The German GLOBEC Project

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The German GLOBEC contribution (www.globec-germany.de) titled ‘Trophic Interactions between Zooplankton and Fish under the Influence of Physical Processes’ aims for a better understanding of the trophodynamic interactions between zooplankton and fish under the influence of physical processes in order to elucidate the principal mechanisms accounting for the high variability of copepod production and of reproductive success of fishes. The results will form the basis for strategic modelling of the recruitment success of fishes. Over the last several decades, herring and sprat, but also numerous copepod populations, in the Baltic and in the North Sea have experienced high fluctuations in recruitment and biomass. Whereas a substantial decrease of individual weight of herrings and sprats at high biomass was documented in the Baltic Sea, a similar relationship was not observed in the North Sea. It is assumed that this phenomenon is caused by food (mainly copepods) limitation in the Baltic Sea. However, it is not clear whether this is due to direct effects of trophic interactions (internal dynamics) in the rather simple Baltic food web or whether the decrease of some copepod populations is a reaction to physical processes (external forcing). An interdisciplinary team of fisheries biologists, planktologists, physiologists, geneticists, physical oceanographers and modellers are investigating these hypotheses. The influence of physical processes on zooplankton and on the spawn of two planktivorous fish species with different life histories, herring and sprat, and on their trophodynamic interactions is studied in the Baltic and the North Sea, two ecosystems with very different oceanographic characteristics. This is done using a combination of field studies, experimental investigations and modelling. The two seas under investigation exhibit a gradient from marine to almost fresh water conditions. Top-down and bottom-up processes are studied comparatively in both ecosystems. The same suite of species will be investigated in both areas: the planktivorous clupeids, herring and sprat, and their main food basis, the copepods *Pseudocalanus* spp., *Acartia* spp. and *Temora longicornis*. The focus is on an intra-seasonal and regional comparison of the reactions of egg and larval cohorts of herring and sprat produced at different periods over the entire spawning season with respect to their continually changing physical and biological environments. A tight coupling between field research and modelling is required to enhance our understanding of the two ecosystems. We expect that an improved understanding of the mechanisms governing population fluctuations at short time scales will finally give us insight into the causal relationships of major population fluctuations and ecosystem changes on the decadal scale.

The project is funded for three years with 4 million EURO by the Federal Ministry of Education and Research (BMBF). Similar funds are contributed by the 8 participating institutions. The project is run by 80 scientists and technicians from seven different research institutions and started two years ago. The first results from the Baltic Sea studies are presented below.

Variation in nutritional condition of larval sprat (*Sprattus sprattus*) caught during the 2002 spawning season in the Bornholm Basin, Baltic Sea

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In marine fish species, rates of mortality and growth are inversely related during the first year of life. Since the growth and survival of larval fish is affected by the abundance and quality of food, understanding recruitment dynamics requires robust estimates of nutritional condition and growth rates of field-caught fish. Within the German Globec programme (www.globec-germany.de), we performed grid sampling with Bongo nets in the Bornholm Basin (Baltic Sea) in March, April, May, early July and late July 2002 to collect sprat eggs and larvae. Results from the sprat egg surveys indicated that the major peak in spawning activity occurred in mid April, followed by a second smaller peak in mid June. Sprat larvae caught in May and early July were the survivors of these two spawning events. To evaluate the condition and growth rates of field-caught sprat, we 1) measured a biochemical growth indicator (RNA/DNA ratio, Clemmesen 1993) in individual field-caught larvae to track changes in larval condition during the 2002 spawning season, 2) conducted four, 10 day laboratory experiments to evaluate the relationship between RNA/DNA ratios and growth rate in post-larval sprat, and 3) analysed the gut contents of larvae to determine how feeding habits changed during the season.

New larval cohorts were observed during the cruises in April, May and early July but not at the end of July, when no newly-hatched or young sprat larvae were encountered. Median values of RNA/DNA ratios were higher in small (4-12 mm) larvae in May and April compared with those of similar sized larvae in July indicating a better nutritional condition during the former period. Differences in nutritional condition of these small sprat larvae corresponded to seasonal differences in the abundance of copepod nauplii, the dominant food of small sprat larvae (Voss et al., 2003).
In contrast to the small larvae, larger larvae (> 12 mm) caught during the July cruises had higher RNA/DNA ratios indicating a good feeding environment for larger larvae and suggesting a higher occurrence of prey eaten exclusively by larger larvae (e.g. larger, later-stage copepods). Gut content analysis of 2002 field-caught larvae supported the RNA/DNA results and revealed that medium sized (8 to 12 mm) larvae fed on a more variable diet and had a lower proportion of nauplii in July (30-50%) compared to March-May (60-90%).

Based on the hypothesis that patterns in RNA/DNA ratios reflect the feeding environment (Pepin et al., 1999; Evans 2000; Clemmesen et al., 2003), different growth and condition scenarios were evident during the 2002 spawning season. Variability patterns in RNA/DNA ratios (differences between 10th and 90th percentiles) were nearly twofold higher for the larvae caught during the cruises in July compared to March and April. The persistence of sprat larvae with lower RNA/DNA ratios in the July population suggests that the environment did not strongly select for fast growing, well nourished individuals. Whereas an increase in RNA/DNA ratio values comprising the 10th percentile with increasing larval size in April and May suggests a loss of the slow growing, less nourished larvae from the population (indicates size- and condition-selected mortality). Highly significant correlations between muscle tissue RNA/DNA ratios and growth rates of post-larval sprat in laboratory calibration experiments were found. None of the analysed field-caught larvae had RNA/DNA ratios below the laboratory-determined threshold for zero growth. Our ongoing approach, coupling field studies and laboratory experiments, will incorporate temperature effects on RNA-DNA ratios, and will include otolith microstructure analyses. All of these techniques will be used to parameterize individual-based models investigating factors affecting early growth and survival of sprat in the Baltic Sea.

References
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The goal of this exercise was to study inter-annual differences in modelled drift patterns of sprat larvae stemming from the Bornholm Basin, one important spawning ground for sprat in the Central Baltic Sea. To achieve that, we made use of the 3D, eddy-resolving, baroclinic circulation model for the Baltic Sea as described by Lehmann (1995) and Hinrichsen et al., (1997). The model was forced by actual meteorological data that were made available by SMHI, Norrköping, Sweden for a time-series of 24 years (1979-2002). Larvae were tracked through the model domain as Lagrangian passive drifters. In each year and at 9 different dates per year (roughly corresponding to an average sprat spawning season) we released 750 particles in a depth layer of 5-10m in all areas of SD 25 deeper than 40m (mainly the Bornholm Basin, Fig. 1). Particles were forced to remain in this layer, because there is no applicable knowledge yet about larval sprat vertical migration patterns. Depending on the seeding day, particles were allowed to drift for a period of 36-116 days until their position was recorded on 15 August (day 227) for each year. We then devised a relatively coarse grid of 15x15nm rectangles (Fig. 1) and counted the number of particles found in
Regression analysis with spawning stock biomass, intermediate water temperature at peak spawning time being as well a proxy for winter temperatures, and the retention index as independent variables is now able to significantly (P<0.001) explain almost 60% of the overall recruitment variability in sprat from SD 25.

As we have seen, the inclusion of our newly derived, simple retention index already led to a considerable improvement of the existing sprat recruitment model. However, there is no way around admitting that the mechanistic reasons for this discovered relationship are clearly not yet understood and will require thorough investigation. Certain preliminary insights, gathered from GLOBEC-Germany’s extensive surveys of the Central Baltic Sea, have already raised our attention and seem to point towards spatio-temporal differences in food-availability and potentially also predation pressure to which larval sprat are exposed. In parallel, there is also a need to refine the current modelling approach in order to minimize assumptions and maybe even increase the explanatory power of the retention index.

**References**


![Figure 3. Correspondence between recruitment success of age 0, Baltic sprat in SD 25 (Central Baltic Sea, black line) and a newly-developed retention index (green line) for a time series of 23 years (1979-2001).](image)

![Figure 4. Time-series of Baltic sprat spawning stock biomass (SSB) in SD 25. Circles depict the suggested two periods of predominantly low and high biomass levels.](image)
A strong impact of winter temperature on spring recruitment of a key copepod species in the Bornholm Basin: potential linkages to climate variability

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Recent analyses of the feeding habits of Baltic sprat demonstrate a strong preference for nauplii and copepodites of Acartia spp., particularly by their larvae (Voss et al., 2003). These copepod species thus form an important link between phytoplankton production and fish recruitment in the food web of the Baltic Sea. Long-term investigations in the Central Baltic, however, revealed inter-annual fluctuations of the standing stocks of calanoid copepods which have been related to changes in hydrographic conditions (Möllmann et al., 2000; Hänninen et al., 2000). An increasing biomass of Acartia spp. in the 1990s contrast with strongly decreasing biomass of another key species, Pseudocalanus sp. (Möllmann et al., 2000; 2003).

The German Globec Project aims to clarify the trophodynamic interactions between zooplankton and planktivorous fish in relation to reproductive success under the impact of physical forcing. A major goal of the project is the identification of critical life-stages or processes which determine the seasonal population dynamics and, thus, can explain the observed long-term fluctuations in the biomass of Acartia. Within this framework, a highly frequent net-sampling programme was carried out in order to investigate the spatio-temporal distribution of Acartia spp. in the Bornholm Basin in 2002. Characteristic seasonal patterns in the abundance and stage composition of Acartia longiremis and A. bifilosa are depicted in Figure 1. In the transition period from winter to spring, a pronounced peak in naupliar abundance generally precedes those of copepodites and adults. During 2003, experiments have therefore been performed to identify the source of the initial naupliar peak and the potential factors controlling the recruitment process.

In these experiments two major mechanisms for the origin of the nauplii have been compared. First, in-situ egg production by females and hatching of eggs was determined by incubation experiments on-board research vessels. Second, hatching of nauplii from eggs hibernating in the sediment was studied in the laboratory by the incubation of sediment cores taken by a multicorer in January 2003.

The results demonstrate that hatching of nauplii from the sediment is by far the most important source for Acartia nauplii in spring. As exemplified by the dominant species A. longiremis, egg production by females in the water column is not only poor during the period from January to April, but hatching success of these eggs is also very low (Fig. 2a). In contrast, very high hatching rates of nauplii have been observed from sediment incubated in the laboratory (Fig. 2b). Hatching of hibernating eggs was particularly important during the period when in-situ egg production and egg hatching was low. Roughly calculated between 120,000 and 205,000 nauplii m⁻² hatched from the sediment in the period January to April, whereas only 8000 nauplii m⁻² can be derived from in-situ egg production. Thus, hatching of resting eggs explains the early occurrence of nauplii in the water column.

Most important, the laboratory experiments revealed a strong temperature control of egg hatching from the sediment. When sediment cores were incubated at 4°C, hatching rates were on average about a factor of 2 to 5 lower than those observed at 10°C (Fig. 2b). The incubation temperatures represent generally the upper and lower limit of the naturally occurring range above the sediment in the Bornholm Sea. Relatively high temperatures were observed in the winter of

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**Figure 1.** Seasonal abundance of developmental stages of Acartia bifilosa (a) and A. longiremis (b) in the Bornholm Sea.

**Figure 2.** Seasonal variation in egg production and egg hatching of A. longiremis (a) and hatching of nauplii from a sediment core (b).
2001/2002 (Fig. 3). At depths below 60m at which peak hatching of nauplii was observed, temperatures above the sea floor were generally above 9°C. In contrast, temperatures in the winter of 2002/2003 dropped to below 5°C in large parts of the Bornholm Sea as a consequence of a major inflow of cold saline water in January.

Although our results obtained need further confirmation by analysis of field samples taken during 2003, they suggest that the recruitment through hatching of resting eggs is a critical process in the population dynamics of Acartia spp. in the Baltic with regard to physical forcing. First, resting eggs are a major source for the first generation of Acartia spp. in the Bornholm Sea as demonstrated for this genus for the northern Baltic (e.g. Katajisto et al., 1998). Second, hatching of resting eggs is restricted to a short time period in winter-spring. And third, hatching depends strongly on the in-situ temperature in deep areas of the Bornholm Sea. These characteristic patterns in the early life cycle of Acartia spp. potentially relate fluctuations in the biomass of these species to the prevailing hydrographic conditions and, thus, to climate variability. Because the hydrographic conditions in the Baltic Sea are mainly controlled by climatic factors (Hänninen et al., 2000), a lack of deep vertical mixing during cold winters or of major inflows of cold water and consequently high temperatures in the deep water may explain the increasing standing stocks of Acartia spp. in the 1990s.

References

A new Individual Based Model approach to derive somatic larval growth characteristics from otoliths
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Otolith microstructure analysis of young fish is utilized amongst others to determine age, daily growth rate estimates, mortality, migratory and environmental history, competition, abundance, condition and taxonomy (Campana and Neilson, 1985; Jones, 1986; Re and Goncalves, 1993). Otolith and fish size are highly correlated for a variety of marine and freshwater species (Campana and Neilson, 1985), thus it is possible to estimate growth-rate histories of individual fish by measuring the widths of otolith increments. Otolith increment width and somatic larval fish growth data (length, weight) of North Sea herring were used to develop an Individual Based Model (IBM) in order to describe daily resolved larval growth rates. Firstly, the model utilizes information from sagittal otolith readings as well as measured standard length and weight data of the larvae by solving an overdetermined set of linear system equations for all parameters using the method of least square residuals. The model solving the linear system consists of a matrix that describes the increment width information of more than 140 larvae, a vector containing their length/weight measurements as well as a vector describing the residuals. The solution vector yields age dependent maximum somatic growth rates of herring larvae. Secondly, measured increment width data are used individually to determine daily resolved nutritional growth parameters of single larvae in relation to their potential maximum somatic growth conditions. The model has been utilized for larvae caught during ichthyoplankton...
surveys from 1991 to 1994 to simulate somatic growth curves of selected larvae in comparison to the maximum larval growth curve (Fig. 1) derived from laboratory experiments (Folkvord et al., 2000). The solid line displays the maximum larval length for each of the otolith increments as well as the inner core. All larvae showed similar sizes at formation of the first increment, highest growth rates were observed for the herring larva represented by the long-dashed line. Lowest growth rates were found for the larvae described by the dotted and dash-dotted lines, which also were defined as being in a bad nutritional condition (Fig. 1). Average herring larval growth rates for the years 1991-1994 are displayed in Fig. 2. Larvae sampled in 1991 showed the worst growth conditions. 1992 had similar mean growth conditions in comparison to 1994. In 1993, larval growth started with extremely high growth rates for the first larval feeding phase and showed the highest variations throughout the feeding period out of all the years. Compared to the low values in 1991 growth rates at around increment 30 were 50% higher. 1994 represents normal or moderate growth conditions and covers the largest larval age spectrum. The area where the herring larvae have been caught is characterized by low stratification and usually has almost constant late-summer temperature conditions between the years as seen in the data from 1991-1994. Thus, with a high degree of confidence variation in otolith increment widths is not caused by temperature effects, but can be assigned to variability in the abundance of available larval prey. In areas with less homogenous environmental conditions, temperature has to be considered as a driving key factor influencing otolith growth. Once the spatially and temporally resolved environment is known the presented method can be extended to a more complex version including both temperature as well as available food. For this specific purpose, this type of individual-based model can be coupled with local or regional circulation models in order to enable larval environmental reconstruction by backward projection (Hinrichsen et al., 1997).

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Fish predation control of key copepod species in the Bornholm Basin

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Although an established concept in freshwater ecology (Kitchell and Carpenter, 1993), top-down controls of plankton communities by fish predation have been rarely documented in the marine environment (e.g. Shiomoto et al., 1997; Cury et al., 2000; Kaartvedt. 2000). For Central Baltic deep basins (Gotland Basins and Gdansk Deep), seasonal time series investigations demonstrated the importance of predation by sprat (Sprattus sprattus) for the interannual dynamics of the copepods Pseudocalanus sp. and Temora longicornis (Möllmann and Köster, 2002). Within the GLOBEC-Germany programme a highly resolved spatio-temporal investigation on the predatory effect of the main planktivores in the Baltic Sea, i.e. beside sprat also herring (Clupea harengus), on the dynamics of the key copepods Pseudocalanus sp., T. longicornis and Acartia spp. was conducted. An almost monthly coverage of the Bornholm Basin between April 2002 and May 2003 included spatially resolved net sampling of copepods, determination of the predator stock size and distribution using combined hydroacoustic and trawl surveys, and an extensive stomach content sampling programme.

Figure 2. Average growth rates of North Sea herring larvae 1991-94.
To date, stomach content data from 738 herring and 883 sprat from surveys in May, June and July 2002 have been analysed. Diet data indicate a switch of both predator species from mainly older copepodite stages (C4-C6) of *Pseudocalanus* sp. in May to *T. longicornis* in June/July (Fig. 1). The pelagic fish community is presently characterized by the dominance of the sprat stock (Köster et al., 2003). During May to July 2002, the stock size of herring in the Bornholm Basin increased due to the return of the fish from their coastal spawning area. In contrast, the sprat stock showed an opposite movement from spawning in the deep basins in May to coastal feeding later in the season (Fig. 2).

Combining daily food intake estimates for single fish [calculated using average stomach contents in a temperature-dependent model of gastric evacuation (Temming, 1996)] with stock size estimates from hydroacoustic surveys allowed the calculation of the population consumption by herring and sprat stocks. These were confronted with potential secondary production estimates of the target copepod species [using a temperature-dependent model of Huntley and Lopez (1992)]. The resulting consumption to production ratios (C/P) indicate a major predatory impact of the sprat stock on *Pseudocalanus* sp. in May with an average C/P of almost 0.6 for adult copepods (Fig. 3). A considerable, although lower impact is demonstrated from herring C/P (max 0.2) on *Pseudocalanus* sp. in May and *T. longicornis* in July.

Resolving a predatory impact on smaller spatial scales is a relatively seldom investigated feature (Fig. 4). Our results clearly demonstrate the high within-basin variability, with high C/P of sprat on *Pseudocalanus* sp. stages in May, concentrating mainly on the north-eastern parts of the Bornholm Basin. Even though the average C/Ps of herring were low, locally predatory hot spots can be identified in May for *Pseudocalanus* sp. and *T. longicornis* with peak C/P of 1. These areas of high predation pressure are, as for sprat, mainly located on the eastern flanks of the basin.

Although these are preliminary results, which will be complemented to a full seasonal scenario by further sample and data analyses, first conclusions with respect to copepod population dynamics can be drawn. (i) *Pseudocalanus* sp. which suffers presently already from unfavourable hydrographic conditions (Müllmann et al., 2003; Schmidt et al., 2003), is under additional stress by the unusual high sprat stock, which feeds heavily on its older developmental stages during the peak reproduction time of the copepod in early spring; (ii) *T. longicornis* is obviously much less affected by fish predation due to the summer migration of sprat out of the basin; (iii) *Acartia* spp., the third target copepod in our study, seems to be unaffected by pelagic fish predation which is mainly due to a lacking vertical predator-prey overlap.

Generally, we stress the importance of spatial variability in the predatory impact on copepods, which will be further evaluated by comparing predation estimates with local copepod population dynamics, i.e. growth and mortality rates.
German GLOBEC Statusseminar: Programme evaluators meet in Hamburg

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This issue of the GLOBEC Newsletter includes a series of scientific reports on the German GLOBEC programme, which recently held a two day review meeting (Statusseminar) in Hamburg, 27 - 28 January, 2004. Topics covered are spring recruitment of copepod species in the Bornholm Basin (Dutz et al.), fish predation on copepods (Möllmann et al.), nutritional condition of larval sprat (Clemmesen et al.), a new IBM approach to derive somatic larval growth characteristics from otoliths (Hinrichsen) and a new retention index for the Central Baltic (Baumann). These five articles provide a flavour of the meeting selected from the 18 scientific presentations and 28 posters, and in addition Jürgen Alheit provides an overview of the project.


References


Seifert (Projekträger, Jülich) representing the funding agency, BMBF. Gus Paffenhöfer (Skidaway Institute of Oceanography) was unable to attend.

The articles elsewhere in this Newsletter provide a selection from the range of topics presented at the meeting, demonstrate the high quality of those contributions, as well as how active and dynamic the German GLOBEC programme is at mid-term. The evaluators enjoyed both the programme of oral presentations and the opportunity to interact with the participants during the evening poster session. The latter was enlivened by one of Jürgen Alheit’s “German wine tasting sessions”, which are world famous in the GLOBEC community.

More than 60 German GLOBEC scientists from 8 participating institutions were at the Statusseminar. A particularly impressive aspect of the meeting was the strong representation of students, who gave excellent oral presentations, together with the degree to which the participating institutions are collaborating, interacting and communicating to achieve a truly integrated programme. To date most of the focus has been on the Baltic Sea with field-work in the North Sea just starting. Once the latter work is completed this will provide the programme with a unique opportunity to compare and contrast the two systems. Such integration and synthesis, particularly allowing data to be matched with the models, will be presented at a final international symposium of the programme which is in the early planning stages.

At the end of the two days the evaluators met formally with the representatives of the funding agency, the German Federal Ministry for Education and Research (BMBF), to review the progress of the programme so far and to consider plans for future development. Consistent with the impressive body of work presented in Hamburg and the exciting plans for future work the outcome of this review was entirely favourable.

Poster session, (left to right) – Francois Carlotti, Roger Harris, Keith Brander, Jürgen Alheit, Axel Temming, Prof. Dr. Udo Schöttler, Dr Peter Seifert and Prof. Dr.Gerd Hubold.