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Effects of photoperiod and temperature on recent growth rates of sprat larvae in the Baltic Sea

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Abstract

Growth rate has been shown to effect survival and recruitment of marine fishes. How growth rates in the field are affected by larval development and environmental variability is poorly understood. Recent growth rates of sprat larvae, a key species in the Baltic Marine ecosystem, were determined by converting RNA/DNA ratios determined from individual larvae into recent growth based on a laboratory calibrated RNA/DNA temperature growth model. Several factors (larval size, temperature and photoperiod) that may contribute to the observed variability in recent growth sampled in the spawning seasons 2002 through 2004 were analyzed with a variety of models. Best fit was found for the Generalized Additive Models (GAMs). Larval size (dry weight), photoperiod and temperature terms explained 29 % and 36 % of the variability observed in recent growth of sprat larvae in the Baltic Sea, respectively.

Keywords: growth rate, temperature, photoperiod, GAM model approach, larval sprat, effect on recruitment

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Introduction

Rapid growth and high mortality characterize the larval stage of most marine fishes. The rates of growth and mortality together determine the rate of change in the biomass of a cohort. Inter-annual variability in these rates coupled with fluctuations in egg production can lead to large fluctuations in recruitment and year-class size (Houde 1989). While larval mortality generally decreases with increasing size (Peterson and Wroblewski 1984; Bailey and Houde 1989; Houde 1997), larval growth and development follow genetically determined patterns that are modified by environmental conditions including photoperiod, water temperature, and prey availability as shown by Buckley et al. (2006). Faster growth and higher survival in relation to prey abundance have been shown for the Japanese anchovy, Atlantic cod and haddock (Beaugrand et al. 2003, Buckley and Durbin 2006, Buckley et al. 2010).

In temperate waters, the increase in growth rate of fish larvae observed in the spring and the decrease observed in the fall has most often been attributed to or correlated with water temperature (Campana and Hurley 1989; Munk et al. 1991; Heath 1992). However, photoperiod changes dramatically at mid and higher latitudes during these same periods and may be a fundamental cause of the change in growth rates. While the differences in growth rates among different stocks at very different latitudes have been attributed to the longer photoperiod at high latitudes (Suthers and Sundby 1996), the role of photoperiod

in determining growth rate within a stock over the larval period has been found to be of key importance (Buckley et al. 2006). Larval growth was shown to be affected by seasonal differences in light irradiance (Fiksen & Folkvord 1999, Porter et al. 2005). Since most marine fish larvae are visual feeders (Blaxter 1986), photoperiod determines the time available for feeding and consequently has a considerable impact on daily ingestion rates in marine fish larvae (Laurence 1977; Suthers and Sundby 1996). Both temperature and photoperiod also indirectly affect larvae through effects on the prey production (Buckley et al. 2010).

As part of the German GLOBEC (Global Ocean Ecosystems Dynamics) Baltic Sea Program we examined the factors affecting growth of larval sprat (*Sprattus sprattus*) over the spawning period 2002-2004. The objective was to take an integrative approach to look across cohorts, months and years in an attempt to identify the dominant variables consistently affecting larval growth which was estimated as recent growth of individual larvae from the ratio of RNA to DNA (R/D) and water temperature based on a laboratory calibration model determined with herring larvae (Harrer, 2006) using a generalized additive model (GAM) approach.

Materials and Methods

Field sampling

Sprat larvae and environmental data were collected on cruises to the Bornholm Basin, Baltic Sea as part of the German GLOBEC Program in April 2002, May 2002, June 2002, July 2002, March 2003, April 2003, May 2003, July 2003, March 2004, May 2004 and July 2004. Sampling was performed with a Bongo net covering most of the Bornholm basin area at a set of standard stations (Fig. 1). Further details on sampling procedures are given in Köster et al. (2003), Voss et al. (2006) and Hinrichsen et al. (2010). Temperature and salinity data were obtained from a CTD profile which was taken prior to the Bongo haul on the same station grid. Photoperiod, defined as the number of hours between civil sunrise and civil sunset, was estimated from the date of capture using longitude 15.4 E and latitude 55.2 N.

On each cruise, sprat larvae from one net of the Bongo were immediately sorted from the catch and frozen at –74°C in 1.5 ml vials for later analysis of dry weight, RNA, and DNA content (Table 1). The time between a net coming on deck and freezing of larvae in at -74°C freezer was minimized as much as possible, never exceeding 30 min. The larvae were sorted on frozen gel packs to avoid nucleic acid degradation taking place.

Biochemical analysis and estimation of growth rate

After storage at -74°C herring larvae were thawed and measured for standard length using a stereomicroscope. Larvae were freeze-dried to constant weight (16 hours, using a Christ Alpha 1-4 freeze-dryer at –51°C) and were weighed to the nearest 0.0001 mg (Sartorius microbalance SC2). The analysis of RNA- and DNA concentrations was performed by a modification of the method described in Clemmesen (1993) and Belchier et al. (2004). The freeze-dried larvae were rehydrated in Tris-SDS-buffer (Tris 0.05M, NaCl 0.01M, EDTA 0.01M, SDS 0.01%) for 15 min. Cells were disrupted by shaking in a cell-mill with glass beads (diameter 2 mm and 0.17-0.34 mm) for 15 minutes. The homogenate was then centrifuged at 6000 rpm at 0°C for 8 min, and the supernatant used for the analysis. The amount of nucleic acids was measured fluorometrically in a microtiter fluorescence reader (Labsystems, Fluorescan Ascent) using the fluorophor ethidiumbromide. Total nucleic acids were measured first, then RNAse was applied to the sample in order to digest the RNA. After the enzyme treatment (30 min at 37°C) the remaining DNA was measured. The RNA fluorescence was calculated by subtracting the DNA fluorescence from the total nucleic acid fluorescence. RNA calibrations were set up every measurement day and the RNA concentration was calculated by linear regression. The DNA concentrations were

calculated using the relationship between RNA and DNA fluorescence described by Le Pecq & Paoletti (1966) with a slope ratio of 2.2.

The equation to calculate recent growth from RNA/DNA ratios was derived from laboratory experiments with herring larvae, a similar clupeid species reared at 8 different temperatures with a feeding and a starvation treatment. RNA/DNA ratios were then correlated to weight specific growth rates (Gi) calculated from samples at 6 day intervals using the equation:

$$Gi = (\ln Wt2 - \ln Wt1) / (t2-t1)$$

with W being the dry weight of the larva, (Wt2 being the individual value and Wt1 the mean of the age group 6 day prior).

Based on these calibration experiments an equation to calculate recent growth (G_i) expressed as the instantaneous dry weight-specific growth rate (d^{-1}) estimated for each larva from water temperature (T) in ºC and RNA/DNA ratio (R/D; dimensionless) was established (modified after Harrer 2006):

$$G_i = -0.1503 + 0.0041(T) + 0.1081(R/D)$$

RNA/DNA ratios of sprat larvae caught during the spawning season 2002-2004 were converted to recent growth rates using the above equation. The temperature experienced by the larvae prior to being caught as a mean of the temperature in the upper 30m of the water column was used, since this is the area where the majority of the sprat larvae in the Bornholm Basin have been found (Voss et al 2006).

Data Analysis

The data were analyzed and statistics performed using SAS software (SAS Institute, 2001). The general approach was to first use all the data for individual larvae to explore the relationships among recent growth rate, larval size, photoperiod, water temperature, and Julian day by using SAS REG procedure for linear regression analysis. Generalized additive models (GAMs) were used with the SAS GAM procedure for nonparametric regression to analyze ontogenetic and seasonal trends in the growth rates. After examining different values for degrees of freedom (df), 4 df in the models to allow for sufficient flexibility in shape without excessive data chasing were chosen. Growth rates from individual larva were fitted to the model:

$$G_i = \text{spline (dry weight, df = 4) spline (environmental variable, df =4)}$$

Where the environmental variable was either julian day (day of the year), photoperiod or temperature.

Results

The numbers of sprat larvae sampled from the different cruises and the mean values for photoperiod, Julian day, temperature, salinity, larval size and dry weight are given in Table1. Mean temperature in the middle of March (JD 74) was approx. 2°C and reached approx. 15°C at the end of July (JD 210). For a given sampling time the temperature at the sampling stations differed between 2°C and 5°C depending on the location in the sampling grid (Fig. 2). Photoperiod increased over the season reaching the peak in hours of daylight (19.4 hours) on June 21 (JD 172) (Fig. 2).

Stepwise linear regression and generalized additive models (GAMs) were analyzed to develop seasonal models of growth rate that included the ontogenetic trend: When larval size (ln DW), water temperature and photoperiod were used in stepwise linear regressions the best 2-parameter models included photoperiod and larval size (Table 2). These size- and photoperiod-dependent growth models explained 29% of the observed variability in growth rate of sprat larvae. Inclusion of a third variable, either temperature or Julian day increased the explained variability to 34%. GAMs explained slightly more of the observed variability (36%) in growth rate of sprat than did the linear models (Table 2).

Predicted growth rates from the GAM model in relation to Julian day showed a seasonal effect with an increase in weight specific growth rates until Julian day 150 (May 30). Thereafter the variability in predicted growth increased and a separation of the data into two different larval size groups, based on standard length, revealed different growth patterns over the season (Fig. 3). Sprat larvae smaller 12mm standard length showed a dome-shape growth- Julian day relationship with a peak in growth rate on Julian day 150 followed by a decline in growth rate later in the season. Whereas sprat larvae larger than 12 mm standard length showed the highest growth rates later in the season (Julian day 210, July 30, Fig. 3).

Growth rates of all sprat larvae increased with temperature until about 8°C and showed increasing as well as declining growth rates at higher temperatures (Fig. 4). When separating the growth data into two size groups (smaller 12mm standard length, larger 12mm standard length) different growth temperature dome-shape relationship became evident depending on larval sizes. The peak in growth for sprat larvae smaller 12mm was found at 8 °C, whereas the peak in growth of sprat larvae larger 12 mm standard length was observed at 12°C (Fig. 4).

Growth rate in relation to photoperiod showed an increase over the season and a decline in growth rate at the highest photoperiod in sprat larvae smaller 12mm (Fig. 5). Larvae larger 12mm showed a slight increase over the season with no reduction at the highest photoperiods (Fig. 5). In this study no effect of salinity in explaining the variability in recent growth rates could be found.

Discussion

Effects of temperature on growth rates

Dome-shape relationships of recent growth were found with temperature and larval sizes and indicated a decrease in growth rate of sprat larvae at the end of the spawning season. Dome-shape temperature growth relationships in the field were also found for cod and haddock larvae on Georges Bank (Buckley et al. 2006) and Takahashi et al. (2005) for Japanese anchovy. The observed effect off a dome shape relationship of temperature on biochemically determined growth rates could also be shown on sprat larvae from the same location when determining the growth rate based on otolith increment width (Hinrichsen et al. 2010).

Temperature affects the rates of development, metabolism and digestion (Brett 1979, Hunter 1981). In well-fed fish larvae, daily ration and growth rate increase with temperature and then fall precipitously as temperature approaches the lethal limit. The temperatures found in the study area are not near sprat's thermal limits, since sprat larvae have been found to grow well at temperatures above 16°C in the North Sea (Huwer 2004, Holtappels 2004). The fact that temperature leads to increase in growth is supported by numerous laboratory experiments demonstrating faster larval growth rates at higher temperatures (Pepin 1991; Buckley et al. 1993; Houde and Zastrow 1993; Otterlei et al. 1999, Malzahn et al. 2003). Due to increased metabolic costs at the higher temperature, consumption has to increase and if the demands are not met by increased consumption decreased growth rate can be found as seen in this study. It has been a matter of discussion in the literature whether food limitation for larval fish can occur in the field. Buckley et al. (2006) showed that the relationship between temperature and growth was variable among years and

support the hypothesis that larval growth can at times be food-limited. Donner (2006), Peschutter (2008) and Paulsen (2009) were able to demonstrate food limitation based on low RNA/DNA ratios in herring larvae in an enclosed water area, the Kiel Canal. Clemmesen et al. (1997) could demonstrate the effect of temperature on nutritional condition of *Engraulis anchoita* in Brasilian waters, with a significant number of analyzed larvae being classified a starving.

Effects of photoperiod on growth rates

The positive effect of photoperiod on larval growth was evident in the study, since photoperiod was show to have a significant effect on sprat growth rates from the field. When comparing the linear regression models, photoperiod had a higher impact on growth rates than temperature. Analysis of the GAM models, which are able to give a better fit to the trend in the data, revealed that photoperiod and dry weight revealed 29% of the observed variability compared to 35% when dry weight and temperature were included in the GAM models. When analyzing the effect of photoperiod in relation to larval size a different pattern was evident. Sprat larvae smaller 12 mm showed a decrease in growth rates at photoperiods higher than 18.5 hours. Longer hours of daylight did not increase growth rate, although these longer hours potentially allow for longer food searching and feeding times. The growth reduction at high photoperiods is comparable to the growth reduction at higher temperatures. The data suggest that there might not have been enough appropriate food available, an idea which is supported by the declining numbers of copepodids, the prime food source for these sprat size groups; found in the study area (Voss et al. 2006, Voss et al. 2008). It has to be considered that photoperiod is a proxy of available feeding time and therefore can effect growth rate, but since the times of sunrise and sunset are a function of the day of the year and the latitude, light at depth and effective photoperiod can vary greatly depending on a variety of factors including cloud cover, fog, sea state and pigment concentration (Suthers and Sundby 1996).

Ontogenetic and seasonal trends in growth rates

Larval size, measured as dry weight, was highly correlated with growth rates of sprat larvae and was the first variable to be included into the regression and GAM models. The GAM model was able to explain 36% of the explained variability in larval sprat growth. This is significantly lower than the results given by Buckley et al. (2006) and might be attributed to the more changing environmental conditions sprat larvae experience in the Baltic Sea. Sprat larvae smaller 12mm standard length showed a different relationship between growth rate and temperature than the larger sprat larvae. Highest recent growth was found at a temperature of 8°C which coincide with the temperature for best survival rates of sprat eggs reared at different temperatures (Petereit et al. 2008). Larval size also influenced the relationship between growth rate and season (Julian day) and growth rate and photoperiod. Since most marine fish larvae are relatively undifferentiated at hatching and development continues at a rapid rate through the first several weeks after hatching (Blaxter 1986). Given the rapid development of visual, locomotive, respiratory and digestive systems that dramatically improve the larva's ability to acquire and process food in the first weeks after hatching (Hunter 1981; Blaxter 1986), an initial increase in growth rate with size would be expected and may explain why growth rates of sprat larvae showed a strong ontogenetic trend.

Over the spawning season temporal windows of survival might emerge which could be coupled with seasonality in growth. Otolith back-calculation indicated that surviving juvenile sprat started first-feeding relatively late in the spawning season with successful recruits mostly stemming from a 'window of survival' of eggs spawned in June (Baumann et al. 2008) indicating positive selection for favorable feeding or environmental conditions for older larvae later in the year. Voss et al. (2009) were able to show the importance of prey availability for medium sized larvae (>11mm) at a size when the thermal optimum seems to be shifting.

Other sprat growth models

Voss et al. 2008 analysed sprat larvae feeding success from the GLOBEC cruise in 2002 and included food fields, stratification and turbulence into the GAM models to evaluate whether the addition of other environmental variables can improve the predictability given by the models. They were able to explain 80 % of the variability from a number of simultaneously acting key environmental parameters, like bottom depth, turbulence, light condition and prey density. The importance of a multi variable approach was also shown by Hinrichsen et al. 2010 when analysing the variables responsible for otolith increment width and concluded that otolith growth was not only affected by feeding directly, but also by endogenous nutrition based on energy reserves. Highest predictive power was found when taking larval age, temperature and prey abundance into the GAM model. The results showed that optimum growth was found in late spring to early summer at favorable temperature conditions for optimal growth rate. MacKenzie and Köster (2004) examined recruitment strength at different water temperatures for the Baltic Sea sprat and suggested that recruitment was highest at water temperatures between 5.0 and 9.0 °C but tended to be lower at temperatures <3 and ≥11°C. The results presented here demonstrate that by using a biochemically derived growth determination an assessment of the environmental variables potentially affected growth can be performed and can point to potential critical windows of survival which can then be analysed in more detail.

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Figure Legends

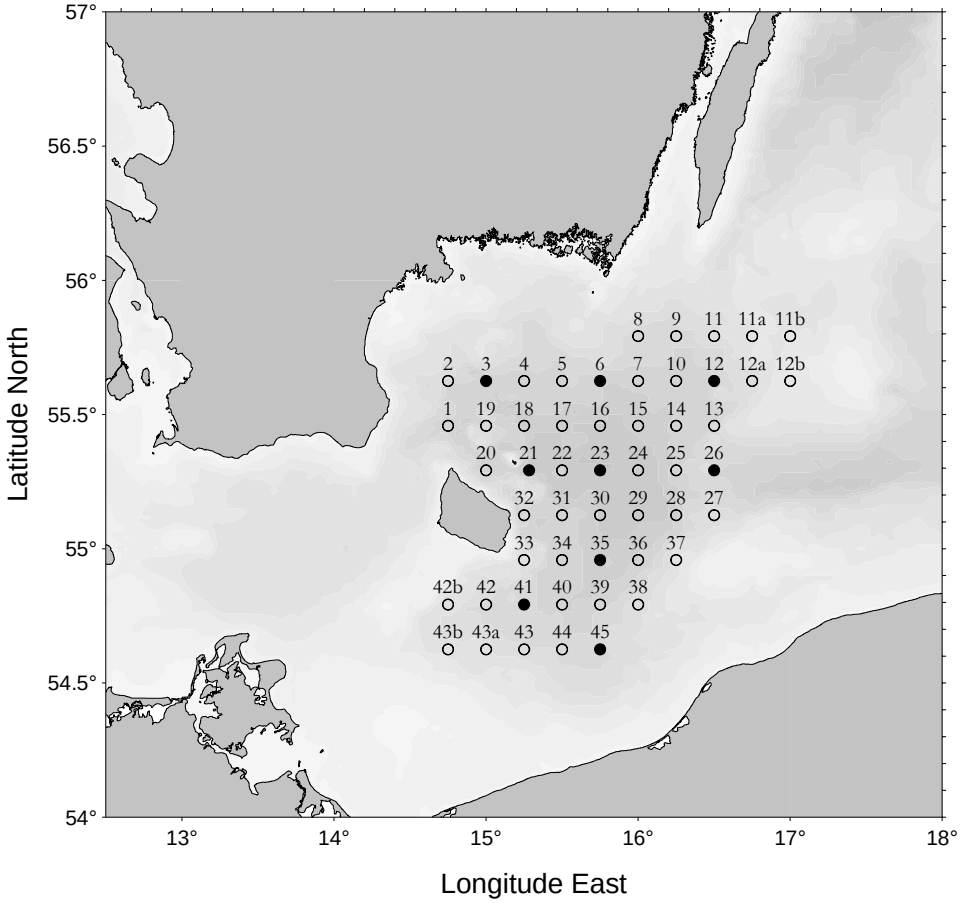
Fig. 1. Sampling locations in the Bornholm Basin, Baltic Sea. Samples for biochemical analysis were taken approx. at every second station.

Fig. 2: Relationship between photoperiod and temperature versus day of the year on the sampling stations in the Bornholm Basin. Temperature data are means of the upper 30 m water column at the station, where the larvae were sampled.

Fig. 3. Relationship between recent growth rate (G_i) and day of the year (Julian day) with observed and predicted G_i of sprat larvae given. Predicted values are from dry weight-, temperature- and photoperiod-specific growth GAMs. Individual data are presented as red triangles, predicted recent growth rates are given as black circles. Upper panel gives the results for all size classes. Middle panel present the results for sprat larvae smaller 12mm in size (standard length). Lower panel gives the data from sprat larvae larger 12mm in size).

Fig. 4. Relationship between recent growth rate (G_i) and temperature (mean of the upper 30m) with observed and predicted G_i of sprat larvae given. Predicted values are from dry weight-, temperature- and photoperiod-specific growth GAMs. Individual data are presented as red triangles, predicted recent growth rates are given as black circles. Upper panel gives the results for all size classes. Middle panel present the results for sprat larvae smaller 12mm in size (standard length). Lower panel gives the data from sprat larvae larger 12mm in size.

Fig. 5. Relationship between recent growth rate (G_i), and photoperiod (in hours) with observed and predicted G_i of sprat larvae given. Predicted values are from dry weight-, temperature- and photoperiod-specific growth GAMs. Individual data are presented as red triangles, predicted recent growth rates are given as black circles. Upper panel present the results for sprat larvae smaller 12mm in size (standard length). Lower panel gives the data from sprat larvae larger 12mm in size.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8 9 11 11a 11b
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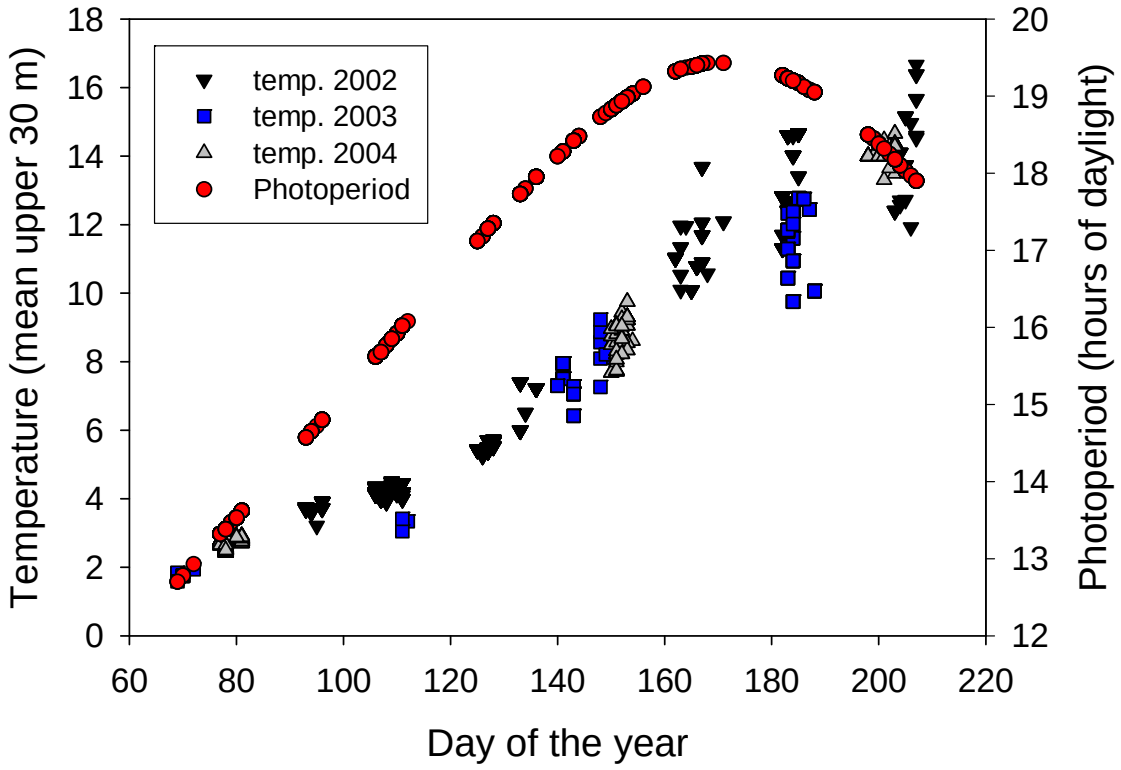
43b 43a 43 44 45

Fig. 1


temp. 2002
temp. 2003
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Photoperiod
Temperature (mean upper 30 m)
Photoperiod (hours of daylight)
Day of the year
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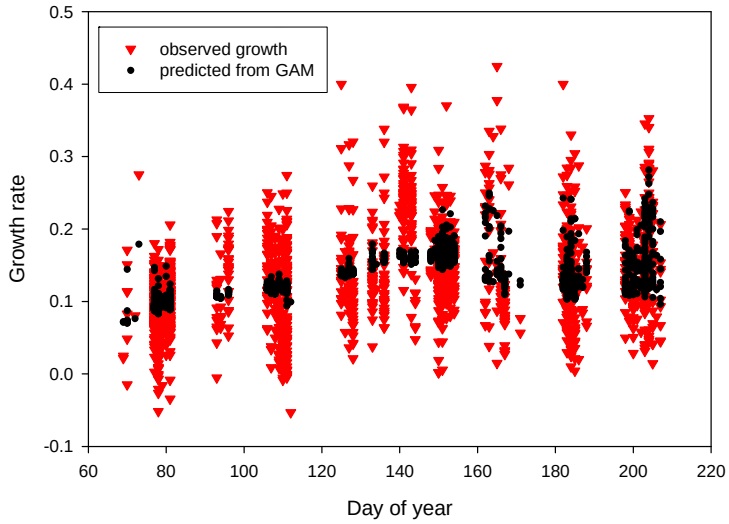
Fig 2:


observed growth
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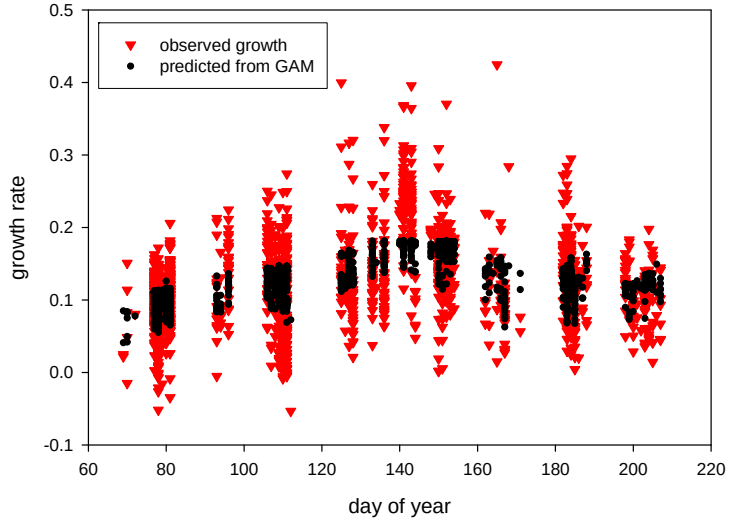
Growth rate
Day of year


observed growth
predicted from GAM
growth rate
day of year

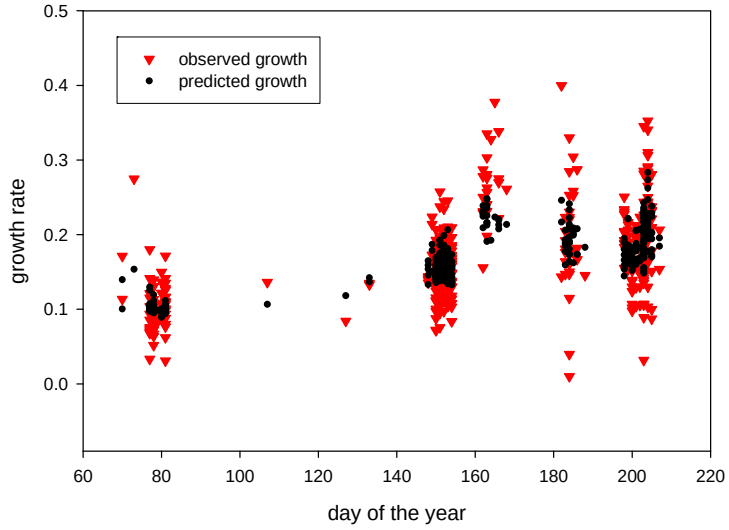
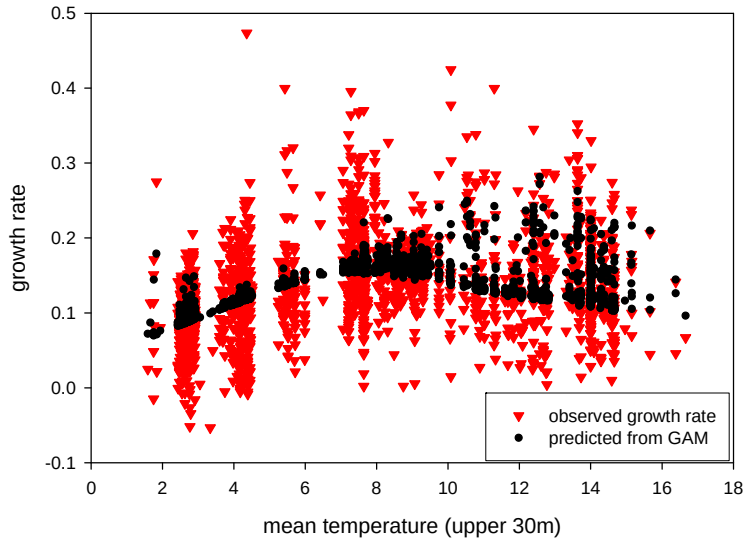
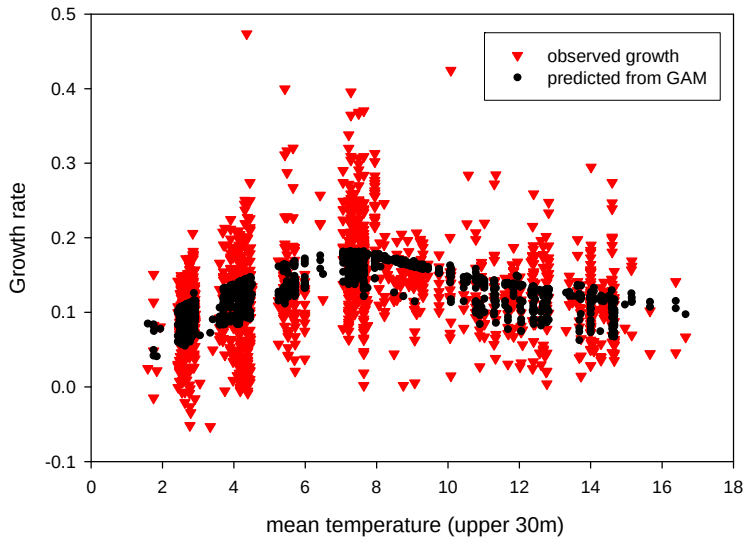

observed growth
predicted growth
growth rate
day of the year

Fig 3:


growth rate
observed growth rate
predicted from GAM
mean temperature (upper 30m)


Growth rate
observed growth
predicted from GAM
mean temperature (upper 30m)

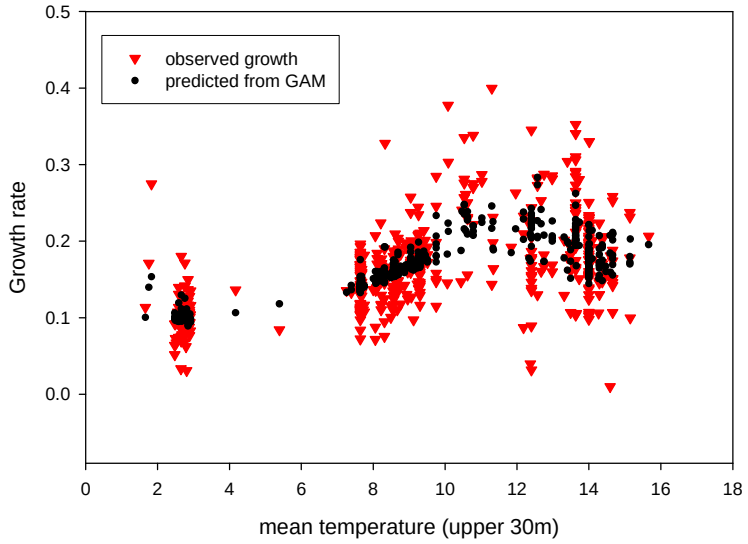
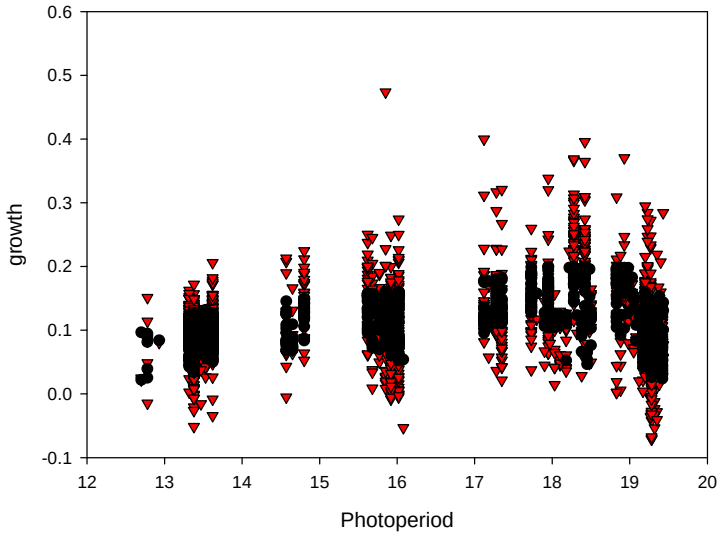

Growth rate
observed growth
predicted from GAM
mean temperature (upper 30m)

Fig. 4


0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
growth
12
13
14
15
16
17
18
19
20
Photoperiod

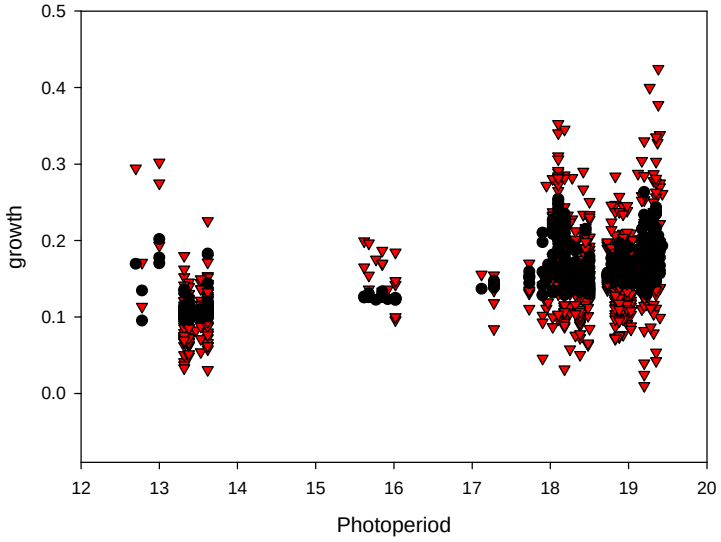

0.5
0.4
0.3
0.2
0.1
0.0
growth
12
13
14
15
16
17
18
19
20
Photoperiod

Fig. 5:

Table 1:numbers of sprat larvae analyzed for growth, mean values and standard deviations of photoperiod (PP), Julian day (JD), temperature, salinity, size(mm) and dry weight (µg) for the three GLOBEC sampling years.
*Temperature = mean of upper 30m, salinity = mean of upper 30m

	2002	2003	2004
March, N=numbers		13	533
PP,		12.79 + 0.085	13.44 + 0.118
JD		70.15 + 1.14	78.93 + 1.54
Temperature*		1.77 + 0.085	2.71 + 0.127
Salinity*		7.23 + 0.056	7.37 + 0.094
size		7.99 + 6.35	9.08 + 2.13
dw		293.78 + 740.41	59.19 + 61.31
April, N=numbers	286	3	
PP	15.66 + 0.45	16.04 + 0.035	
JD	106.81 + 5.63	111.33 + 0.577	
Temperature*	4.18 + 0.23	3.27 + 0.19	
Salinity*	7.26 + 0.082	7.14 + 0.045	
size	7.27 + 1.84	5.15 + 0.32	
dw	35.73 + 26.99	14.33 + 5.92	
May, N=numbers	171	114	226
PP	17.53 + 0.30	18.41 + 0.17	18.93 + 0.073
JD	130.40 + 4.00	143.00 + 2.75	152.09 + 1.51
Temperature*	6.24 + 0.84	7.59 + 0.54	8.74 + 0.51
Salinity*	7.26 + 0.079	7.29 + 0.036	7.33 + 0.087
size	7.78 + 1.59	9.50 + 1.49	12.15 + 1.64
dw	38.74 + 34.55	79.95 + 57.77	183.11 + 100.456
	2002	2003	2004
June, N=numbers	96		
PP	19.38 + 0.037		
JD	165.08 + 2.12		
Temperature*	11.12 + 0.90		
Salinity*	7.19 + 0.032		
size	8.88 + 3.94		
dw	259.39 + 497.89		
July, N=numbers	225	108	134
PP	18.74 + 0.56	19.18 + 0.056	18.34 + 0.12
JD	192.19 + 10.33	184.37 + 1.53	200.52 + 1.91
Temperature*	13.43 + 1.11	11.52 + 1.006	14.09 + 0.27
Salinity*	7.08 + 0.045	7.24 + 0.040	7.35 + 0.091
size	11.88 + 4.81	9.44 + 2.54	12.19 + 2.67
dw	1160.57 + 2100.85	120.46 + 161.66	305.11 + 327.096

Table 2: Models relating sprat larval growth to larval dry weight, photoperiod, and temperature for the years 2002 through 2004. Data are observations for individual larvae. dw is dry weight in µg●larva^{-1} and ln(dw) the natural log of dw. PP is the photoperiod (h). T is the temperature in ºC. The R^2 values reported for the generalized additive models (GAMs) are for a linear relationship between observed and predicted values for growth. For all models, the probability of a greater F value is <0.0001 and all variables are significant at p<0.0001.

Sprat growth GLOBEC 2002; 2003, 2004							
X1	**X2**	**X3**	**R^2**	**Model**			
Linear regression				#			
ln (dw)			**0.23**	1	Gi = 0.025X1 + 0.027		
ln (dw)	**PP**		**0.29**	2	Gi = 0.020 X1 + 0.008X2 – 0.078		
ln (dw)	**T**		**0.23**	3	Gi = 0.022X1 + 0.0017X2 + 0.026		
ln (dw)	**PP**	**T**	**0.34**	4	Gi = 0.025 X1 + 0.018X2 – 0.007X3 – 0.219		
ln (dw)	**PP**	**JD**	**0.34**	5	Gi= 0.026 X1 + 0.021 X2 – 0.0008 X3- 0.219		
GAM				*Chi-Square*			
					X1	**X2**	**X3**
dw	**T**		**0.35**	5	217	399	
dw	**PP**		**0.29**	6	130	50	
dw	**PP**	**T**	**0.36**	7	220	39	32