Petereit C, Haslob H, Kraus G, Clemmesen C (2008) The influence of temperature on the development of Baltic Sea sprat (*Sprattus sprattus*) eggs and yolk sac larvae. Mar Biol 154:295–306

Petereit C, Hinrichsen HH, Voss R, Kraus G, Freese M, Clemmesen C (2009) The influence of different salinity conditions on egg buoyancy and development and yolk sac larval survival and

morphometric traits of Baltic Sea sprat (*Sprattus sprattus balticus* Schneider). Sci Mar 73(S1): 59–72

Petrova EG (1960) On the fecundity and the maturation of the Baltic sprat. Trudy Vsesojuznyj naucno issledovatelskij Institut Morskogo Rybnogo Xozjajstva i Okeanografii 42:99–108

Pörtner HO, Farrell AP (2008) Physiology and climate change. Science 322:690–692

Pörtner HO, Peck MA (2010) Climate change impacts on fish and fisheries: towards a cause and effect understanding. J Fish Biol 77:1745–1779

Raab K, Nagelkerke LAJ, Boerée C, Rijnsdorp AD, Temming A, Dickey-Collas M (2011) Anchovy *Engraulis encrasicolus* diet in the North and Baltic Seas. J Sea Res 65:131–140

Rosenberg AA, Doyle RW (1986) Analysing the effect of age structure on stock-recruitment relationships in herring (*Clupea harengus*). Can J Fish Aquat Sci 43:674–679

Rudstam LG, Aneer G, Hildén M (1994) Top-down control in the pelagic Baltic ecosystem. Dana 10:105–129

Schaber M, Haslob H, Huwer B, Harjes A, Hinrichsen HH, Storr-Paulsen M, Schmidt JO, Voss R, Neumann V, Köster FW (2011) Spatio-temporal overlap of the alien invasive ctenophore *Mnemiopsis leidyi* and ichthyoplankton in the Bornholm Basin (Baltic Sea). Biol Invasions 13:2647–2660

Schiemer F, Keckeis H, Kamler E (2003) The early life history stages of riverine fish: ecophysiological and environmental bottlenecks. Comp Biochem Physiol A 133:439–449

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60:1129–1157

Travers M, Shin Y-J, Jennings S, Cury P (2007) Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. Prog Oceanogr 75:751–770

Tsuruta Y (1992) Reproduction in the Japanese anchovy (*Engraulis japonica*) as related to population fluctuation. Bull Nat Res Inst Fish Eng 13:129–168

Voss R, Schmidt JO, Schnack D (2007) Vertical distribution of Baltic sprat larvae: changes in patterns of diel migration? ICES J Mar Sci 64:956

Voss R, Dickmann M, Hinrichsen HH, Flöter J (2008) Environmental factors influencing larval sprat *Sprattus sprattus* feeding during spawning time in the Baltic Sea. Fish Oceanogr 17:219–230

Voss R, Hinrichsen HH, Stepputtis D, Bernreuther M, Huwer B, Neumann V, Schmidt JO (2011) Egg mortality: predation and hydrography in the central Baltic. ICES J Mar Sci 68(7):1379–1390

Zenitani H, Kimura R (1997) Increase in late winter egg production of the Japanese anchovy as related to recovery of the stock size along the Pacific coast of Japan. Nippon Suisan Gakkaishi 63:665–671