

Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival

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Der Dekan

Wenn [...] haline Schichtung in der Natur auf kurzfristige Vertikalbewegungen hemmend einwirkt, dürfte es sich nicht um ein physiologisches, sondern eher um ein psychologisches Problem handeln.
Banse 1959

Nothing in the world is purely spatial or purely temporal; everything is process
Blaut 1961

Summary

This thesis shows different aspects of the distribution of zooplankton and the resulting influence on larval fish survival.

The vertical distribution of the key calanoid copepod species in the Bornholm Basin (Baltic Sea), *Pseudocalanus acuspes* (Giesbrecht 1881), *Temora longicornis* (Müller 1792), *Acartia bifilosa* (Giesbrecht 1882), *Acartia longiremis* (Lilljeborg 1853) and the only cyclopoid copepod *Oithona similis* (Claus 1863), were investigated. Sampling was carried out with multiple opening/closing nets. The results showed distinct seasonal differences in the vertical distribution for all species. For *P. acuspes* an ontogenetic migration was detected, with the younger stage dwelling near the surface and the older stages moving successively deeper. The adults inhabited the water layers around the halocline. In November the vertical distribution disintegrated and all stages were distributed over the whole water column. However in this period the older stages (C4, C5) dominated the community. A diel vertical migration was observed for *T. longicornis* in the summer months (June 2001, July and August 2002). The migration was most distinct for the older stages, moving from 20 metre at night to almost 60 metre at day. No diel migration was observed in April and November. For *Acartia* species an extended daily migration was not observed, even though the weighted mean depth of *Acartia longiremis* in July shifted from 10 metre at night to 20 metre at day. Both *Acartia* species inhabited the water column above the thermocline in spring and summer. However, in November the distribution was broader for all stages in both species. All stages of *O. similis* inhabited the water layers around the halocline irrespective to the season, showing no vertical migration.

The distribution of reproducing female *P. acuspes* was investigated with the Video Plankton Recorder, an *in situ* imaging device. The distribution was closely related to high salinity although low oxygen values were avoided. Based on images of female *P. acuspes* carrying egg sacs the number of eggs per clutch was calculated and using the temperature dependent development time an *in situ* egg production rate was estimated. Albeit the production was the same between years, the naupli to female ratio was higher in 2003 leading to the conclusion that the naupli mortality might have been reduced.

A simple individual based model of *P. acuspes* connected to a circulation model of the Baltic Sea was used to reveal possible influence of drift to biomass changes. The results showed that in contrast to the 1980's during the 1990's the prevailing barotropic circulation forced the majority of *P. acuspes* out of the Bornholm Basin into easterly Basins and shallow coastal regions. However, the transport of organisms produced in the eastern Basins (Gotland Basin and Gdansk Deep) back to the Bornholm Basin was limited. Lower salinity and higher temperature in the near shore water might influence the survival and reproduction.

The same circulation model was used to investigate the drift of larval cod and possible consequences on the overlap with food organisms. Again, a shift in the baroclinic circulation between the 1980's to the 1990's led to an increased dispersion of larvae in the latter period. It was shown that this decreased the overlap with larval prey and thus decreased the survival probability of larval cod.

Furthermore, the influence of variability in prey abundance and diversity on the results of an individual based model on larval cod growth

and survival was investigated. It was shown, that the use of idealized mean prey fields led to an overestimation of larval survival. Using field data derived from net sampling the survival was partly reduced to 50%. Another investigated

factor was the size of prey organisms. Again, the use of mean value led to an overestimation of survival. Using measurements from samples reduced the survival up to 75%.

Zusammenfassung

In dieser Arbeit werden verschiedene Aspekte der Verteilung von Zooplankton und der daraus resultierende Einfluss auf das Überleben von Fischlarven gezeigt.

Die Vertikalverteilung der wichtigsten calanoiden Copepoden im Bornholm Becken, *Pseudocalanus acuspes*, *Temora longicornis*, *Acartia bifilosa*, *Acartia longiremis* und dem einzigen cyclopoiden Copepoden *Oithona similis*, wurde mit Hilfe von Multischließnetzen untersucht. Die Ergebnisse zeigen deutliche saisonale Unterschiede in der Vertikalverteilung aller Arten. Dabei konnte für *P. acuspes* eine ontogenetische Vertikalwanderung gezeigt werden, bei der sich die jungen Stadien in den oberen Wasserschichten aufhalten und die Älteren sukzessive in tiefere Wasserschichten abwandern. Dabei halten sich die Adulten im Gebiet der Salzgehaltssprungschicht auf. Gegen Winter (November) löst sich diese Vertikalstruktur auf und alle Stadien verteilen sich über den gesamten Wasserkörper. Allerdings dominieren zu diesem Zeitpunkt ältere Copepodidstadien (C4, C5) die Stadienzusammensetzung. Für *T. longicornis* konnte eine tägliche Vertikalwanderung in den Sommermonaten (Juni 2001, Juli und August 2002) gezeigt werden. Am ausgeprägtesten war die Wanderung für die älteren Stadien, die von 20 Meter Wassertiefe in der Nacht bis auf 60 Meter am Tag wandern. Für April und November konnte keine Wanderung gezeigt werden. Die *Acartia* Arten zeigten keine solche ausgedehnte Wanderungsbewegung, auch wenn sich der Verteilungsschwerpunkt bei *A. longiremis* von 10 Meter am Tag auf 20 Meter in der Nacht verlagerte. Beide Arten halten sich im Frühjahr und den Sommermonaten vorwiegend über der Temperatursprungschicht auf. Diese Bindung verschwand im Winter (November), wo sich alle Arten brei-

ter über die Wassersäule verteilen. Alle Stadien von *O. similis* hielten sich über das ganze Jahr hinweg im Bereich der Salzgehaltssprungschicht auf, ohne Wanderungsbewegungen zu zeigen.

Die Untersuchung der Verteilung von sich reproduzierenden *P. acuspes* Weibchen mit Hilfe des Videoplankton Rekorders in zwei hydrographisch unterschiedlichen Jahren zeigte eine enge Bindung an hohe Salzgehalte (13.25) und die Vermeidung zu niedriger Sauerstoffgehalte (0.88 ml/l). Zusätzlich zur Darstellung der Vertikalverteilung konnte mit Hilfe der Aufnahmen eisacktragender Weibchen die Anzahl der Eier pro Eisack bestimmt werden und über die temperaturabhängige Entwicklung die Eiproduktion. Obwohl die Produktion in beiden Jahren gleich war, lag das Verhältnis von Nauplien zu Weibchen im Einstromjahr höher, was auf eine erhöhte Sterblichkeit in dem Stagnationsjahr schließen lässt.

Ein vereinfachtes individuen-basiertes Modell für *P. acuspes*, gekoppelt mit einem Zirkulationsmodell der Ostsee, wurde benutzt, um den Einfluss zu untersuchen, den die Drift von diesen Copepoden auf eine Abnahme ihrer Biomasse haben kann. Die Ergebnisse zeigen, dass in den 1990er Jahren, im Gegensatz zu den 1980er Jahren, die vorherrschenden barotropen Strömungen zu einer starken Verdriftung aus dem Bornholmbecken in die östlichen Becken und in die Küstenbereiche führten. Der Rückstrom aus den östlichen Becken zurück in die Bornholmsee war hingegen zu keiner Zeit signifikant. Die niedrigeren Salzgehalte und die höheren Temperaturen im küstennahen Wasser könnten einen negativen Einfluss auf das Überleben oder die Reproduktion gehabt haben.

Dasselbe Zirkulationsmodell wurde benutzt, um die Drift von Dorschlarven und die Konsequenz

in Hinsicht auf Überlappung mit ihrer Nahrung zu untersuchen. Auch hier konnte gezeigt werden, dass eine Veränderung der baroklinen Strömungen in den 1990er Jahren im Gegensatz zu den 1980er Jahren, zu einer erhöhten Dispersion der Larven führten. Es konnte gezeigt werden, dass dies zu einer Verringerung der Überlappung mit der Nahrung führte, welches ein niedrigeres Überleben zur Folge hatte. Untersucht wurde weiterhin der Einfluss der Variabilität in der Abundanz und Diversität der Zooplankton-Nahrungsfelder auf die Ergebnisse eines individuen-basierten Modells zum

Wachstum und Überleben von Dorschlarven. Es konnte gezeigt werden, dass die Verwendung von idealisierten mittleren Nahrungsfeldern zu einer Überschätzung des Überlebens führen kann. Werden ‚echte‘ Nahrungsfelder in dem Modell benutzt, lag das Überleben zum Teil um 50% niedriger. Als weiterer Faktor wurde die Größe der Nahrungsorganismen identifiziert. Auch hier zeigte sich, dass die Annahme einer mittleren Größe zu einer Überschätzung führt, und die Benutzung realer Größen das Überleben um bis zu 75% verringert.

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I General Introduction

Fisheries are supposed to have an important influence on the development of fish stocks (Pauly *et al.* 1998). However, the recovery of collapsed fish stocks, e.g. the Canadian cod stock, failed, although the fishery was closed (Bundy and Fanning 2005). One of the many reasons discussed for this failure (Dutil *et al.* 2003, Bundy and Fanning 2005) was the environmental impact on the early larval stage. The impact of variability in the environment on early life stages is well known (Hjort 1926, Lasker 1981, Hewitt *et al.* 1985, Cury and Roy 1989). Hjort (1914) hypothesised a 'critical period' in the ontogenetic development of fish being responsible for recruitment failure. This period is often stated as the first-feeding stage of fish larvae when larvae shift from

endogenous to exogenous feeding (Hewitt *et al.* 1985; Houde 1989) In his match-mismatch hypothesis Cushing (1974) proposed the timing of peak production of invertebrate zooplankton to the peak spawning of fish to be the relevant process of recruitment variability of fish. The association of plankton biomass and fish recruitment success was shown for cod and herring in the North Sea (Rothschild 1998). Astthorsson *et al.* (1994) showed the dependence of fish stock recruitment on the food supply for larval fish. Since invertebrate plankton and fish larvae are not evenly distributed in space (Hardy and Gunther 1935, Mackas *et al.* 1985, Owen 1989, Powell and Okubo 1994), the match-mismatch hypothesis has to be extended to the spatial overlap of

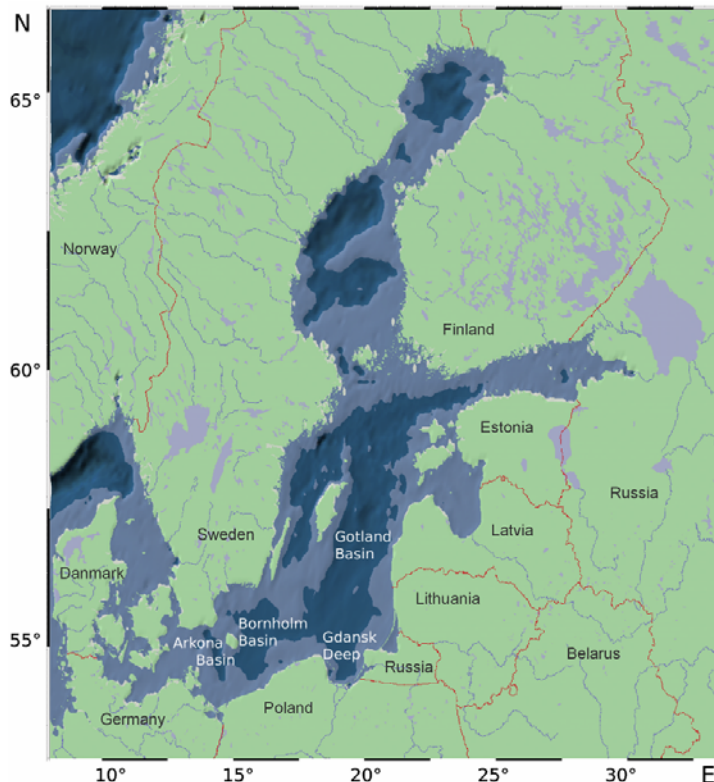


Fig. I-1 The Baltic Sea with adjacent countries; the area investigated in this study is the Bornholm Basin in the south-west between Sweden and Poland; darker blue marks water deeper than 60 metre

predator and prey (Letcher and Rice 1997). The affect of the distribution of prey in the water column on the foraging and ultimately the survival of larval fish was investigated by Lasker (1975, 1978).

Another hypothesis, discussed in parallel, propagate the importance of transport of fish larva by ocean circulation (Hjort 1914, Parrish *et al.* 1981, Bakun and Parrish 1982, Iles and Sinclair 1982, Sinclair and Tremblay 1984). However, the ‘member-vagrant’ hypothesis formulated by Iles and Sinclair (1982) address the importance of retention of individuals in the group (members) having higher survival probability, against those forced out of the group (vagrants). Others discussed the dependence of recruitment success of the fish stock on retention of the larva in areas with favourable environmental conditions.

Besides mere field sampling, the influence of

ocean currents on the transport of eggs or larva of fish was investigated using circulation models. Bartsch *et al.* (1989) investigated the influence of drift of herring larvae in the North Sea to their nursery areas using a baroclinic numerical model. Hannah *et al.* (2000) showed varying transport of larval cod and haddock spawned on Browns Bank with the help of a 3D prognostic advanced turbulence model (Lynch *et al.* 1996). Influence on the survival of larval cod and haddock were described with a retention-survival index (Shackell *et al.* 2000). To take a step forward and consider the influence of environmental factors (temperature, prey field) on growth and survival of individual larva, individual based models were developed (Hinckley *et al.* 1996, Letcher *et al.* 1996, Werner *et al.* 2001, Fiksen and MacKenzie 2002, Hinrichsen *et al.* 2002, Adamack 2003, Lough *et al.* 2005).

I.1 The Baltic Sea

The Baltic Sea (Fig. I-1) is one of the largest brackish water bodies of the world. Its water balance is controlled by freshwater inflow over a number of larger and smaller rivers, inflow of North Sea water through the Danish straits and precipitation and evaporation. The freshwater surplus in the upper layers leads to a constant

outflow of Baltic Sea water. On the other hand, North Sea water is transported into the Baltic Sea in deeper water layers. This creates a surface salinity gradient from the southwest with a value of 10 to northeast with values around two (Fig. I-2).

The bottom topography is characterised by a

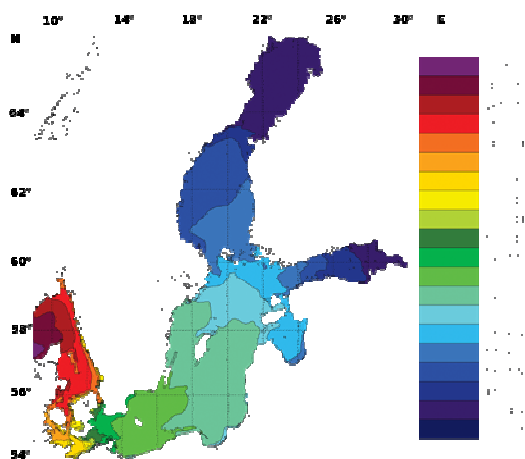


Fig. I-2 Sea surface salinity for July; ten year average (1986-1995); (after Lehmann *et al.* 2002)

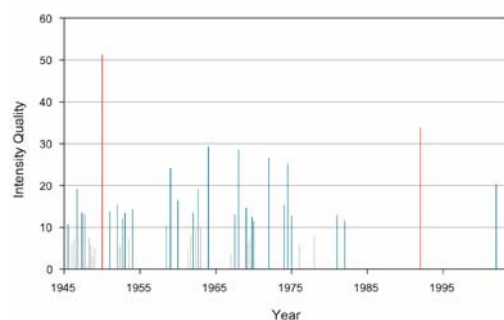


Fig. I-3 Inflow events with their relative strength (after Matthäus and Schinke 1994); The inflow in 2003 was added by the author

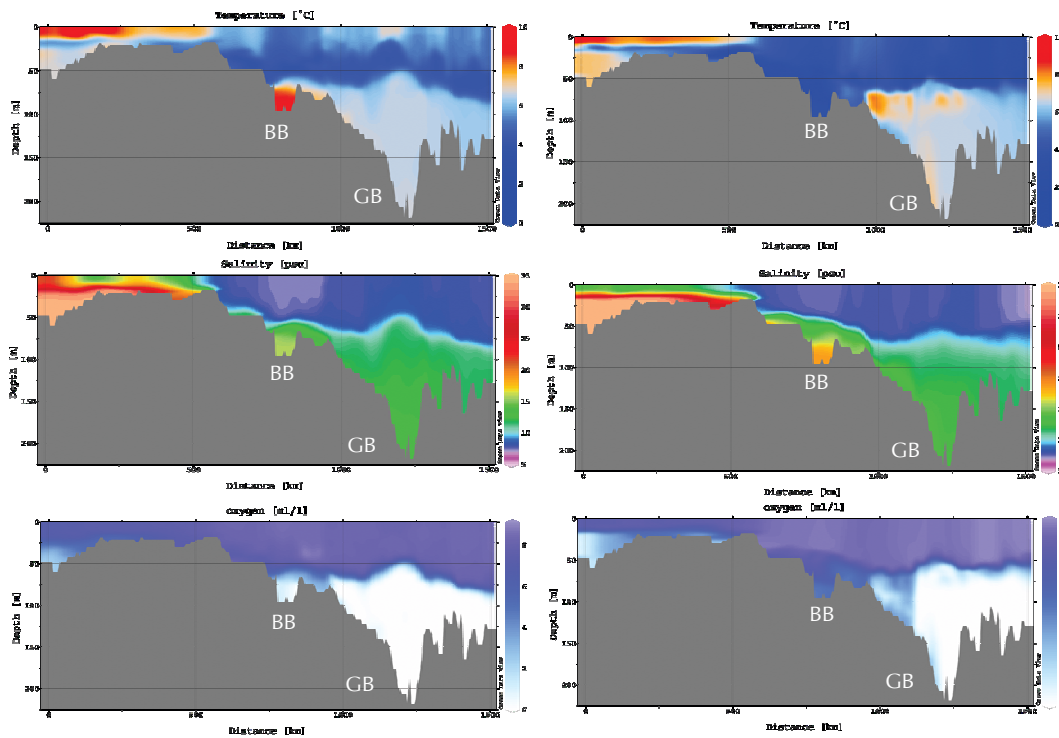


Fig. I-4 Transect through the Baltic Sea; left column 1st May 2002; right column 1st May 2003; in the Center the Bornholm Basin with the most distinct differences in temperature, salinity and oxygen content

series of deep basins, one of those is the Bornholm Basin, separated by sills (Fig. I-1). The water column is permanently stratified separating the dense, saline water in the deep and the freshwater in the upper water layer. This leads to a limited transport of oxygen from the surface to deeper water. Due to breakdown of organic matter at the bottom, this in turn causes oxygen depletion in the near bottom water in the deep basins. Dispersion concurrently leads to a slow decrease in the salinity. Only infrequent strong inflows of North Sea water can renew the deep water, increasing both the salinity and the oxygen content. The North Sea water enters the Baltic Sea over the Danish Straits and flows over the sills in the deeper basins. Depending on the strength of the inflow event the water reaches more of the eastern basins. Those strong inflows are mainly forced by strong wind events and are coupled to the North Atlantic

Oscillation (NAO) (Matthäus and Schinke 1994, Schinke and Matthäus 1998). In the last few decades such inflows were very rare (Fig. I-3). Figure I-4 shows a transect through the Baltic Sea from the Kattegatt to the Gotland Basin. Temperature, salinity and oxygen are plotted for the first May 2002 (Fig. I-4, left column), a year after ten years of stagnation, and the first May 2003 (Fig. I-4, right column), a year after a moderate inflow event. It can be seen, that the inflow reached the Bornholm Basin indicated by increased salinity and oxygen values and a reduced temperature. The effect was less pronounced eastwards, so that only a slight increase in the oxygen content could be reported for the Gdansk Deep. The hydrography itself is no central topic of this thesis, but implications of the special hydrographical situation play a major role in distribution and interaction of organisms.

I.II The pelagic ecosystem of the Baltic Sea

The Baltic Sea is considered a rather simple ecosystem in terms of species diversity and trophic structure. Therefore, it might be easier to understand than other systems (STORE 2001). The upper trophic levels comprise cod (*Gadus morhua*) as the dominant top predator and sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) as the two most abundant planktivorous fish. Marine mammals and seabirds might be locally important, but play only a subordinate role in the Bornholm Basin. The Zooplankton compartment of the ecosystem is composed mainly of different copepod species of which four are predominant in the system, namely *Pseudocalanus acuspes*, *Temora longicornis*, *Acartia bifilosa* and *Acartia longiremis*. The Phytoplankton flora consists of a series of abundant species partly forming large algal blooms in spring and summer. The distribution and interactions of the different compartments of the biotic environment are strongly influenced by the vertical structure of the water column. Cod migrate into the deeper basins during spawning time from May to July, staying in the deeper water layers around the halocline, avoiding the oxygen deficiency layer. They prey on herring and sprat who share temporarily the same habitat. However, sprat performs daily

migrations, staying near the surface at night, which is supposed to be related with the spawning procedure. As they do not feed at night, they prey, as well as herring, mainly on the plankton community around the halocline, including cod eggs. The cod eggs are limited in their distribution to water layers where they can float, which is strongly correlated to the salinity. The larvae of cod dwell in depths of 20 to 40 metre, preying on the plankton community, which appears there. Sprat larvae dwell shallower in depths of 10 to 20 metres. Spawning time of cod and sprat as well as the peak of secondary production differ between the years, interactions between these compartments is not only a question of spatial but also of temporal overlap. Studies related to the recruitment of cod have been performed in two EU funded projects in the past, CORE and STORE. The consumption of cod eggs by sprat and herring, the growth and survival of cod larvae and the impact by larvae and adult sprat and herring on the zooplankton community has been examined and published in a series of articles. Therefore, basic knowledge on the distribution of the main copepod species as well as the interactions with adult fish and fish larvae are known (Köster *et al.* 2003, Möllmann *et al.* 2003a, Voss *et al.* 2003).

I.III Vertical migration

Although general relations of the plankton biomass and the recruitment of sprat and cod were investigated (Möllmann *et al.* 2003a, Möllmann *et al.* 2005, Köster *et al.* 2005) the spatial component was not taken into account. In chapter one data are presented on the diel vertical migration of the main copepod species in the Baltic Sea *Pseudocalanus acuspes*, *Temora longicornis*, *Acartia bifilosa*, *Acartia longiremis* and *Oithona similis*. Conventional multiple opening-closing nets were used to collect the

copepods. Those nets were regularly used for similar studies (Wiebe and Benfield 2003) and display a robust sampling methodology. However, the spatial resolution is limited and small scale processes could not be resolved properly. Sampling was performed in the central Bornholm Basin in June 2001 and in April, July, August and November 2002. A conventional analysis (WMD, Frost and Bollens 1992) and visualization were used to compare day and night distribution.

I.IV Optical methods

During the last decades systems emerged to overcome some of the problems that mark conventional net sampling, i.e. the low spatial resolution or the time consuming analysis of the samples (Wiebe and Benfield 2003). Those systems are mainly based on optical and electronic sensing, either counting particles and sizing them (Coulter Counter (Boyd and Johnson 1969), Optical Plankton Counter (OPC, Herman 1992)) or providing images of the organisms (Ichthyoplankton Recorder (IPR, Lenz *et al.* 1990), Video Plankton Recorder (VPR, Davis *et al.* 1992a)). The Video Plankton Recorder was intensively used on the Georges Bank in the U.S. GLOBEC project (Ashijan *et al.* 2001, Benfield *et al.* 1996, Benfield *et al.* 1998, Davis *et al.* 1992b, Norrbin *et al.* 1996) to reveal distribution patterns of prevailing zooplankton species. However, beyond mere

information of distribution, the images contain information on the orientation of the animals (Benfield *et al.* 2000). In chapter two the distribution pattern of female *P. acuspes* being in the state of reproduction, i.e. carrying egg sacs, were shown. The sampling was performed in two hydrographically contrasting years. 2002 was a year after a long lasting stagnation period (1993-2002) leading to degraded salinity and oxygen values in the deep basins. In January, February 2003 a medium inflow of North Sea water was measured, thus increasing the salinity and oxygen values, especially in the Bornholm Basin (Meier *et al.* 2004, Feistel *et al.* 2003). Besides mere information of the distribution of the reproducing females, images were used to calculate an *in situ* egg production for the two periods.

I.V Modelling

Although the influence of transport on survival was shown for larval fish (Hinrichsen *et al.* 2001), the same was not performed for invertebrate plankton in the Baltic Sea.

In chapter three a very simplified individual based model coupled to a circulation model of the Baltic Sea was used to investigate the consequences of different climate regimes on the transport and development of *P. acuspes*.

In the Baltic Sea the survival of cod and sprat larvae were related to the dynamics of the major copepod species *Pseudocalanus acuspes* and *Acartia* spp. (Hinrichsen *et al.* 2002, Möllmann *et al.* 2003b, Voss *et al.* 2003). The match of peak production of the copepods and the spawning time of the fish may be as important as the spatial distribution and overlap of both. Chapter four comprises two already published manuscripts on the use of circulation models to study the drift of fish larvae and the interaction with their prey due to spatial and

temporal overlap. The role of dispersion versus retention is discussed on the background of seasonal and spatial development of zooplankton. An overlap coefficient was calculated to display the relation of larval survival to different circulation patterns. The individual based model in the study of Baltic Sea cod was developed by Hinrichsen *et al.* (2002). It is based on a generic model for fish larval growth and survival from Letcher (1996). The metabolism of the larva as well as the prey density and size are the two parts of the model that have the largest influence on the results, as it is proofed by sensitivity analysis (Hinrichsen *et al.* 2002). However, the prey fields used in the model were idealized averaged abundances over the basins. The results from the model by Hinrichsen *et al.* (2002) runs showed a good correlation with field data, identifying the youngest larval stage, i.e. the first feeding larva was identified to be most vulnerable to

starvation. In chapter five the idealized zooplankton abundance was replaced by natural variability in the zooplankton prey field.

Data derived from field sampling in 2001 and 2002, were coupled with the IBM of cod larval, and the influence on survival is shown.

1 Vertical distribution and diel vertical migration of main mesozooplankton species in the Bornholm Basin (Baltic Sea)

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1.1 Abstract

In June 2001 during a survey with RV "Alkor", an intense sampling of hydrographic data, fluorescence, zooplankton, fish-larvae and adult fish was conducted, with the aim to investigate the interaction between the upper trophic level and their prey. The vertical distribution of the main copepod species *Pseudocalanus acuspes*, *Acartia* spp., *Centropages hamatus*, *Temora longicornis* and *Oithona similis* was measured using a conventional multiple opening-closing net. Additional sampling was performed in 2002 in April, July, August and November during four surveys conducted within GLOBEC Germany to resolve the seasonal impact. The hydrography was recorded concurrently.

The results showed a similar vertical pattern for both *Acartia* species, whereby all developmental stages concentrate in the upper water layer around 20 m depths with no diel migration. The pattern was found in all sampling periods except November where the animals were more dispersed over the water column. *O. similis* was found in the lower water layer around 60 m depths with no migration and no seasonal differences. *P. acuspes* showed an ontogenetic migration with the C1 – C3 in the upper water layer (20 m), C4 in intermediate water and C5 and the adults in the deep water at 70 m. This pattern was conserved in all sampling periods, however in April the adults tended to dwell slightly deeper. *T. longicornis* showed a daily vertical migration (DVM), occupying the upper water layer in the night (20 m) and moving down by day (45 m). This migration was only observed in summer. Comparing the examined patterns to hydrography showed a concentration of species in the thermocline at 20 m and the halocline at 70 m. The fluorescence signal in June 2001 was highest at 10 m depth, showing that the phytoplankton was more or less limited to the upper and intermediate water layers. Therefore, the food for *O. similis* as well as for *P. acuspes* has to be other than living phytoplankton. A potential food source for these two species may be the marine snow slowly falling down and accumulating at the halo (pycno-) cline. The distribution of adult fish, measured hydroacoustically, showed a clear daily vertical migration staying near surface at night and in the deep water during day (in May 2001 under the halocline at 70 m) showing a similar pattern as *T. longicornis*. Therefore, the predator avoidance theory cannot be an explanation for the migration behaviour of *T. longicornis*.

1.2 Introduction

Diel (Daily) or Diurnal Vertical Migration (DVM) of zooplankton was first observed and documented by Cuvier (1817) in his book „Le Règne Animal“. Since than hundreds of studies dealing with this issue were carried out, published and regularly reviewed (Russel 1927, Cushing 1951, Bainbridge 1960, Banse 1964, Longhurst 1976, Haney 1988, Hays 2003, Jarvis 2003). Vertical migration is described for freshwater systems and marine systems for a variety of planktonic organisms and for very different investigation areas. The dominant pattern described is an ascend of organisms to the surface at dusk and the descend at dawn (DVM). The opposite of this pattern (RDVM, reversed diel vertical migration), i.e. ascend at dawn and descent at dusk, is also observed in a few cases (e.g. Ohman *et al.* 1983, Bayly 1986, Neill 1990, Herwig and Schindler 1996). Additionally there are seasonal vertical migrations (SVM) as well as ontogenetic vertical migrations (OVM) in some species (Marshall and Orr 1955, Longhurst 1976, Osgood and Frost 1994). Hays *et al.* (2001) stated that not all individuals of a population migrate in the same way, e.g. for *Meganocyttiphanes norvegica* (northern krill) a sex specific migration is described by Tarling (2003). The reason for all this migration behaviour could be split in proximate factors, i.e. the immediate or causal factors stimulating the movement, and ultimate factors, i.e. the functional factors, the biological advantage for a vertical migration.

However, despite the overwhelming number of publications, the reason and perhaps ecological significance for this behaviour of zooplankton is not clearly understood in all cases. The most likely ultimate factor is the avoidance of predators at day in deeper water layers and feeding at night near the surface, i.e. a trade off between eating and being eaten (Huntley and Brooks 1982, Dagg 1985, Johnsen and

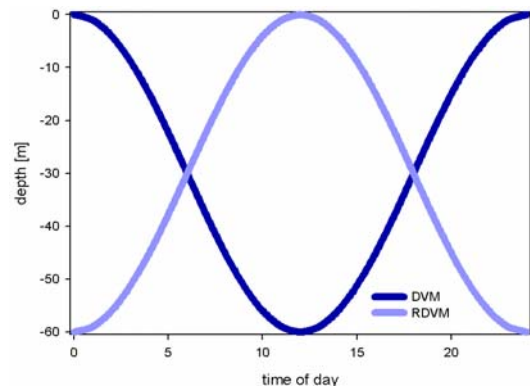


Fig. 1-1 schematic presentation of the two primary types of diel vertical migration after Neilson and Perry (1990)

Jakobsen 1987, Pijanowska and Dawidowicz 1987, Han and Straskraba 2001). Adaption of this behaviour in the migration patterns of predators could result in recursive behaviour in prey leading to observed RDVM (Ohman *et al.* 1983). However, for small Copepods like *Oithona*, *Paracalanus* and *Centropages* no significant migration at all was observed (Bogorov 1946).

Several studies on Baltic Sea zooplankton distribution were carried out in the past, starting in the early 19th century with german expeditions by Ehrenberg and others (Aurivillius 1896). Since 1870 regular expeditions were performed in the framework of the 'Kieler-Kommission zur wissenschaftlichen Untersuchung der deutschen Meere'. Later on, studies were conducted irregularly with different focuses, i.e. restricted areas (Banse 1959, Waldmann 1959, Ackefors and Hernroth 1972, Burris 1980, Dahmen 1997). Dippner (2000) and Möllmann (2000) performed detailed analysis in respect of dependence on biotic or abiotic factors and long-term dynamics. However, the latter studies were based on long-term data series from the Gotland Basin (Fig. 1-1) with no vertical resolved sampling. The latest study in respect of vertical distribution was performed by Dahmen (1997), although he did not resolve day and night

differences. Mankowski and Ciszewski (1961) gave explicit information on day night differences. They reported vertical migration for *A. longiremis*, *P. acuspes* and *T. longicornis* in the Gdansk Deep. However, results of this study were based on single profiles, disregarding plankton patchiness. Studies of the vertical migration of copepods with replicate sampling were not performed in the Baltic Sea. In the present study, the vertical distribution is examined for the key calanoid copepod species in the Bornholm Basin *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes* as well as the only present cyclopoid copepod *Oithona similis*. For June 2001, the zooplankton

sampling was accompanied by sampling of the hydrography, the phytoplankton and fish. Therefore, the distribution and migration could be related to one of the aforementioned factors. Results are shown from day and night distributions to reveal potential migration patterns. Information on the seasonality of vertical distribution as well as migration behaviour data from the Baltic Sea in April, July, August and November 2002 was added covering three vertically resolved day and three night profiles, for each sampling date. The latter data was attained in the frame of the German GLOBEC programme.

1.3 Material and Methods

1.3.1 Zooplankton

Sampling was performed in the central Bornholm Basin, Baltic Sea (Fig. 1-2) onboard of RV "Alkor" in June 2001 (St. 15) and in April, July, August and November 2002 (St. 23). In June 2001, April and August 2002 three vertical distributions were sampled during daytime and three during nighttime. For July and November 2002 only two day and two night distributions were available.

Zooplankton samples were collected with a 0.25 m² multi opening/closing net system (Multinet, Hydro-Bios Kiel). The Multinet was equipped with 5 nets of 50 µm mesh size (100µm in 2001). The gear was operated vertically with a speed of 0.2 m/s, resolving the water column in 10 m intervals from the bottom up to the surface.

Samples were preserved in 4% borax buffered formalin-seawater solution for analysis in the laboratory. Mesozooplankton was identified and counted under a binocular microscope on subsamples no less than 1/100 of the total sample or at least 500 individuals. Subsamples were obtained using a Kott-splitter device. The

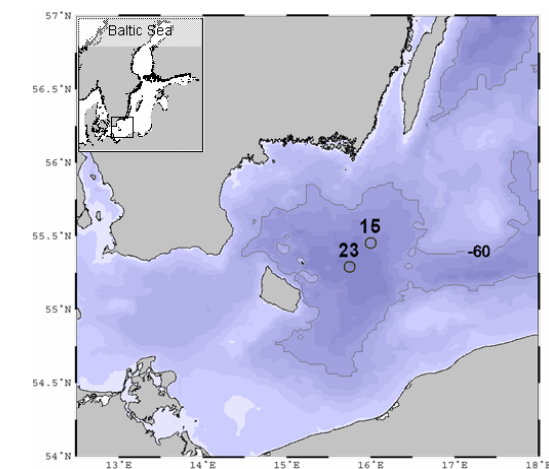


Fig. 1-2 Map of the investigation area Bornholm Basin

copepods were identified to species, *Pseudocalanus acuspes*, *Temora longicornis*, *Centropages hamatus* and *Oithona similis*. *Acartia* species were differentiated in *A. bifilosa* and *A. longiremis* in 2002, but not in 2001. Copepodites were classified to developmental stage. Abundances were calculated as number

per square meter water column for each species. A weighted mean depth was calculated for each period, each species and each stage:

$$\left(\frac{\sum n_i d_i}{\sum n_i} \right) \quad (1-1)$$

with n_i is abundance (number/m³) at depth d_i ($d_i = 5, 15, 25, 35, 45, 55, 65, 75$).

1.3.2 Hydrography

Hydrography was measured prior to each series of zooplankton sampling, covering a vertical profile from 0 to at least 80 metres. Temperature, salinity and oxygen were measured using a Multiparameter CTD Probe

OTS 1500 (ME Meerestechnik-Elektronik GmbH) equipped with an oxygen sensor in 2001 and with an ADM CTD (Analoge und Digitale Meßsysteme GmbH) in 2002.

1.4 Results 2001

1.4.1 Hydrography

The watercolumn in June 2001 in the Central Bornholm Basin showed a stratification with a surface water layer from 0 to 20 metre depth, an intermediate layer from 20 to 50 metre depth and a bottom layer from 50 metre to the bottom (Fig. 1-3). The surface layer was totally mixed with a temperature of about 10°C, a salinity of 9 and an oxygen content of 7.6 ml/l. The intermediate water was characterized by a decrease in temperature to 3.5 °C and a slight decrease in salinity and oxygen content. In the bottom layer the temperature increased again to a maximum value of nearly 7°C at the bottom. A sharp increase was measured in the salinity with a bottom value of 17. The oxygen was decreasing further to 0 ml/l in 80.5 metre depth

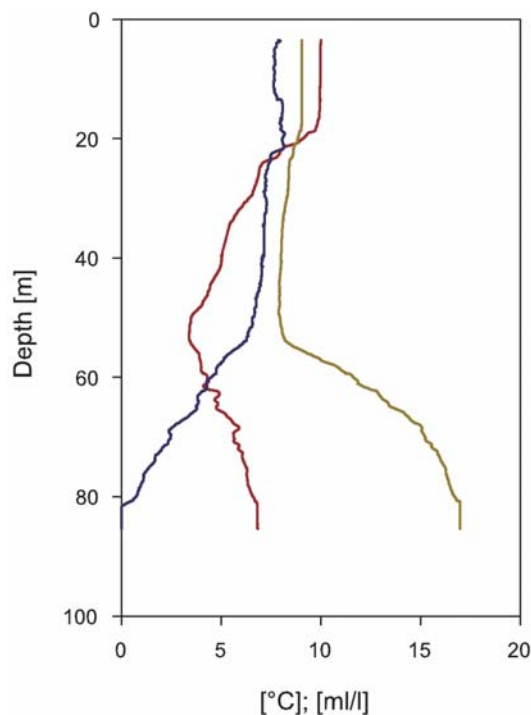


Fig. 1-3 The Hydrography in June 2001 in the Central Bornholm Basin; red – temperature [°C]; dark yellow – salinity; blue – oxygen [ml/l]

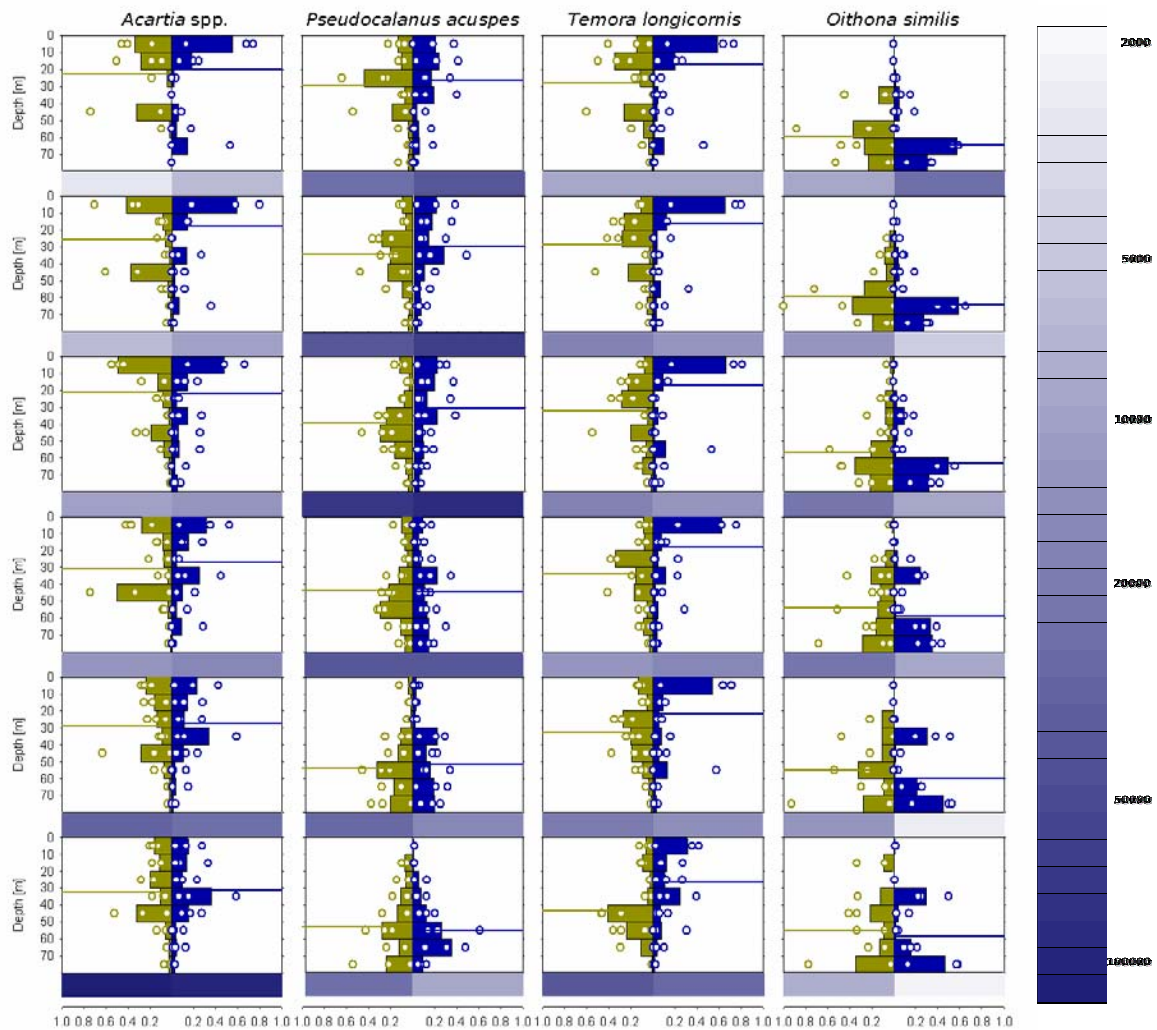


Fig. 1-4 Vertical Distribution of a) *Acartia* spp., b) *P. acuspes*, c) *T. longicornis* and d) *O. similis* in June 2001; from upper row to bottom row (C1, C2, C3, C4, C5, adults); right, dark blue bars show the night distribution (n=3); left, dark yellow bars show the day distribution (n=3); dots show relative values of each individual profile; lines indicate the weighted mean depth (WMD), blue colouring displays the abundance in n/m² in logarithmic scale

1.4.2 Zooplankton

The vertical distribution of the four examined species is shown in Fig. 1-4. Younger stages of *Acartia* spp. tend to stay higher in the watercolumn with WMD's around 20 metres in the depth of the upper thermocline. Stages older than C4 had a broader distribution with WMD around 30 metre, just beneath the thermocline. No difference between the day

and the night distribution could be revealed as shown by the WMD. This is true for *O. similis*, too. Although the orientation is different with WMD around 55 to 60 metres for all stages in the depth of the halocline. However, the distribution is bimodal for C4 to adults with a large proportion sampled in the deepest layer from 70-80 metres. *P. acuspes* shows an

ontogenetic vertical migration, whereas the younger stages dwelled in upper water layers just beneath the thermocline. Older stages were found deeper in the watercolumn. The adults inhabited water layers around 50 to 60 metres. However, the WMD revealed no significant difference between day and night distributions. For *T. longicornis*, diel vertical

migration seemed obvious looking at the WMD. At night, the majority of individuals in each stage could be found in the upper ten metres. The distribution of all stages was more dispersed during day, whereas the majority of the adults shifted to water layers deeper than 40 metre.

1.5 Results for 2002

1.5.1 Hydrography

In 2002 the seasonal succession of hydrography was recorded (Fig. 1-5). In April a typical spring situation could be found with a mixed upper water column from the surface down to 45 metre with a temperature of 4°C, a salinity of 7.5 and an oxygen content of 8-9 ml/l. Below 45 metre temperature increased with depth as well as salinity whereas the oxygen content showed an opposite trend towards a content of 0 ml/l below 80 metre on. In July,

the upper thermocline was well developed in 25 metre. Temperatures in the upper water column were around 15°C in July increasing towards August to 20°C. The salinity showed the same trend for July and August as in April. In November, the upper water column already cooled down and is mixed to a depth of 40 metre. Near the bottom an increase in temperature, salinity and oxygen could be observed.

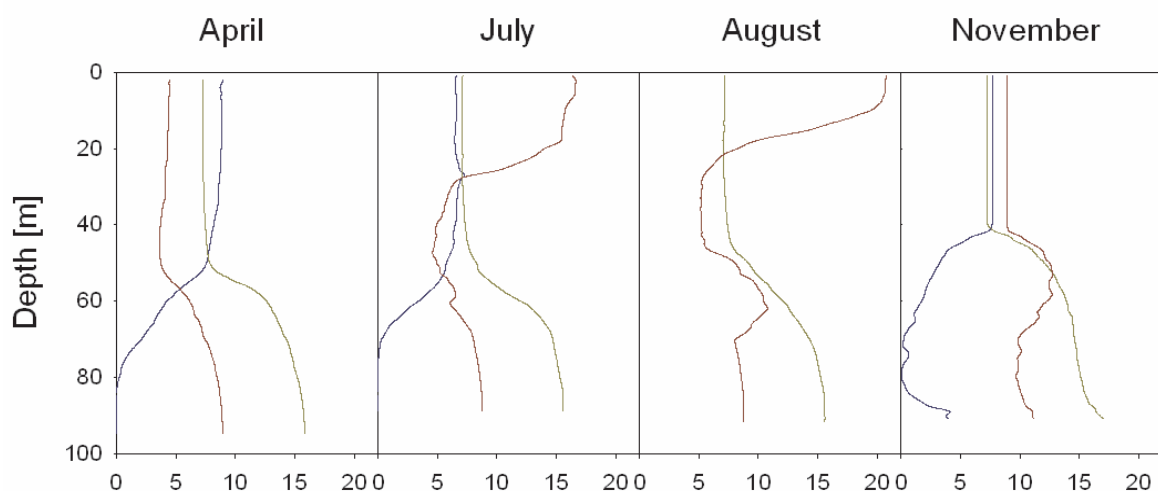


Fig. 1-5 Hydrography at the four sampling periods in 2002; blue line – oxygen content [ml/l], dark yellow – salinity, red line – temperature [°C]; oxygen is missing in August due to a failure of the oxygen sensor

1.5.2 Zooplankton distribution

The results from 2002 showed a distinct seasonal pattern as well as species specific distribution and migration patterns between the stages. The results for *P. acuspes* in 2002 reflect the ontogenetic shift from younger stages dwelling near the surface to adults inhabiting the water around and under the halocline as found in 2001 (Fig. 1-6). However, the trend was plainest for April. In July and August, the distribution of older stages C4 to adults was broader and not as deep as in April. In November, the distribution was broadest most notably for C3 to C5 which were much more abundant than the other stages. Over the year, the abundance of nauplii was highest in April even though they were present in July and August in considerably high numbers, too. In July all stages were very abundant. In August the abundance of C1, C2 and adults were declining, compared to July.

Acartia species showed different distributions, although both species tend to inhabit the upper water layer.

For *A. bifilosa* all stages dwelled near the surface in April, July and August (Fig. 1-7). In November, all stages were evenly distributed from the surface down to 40 metres. The abundance of nauplii was similar high in all four sampling periods, although it has to be looked at carefully, because the data presented in Fig. 1-7 and 1-8 show the distribution of *A. bifilosa*

and *A. longiremis* nauplii grouped together.

A. longiremis exhibited a broader distribution in April and November for all stages and in July and August for the adults (Fig. 1-8). The other stages dwelled in upper water layers in July and August. Contrary to *A. bifilosa*, *A. longiremis* showed a slight shift in the distribution from 10 metre at day to 20 metres at night.

T. longicornis generally inhabited the upper water layers (Fig. 1-9). However, in April the abundance of C2 to C5 was too low to reveal trustable results. Differences between day and night were shown in July and August for the different stages. At day the younger stages stayed in the uppermost water layer and the older stages gradually dwelled deeper with an even distribution over the whole water column in C5 and adults. The WMD revealed differences between day and night distribution for C4 to adult stages. In November, all stages were distributed in the same manner at day as well as at night, evenly distributed from the surface down to 40 metre.

In *O. similis* all stages were restricted to the deep water layers in and under the halocline (Fig. 1-10). The distribution was deepest in April with WMD for all stages between 70 and 80 metre. The WMD for the other periods observed was between 50 and 60 metre. The abundance was highest in July for C1 to adults.

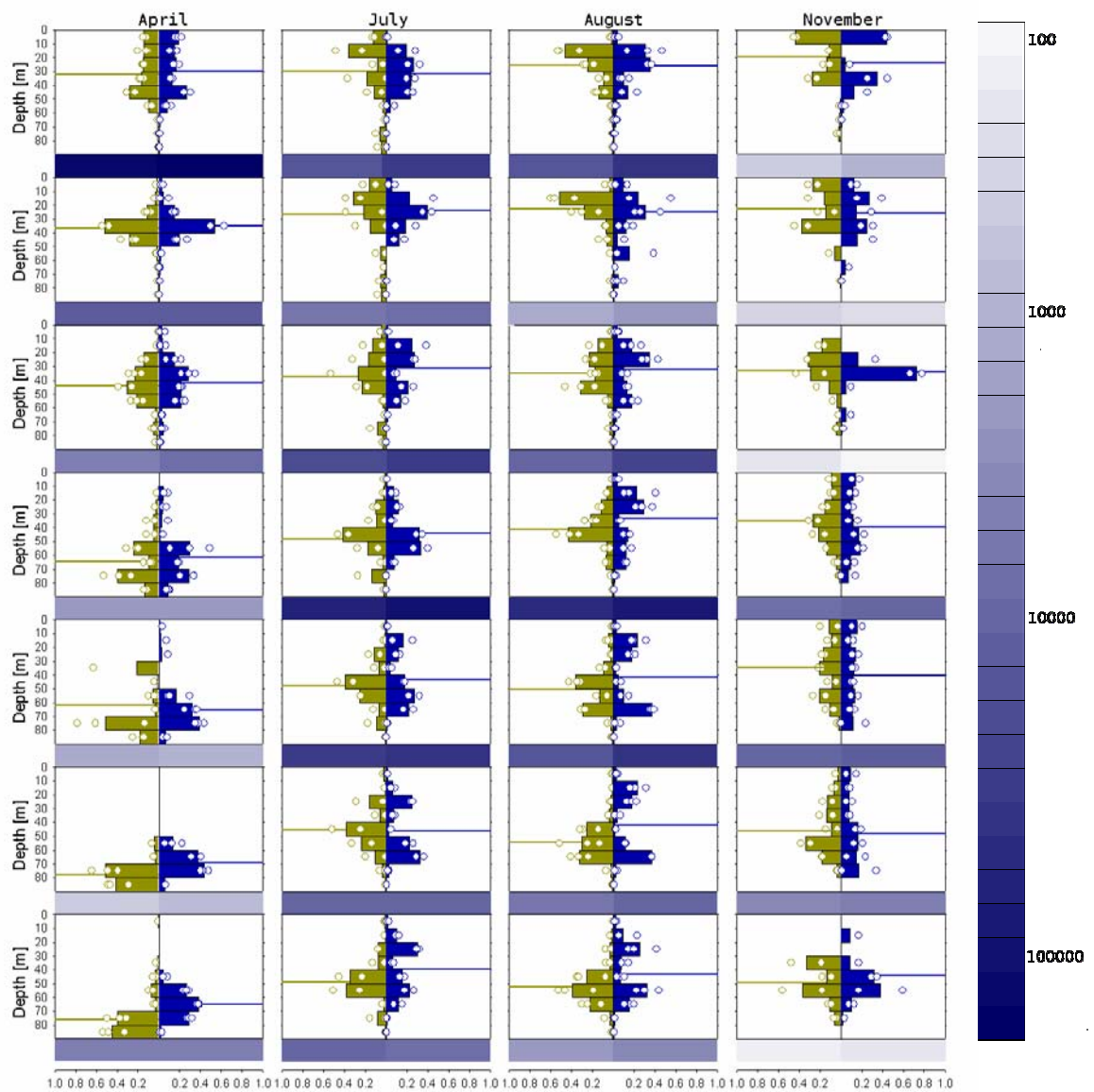


Fig. 1-6 Vertical distribution of *Pseudocalanus acuspes* life stages from upper row to bottom row (nauplii, C1, C2, C3, C4, C5, adults) for four investigation periods in 2002. Samples were taken on Station 23 (Fig. 1-2); bars show mean relative distribution, dots show individual values for each sample (three day, three night in April and August and two day, two night in July and November); dark yellow represents day, dark blue represents night; blue colouring displays the abundance in n/m^2 in logarithmic scale

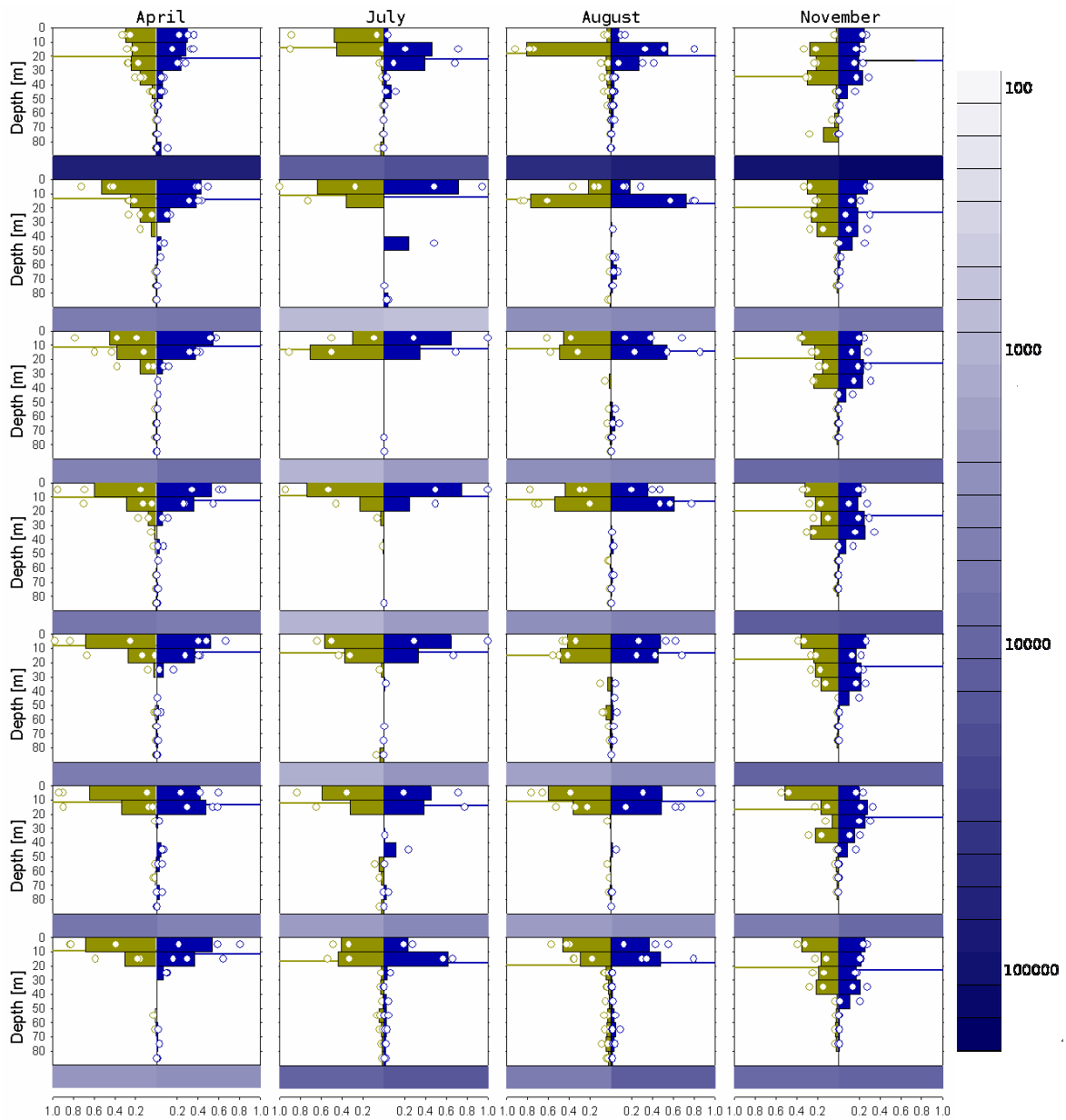


Fig. 1-7 Vertical distribution of *Acartia biflosa* life stages from upper row to bottom row (nauplii, C1, C2, C3, C4, C5, adults) for four investigation periods in 2002. Samples were taken on Station 23 (Fig. 1-2); bars show mean relative distribution, dots show individual values for each sample (three day, three night in April and August and two day, two night in July and November); dark yellow represents day, dark blue represents night; blue colouring displays the abundance in n/m^2 in logarithmic scale

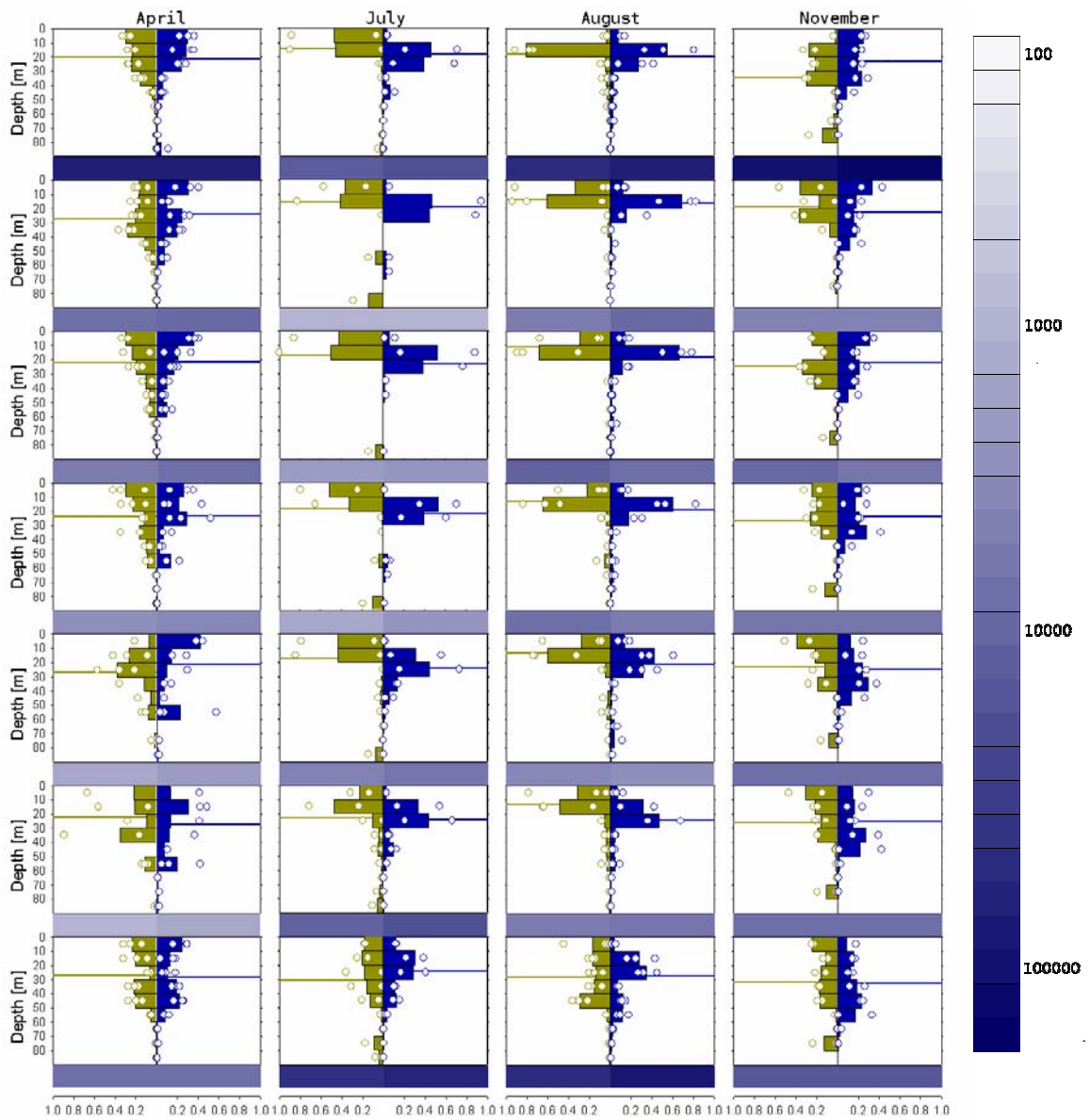


Fig. 1-8 Vertical distribution of *Acartia longiremis* life stages from upper row to bottom row (nauplii, C1, C2, C3, C4, C5, adults) for four investigation periods in 2002. Samples were taken on Station 23 (Fig. 1-2); bars show mean relative distribution, dots show individual values for each sample (three day, three night in April and August and two day, two night in July and November); dark yellow represents day, dark blue represents night; blue colouring displays the abundance in n/m^2 in logarithmic scale

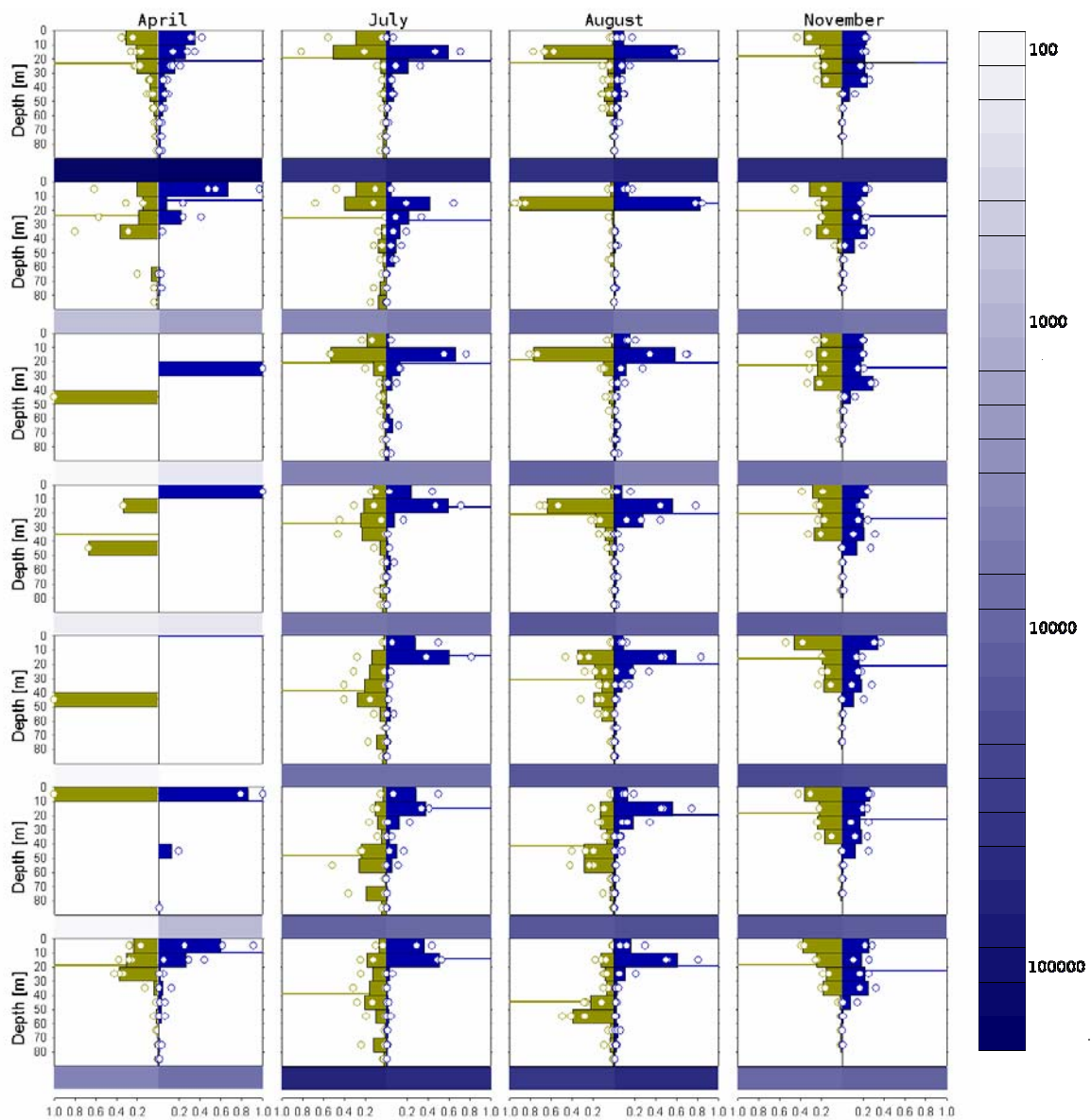


Fig. 1-9 Vertical distribution of *Temora longicornis* life stages from upper row to bottom row (nauplii, C1, C2, C3, C4, C5, adults) for four investigation periods in 2002. Samples were taken on Station 23 (Fig. 1-2); bars show mean relative distribution, dots show individual values for each sample (three day, three night in April and August and two day, two night in July and November); dark yellow represents day, dark blue represents night; blue colouring displays the abundance in n/m^2 in logarithmic scale

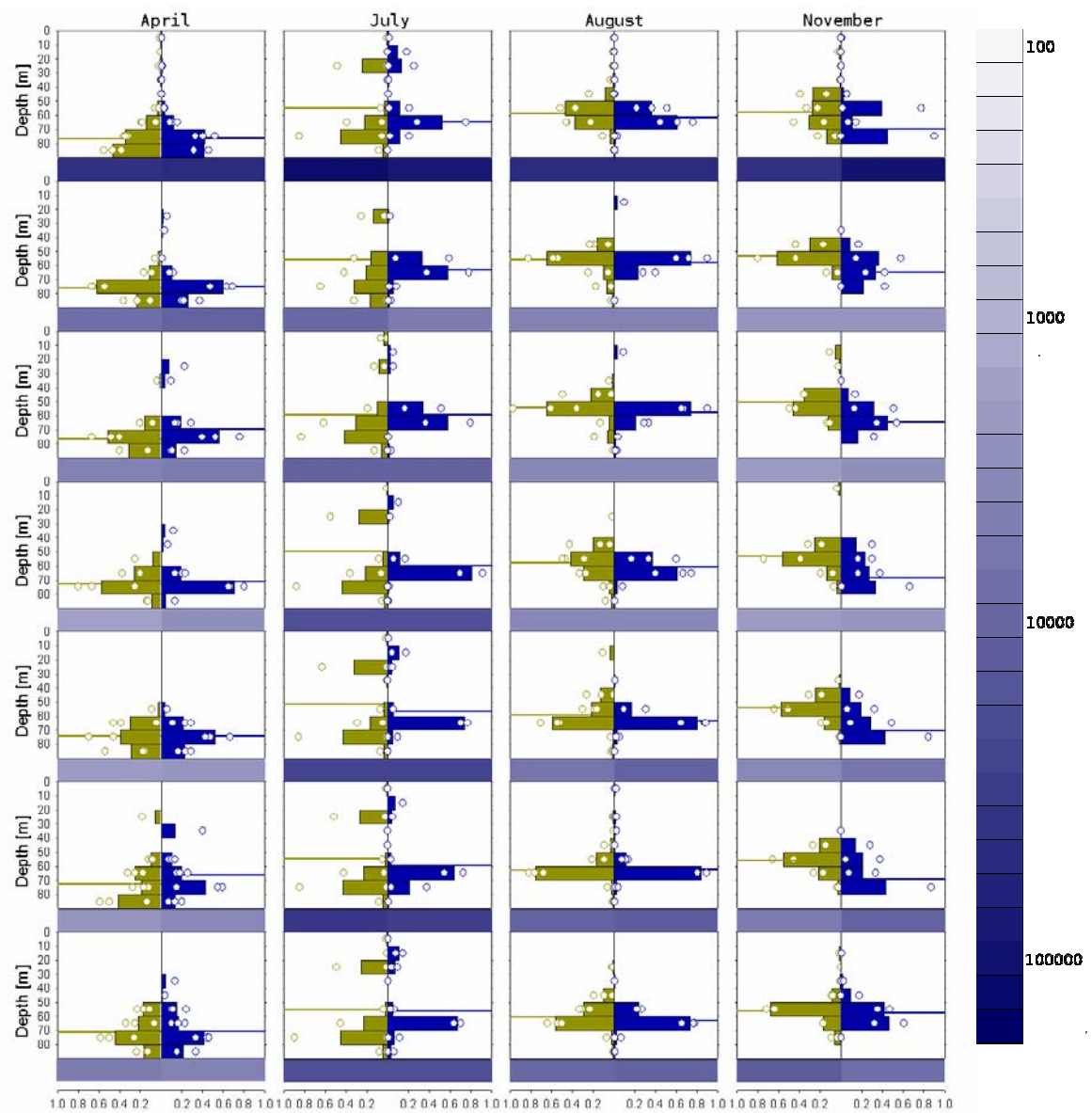


Fig. 1-10 Vertical distribution of *Oithona similis* life stages from upper row to bottom row (nauplii, C1, C2, C3, C4, C5, adults) for four investigation periods in 2002. Samples were taken on Station 23 (Fig. 1-2); bars show mean relative distribution, dots show individual values for each sample (three day, three night in April and August and two day, two night in July and November); dark yellow represents day, dark blue represents night; blue colouring displays the abundance in n/m^2 in logarithmic scale

1.6 Discussion

The aim of this study was to investigate the daily vertical migration behaviour of the main copepod species in the Bornholm Basin (Baltic Sea). Two different field studies were used to firstly explore the influence of environmental parameters, i.e. abiotic like temperature or biotic like prey and predator distribution, on the distribution and migration. Secondly, sampling during different month was performed to reveal possible seasonal differences. Major differences were found in the vertical distribution and migration among the investigated species. The observed patterns were discussed in consideration of the seasonal aspect as well as the relation to environmental factors. The accompanying data on fish and phytoplankton distribution was relatively sparse, observed patterns are described only, rather than analysing the relationship statistically.

Vertical migration over more than 10 metre has only been observed for *T. longicornis* in June 2001 and July, August 2002. The pattern was most distinct and significant for stages older than C3. At night, the animals dwelled at 10 to 15 metre, whereas at day they inhabited deeper water layers beneath 30 metre. The ultimate reason for this behaviour could be predator avoidance (Lampert 1993, Hays 2003). However, the planktivorous fish showed a similar migration, inhabiting water depth of 60 metre at day and moving up in dusk to the surface (Fig. 1-11). Therefore it could be argued, that the avoidance effect is only limited and other reasons are more likely. Staying in deeper, colder water at daytime is energy saving, thus beneficial if the saving counterbalance the energy lost for migration. Another reason could be the avoidance of invertebrate predators, e.g. chaetognaths. However, as no data was collected regarding those hypotheses this remains unclear.

Other studies performed in the Baltic Sea also

revealed migration behaviour of *T. longicornis* (Mankowski and Cziskewski 1961, Hansen *et al.* 2006). However, they did not discuss possible reasons. In general, this species inhabited the upper 40 metre of the water column, avoiding the water masses beneath the halocline with low temperatures. Chojnacki *et al.* (1984) described *T. longicornis* as thermophilic and Möllmann *et al.* (2000) as well as Dippner *et al.* (2000) showed, that the development throughout the year was positively correlated with temperature. Therefore, the preference to the upper water layers in general could be explained. The same positive relationship to temperature was described for *Acartia* species. In our study both sibling species inhabited mainly the upper water layers. This was also reported from other studies in the Baltic Sea (Dahmen 1997, Hansen *et al.* 2006). *A. bifilosa* inhabited the uppermost 20 metres in all sampled periods, except November, where the distribution was more dispersed from the surface down to 50 metres. No differences could be seen between night and day distribution. The broader distribution was also observed for *A. longiremis* in November as well as in April and for the

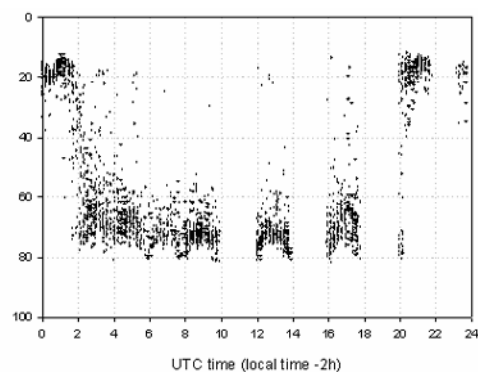


Fig. 1-11 Distribution of echoes derived from hydroacoustic measurements on the triangle transects over 24 hours (Stepputtis 2001)

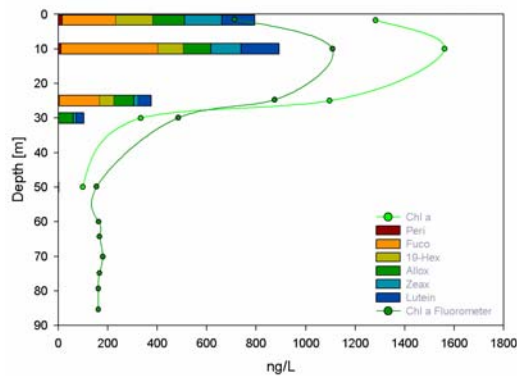


Fig. 1-12 Vertical distribution of marker pigments derived from HPLC analysis (Wright *et al.* 1991) of filtered seawater from June 2001; light green line shows *chl a* concentration derived from fluorometer measurements mounted on the CTD

adults in all sampled periods. In July, the majority of individuals dwelled slightly higher at day than at night. This migration could not be explained with available environmental data. However it could be suspected, that they feed on different parts of the phytoplankton community during day and night, although it could not be proved.

For *P. acuspes* no daily migration could be reported. However, the ontogenetic vertical migration was distinct, with the younger stages (nauplii to C2) inhabiting the upper part of the water column, and the older stages continuously dwelling deeper and deeper with the adults living in and below the halocline. This pattern was most distinct in April, but could also be seen in the summer month. In November, the majority of *P. acuspes* were in stage C3 to C5 and distributed broader over the water column. The few individuals in the other stages conserved the distribution from spring and summer. The need to grow fast counterbalances the risk to be eaten (Bollens and Frost 1989, Lampert 1993). Therefore, young stages dwell in shallow water layers,

where food is available and the high temperature accelerate development. Their small size makes them less vulnerable to predation. As they grow, they have to move to deeper water layers to minimize the risk to be eaten and start diel vertical migration, to take advantage of the food near the surface (Fig. 1-12). This hypothesis could not totally explain the ontogenetic migration for *P. acuspes* in our study, as the older stages did not migrate to the surface at night. However, as the older stages dwell around the halocline they could perhaps switch their feeding to other prey like detritus particles or mikrozooplankton grazing on detritus and accumulating at the halocline (Kioerboe and Sabatini 1994). Another reason for the older stages to dwell deeper could be the physiological need of higher salinity as stated by Hansen *et al.* (2006) and reported from Vinogradov *et al.* (1985) for the Black Sea. In chapter two, differences are shown in the distribution of reproducing female *P. acuspes* for two years with different hydrographic situations indicating a limitation to high saline waters.

The only cyclopoid species in the study was *O. similis*. This genus has been described as the most ubiquitous and abundant copepod in the world (Bigelow 1926, Gallienne and Robins 2001). All developmental stages of *O. similis* dwelled in the depth of the halocline, showing no difference between day and night distributions. Hansen *et al.* (2004) reported the same pattern, suspecting that the need of higher salinity was the reason. However, *O. similis* exists over a wider range of temperatures and salinity than most other marine copepods from temperate brackish coastal waters to subtropical oligotrophic oceans (Nishida 1985, Mazzocchi *et al.* 1995). Therefore it could be suspected, that this species lives at the absolute margins of its distribution.

2 Small-scale distribution of reproducing female *Pseudocalanus acuspes* Giesbrecht

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2.1 Abstract

During two cruises in May 2002 and April 2003 the Video Plankton Recorder (VPR) was towed on two transects from the central Bornholm Basin (100m depth) to its southern margin (60m depth isoline). The VPR allowed recording non-invasively the distribution of egg-sac carrying (reproducing) female *Pseudocalanus acuspes* to a spatial resolution of a few centimetres. Concurrently the hydrography was recorded using a Seabird CTD equipped with an oxygen sensor, deployed on a regular station grid (10 nm). The investigation revealed very different hydrographic conditions between the two years due to an inflow of high saline, oxygen-rich water from the North Sea into the Baltic in January 2003. This resulted in an exchange of the bottom near water mass with increasing salinity from a maximum of 15 in 2002 to a maximum of 19 in 2003. Additionally the oxygen content increased from a minimum of 0.0 ml/l in 2002 to a minimum of 5 ml/l in 2003. The vertical distribution of reproducing *P. acuspes* females changed from 2002 to 2003 slightly, with the individuals dwelling deeper in the water column in 2003 signifying a dependency on ambient hydrographic conditions. The *in situ* egg production was measured directly via image analysis and revealed a higher number of eggs per female in 2003. However, the egg production per day was slightly higher in 2002 because of higher temperatures.

2.2 Introduction

The calanoid copepod *Pseudocalanus acuspes* formerly frequently called *P. elongatus* (Renz and Hirche 2005), is a key species in the Central Baltic Sea, serving as a major food item for commercially important pelagic fish species herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) (Möllmann and Köster 2002, Möllmann *et al.*, 2004). Changes in the availability of the copepod have been shown to

strongly influence growth and condition of Baltic clupeid fish (Möllmann *et al.* 2003a, 2005, Rönkkonen *et al.* 2004). Further *P. acuspes* population size was found to be crucial for larval survival and eventually recruitment of Central Baltic cod (*Gadus morhua* L.) (Hinrichsen *et al.* 2002).

The semi-enclosed Baltic Sea is the largest brackish water system of the world,

characterized by strong vertical salinity gradients due to a positive freshwater balance (Matthäus and Franck 1992). The vertical stratification is characterized by a halocline in the deep basins, which prevents mixing with the upper low salinity but oxygenated water bodies. Ventilation of the deep water is only possible through inflows of saline and oxygenated water originating from the North Sea (Matthäus and Schinke 1999). Consequently, oxygen conditions deteriorate during periods without inflows, called “stagnation periods”.

P. acuspes shows an ontogenetic vertical distribution related to the vertical stratification of the habitat. While naupliar and younger copepodite stages dwell in the food-rich surface layers, later copepodite stages and adults concentrate in the permanent halocline (Hansen *et al.* 2004, Renz and Hirche 2005). Consequently, the vertical distribution is positively related to salinity especially for older developmental stages (Renz and Hirche 2005). Female *P. acuspes* reproduce in the high salinity

deep-water layer with a reproduction peak in spring. Their vertical distribution is restricted from below by low oxygen conditions (Hansen *et al.* 2004, Renz and Hirche 2005).

The population size of *P. acuspes* declined during the last decades, a trend correlated to the salinity level (Möllmann *et al.* 2000, 2003b). Deep water salinity as well as oxygen levels in the Central Baltic Sea decreased during recent decades due to a low frequency of major Baltic inflows (Fonselius and Valderrama 2003), hypothesized to be a result of the persisting positive state of the North Atlantic Oscillation since the late 1980s (Hänninen *et al.* 2000, Möllmann *et al.* 2003a, 2005). The process behind the relationship between *P. acuspes* population size and salinity remained, however, unclear. Renz and Hirche (2005) observed a strong increase in adult and nauplii abundances after a major Baltic inflow in 2003. They discussed possible explanations, e.g. (i) a direct physiological effect of low salinity on growth and reproduction, (ii) advection of *P. acuspes* populations with the inflow, and (iii) an increase in total biomass but not concentration due to an increase in suitable habitat volume. However, based on their data they could not identify the mechanism behind the post-inflow increase in abundance (Renz and Hirche 2005).

The effect of salinity on *P. acuspes* may, however, be indirect via the in parallel low oxygen level. Due to their physiological preferences, low salinity may force reproducing adult females into deeper waters. Here they encounter detrimental oxygen conditions affecting potential egg production or survival of adults, the attached eggs or early nauplii. However, a prerequisite for investigating the above hypothesis is to record the small-scale ambient salinity and oxygen concentrations of reproducing females, which is impossible with conventional net sampling, usually resolving the water column only in intervals of a few metres. Further, reproducing female *P. acuspes* cannot be directly identified from net samples, due to the loss of the

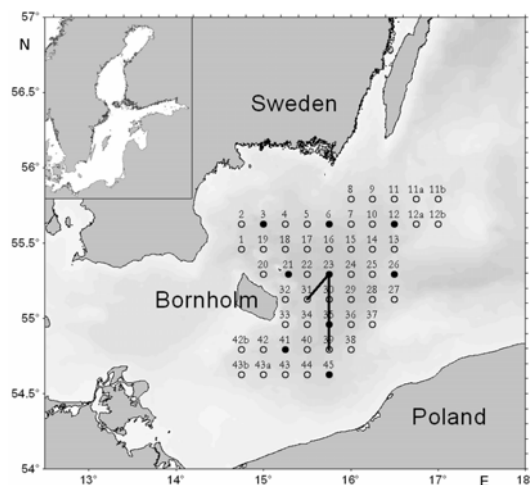


Fig. 2-1 Bornholm Basin (Baltic Sea); white dots represent stations where CTD measurements were conducted; black dots represent stations where additional multinet samples were made; black lines represent the two transects where the VPR was deployed

attached egg sacs during the sampling process. An alternative to conventional net sampling is modern underwater imaging technology such as the Video-Plankton Recorder (VPR). The VPR gives the opportunity to examine non-invasively the distribution of zooplankton organisms on scales of a few centimetres (Davis *et al.* 1992b, Benfield *et al.* 1996). Using a VPR in contrasting environmental conditions, i.e. pre- and post

inflow in 2002 and 2003, here the combined effect of salinity and oxygen conditions on the small-scale distribution of reproducing female *P. acuspes* was investigated with the goal to identify the mechanism behind the salinity-related decline in the population of the copepod.

2.3 Materials and Methods

2.3.1 Video Plankton Recorder (VPR) observations

The VPR was deployed on two cruises in May 2002 and April 2003 in the Bornholm Basin, Central Baltic Sea, conducting two transects from the centre of the Basin to its southern margin (Fig. 2-1). The instrument was towed, undulating from approximately five metre below the surface to eight metre above the bottom.

The VPR consists of a single video camera and synchronized strobe, monitoring a volume of water at a rate of 25 Hz. The photographed area is 0.85 x 0.85 cm and the depth of the recorded water body lies between 0.70 and 0.85 cm, resulting in a water volume of approximately 0.5 cm³ to 0.61 cm³ per image.

The digitized video stream is transmitted to the board-unit via fibre-optic cable where each frame is pre-processed eliminating empty images and objects out of focus. Objects remaining in focus are saved as regions of interest (ROI) and time-code from a GPS system is added to each image. The same time-code is added to a log-file containing the position and depth of the VPR at the same time the image was recorded. Data is archived on a computer hard drive for later analysis. The final analysis was carried out manually by sorting out the ROI showing *P. acuspes* females with egg sacs (Fig. 2-2) and combining each image with data from the log-file. Afterwards, each positive observation was related to the concurrently measured

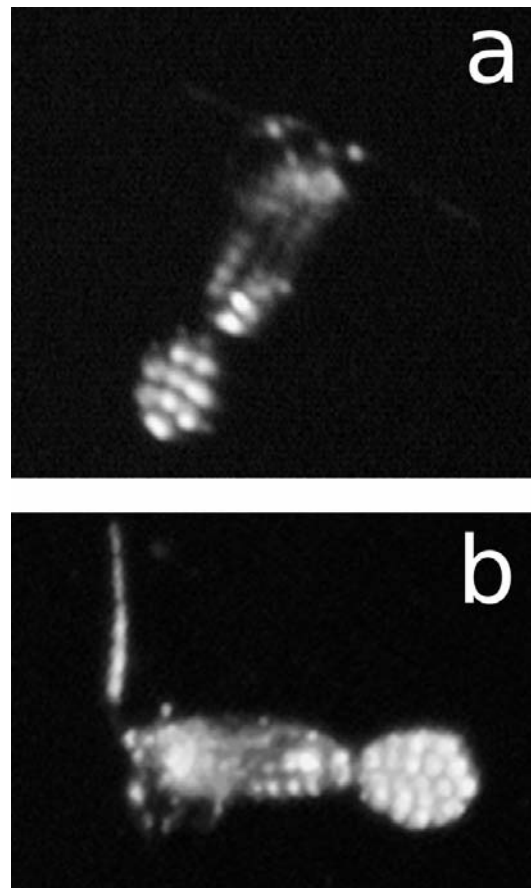


Fig. 2-2 VPR-images of female *P. acuspes* carrying egg-sacs; a) May 2002 b) April 2003

hydrographic situation derived from interpolated CTD-data from profiles on the transect.

2.3.2 Hydrographic measurements

Hydrographic data was obtained from CTD casts applied on a regular station grid (10 nm grid point distance, Fig. 2-1) using an ADM-CTD (Analoge und Digitale Messsysteme GmbH) equipped with an oxygen sensor. The

data was interpolated over the VPR transect using the kriging algorithm (Oliver 1990) implemented in the Surfer software (Golden Software Inc. 2003).

2.3.3 Conventional net sampling

For comparison of the VPR-derived distributions of *P. acuspes* females and evaluating the influence of different hydrographic conditions on the population dynamics of the copepod, parallel net sampling was conducted on the station-grid in the Bornholm Basin (Fig. 2-1). The sampling was conducted on the same two cruises where the VPR was deployed and additionally on two cruises in April 2002 and May 2003. Vertically stratified samples were obtained using a HYDRO-BIOS multinet (50 µm

mesh size) in 10 m depth strata to a maximum depth of 90 m. Samples were preserved in 4% formalin-seawater solution for analysis in the laboratory. Mesozooplankton was identified and counted under a binocular microscope on subsamples no less than 1/100 of the total sample. Subsamples were obtained using a Kott-splitter device (Kott 1953). *P. acuspes* were identified to developmental stages (N- nauplii, C1-5 copepodites) and adults to sex (C6 females, C6 males).

2.3.4 Statistical analysis

For both the distribution derived from VPR recordings as well as from net sampling, a weighted mean depth (WMD) was calculated:

$$\left(\frac{\sum n_i d_i}{\sum n_i} \right) \quad (2-1)$$

with n_i is abundance (number/m³) at depth d_i . The depth distributions were compared using a Kruskal-Wallis ANOVA and Median test.

2.3.5 Indices of habitat size and quality

Based on the distribution of female *P. acuspes* recorded with the VPR, two indices were calculated characterizing the reproductive habitat for the copepod. The volume of the reproductive habitat (VRH) was calculated for both sampling dates using an objective analysis after Bretherton *et al.* (1976) based on CTD data obtained on the station grid (Fig. 2-1).

Threshold values were derived from the VPR-recorded distribution of reproducing female *P. acuspes*, using limits within 95% of the individuals were found, i.e. a salinity ≥ 13.25 and an oxygen content ≥ 0.88 ml/l oxygen respectively. As an index of the quality of the reproductive habitat (QRH), the mean oxygen content in the VRH was computed.

2.3.6 Direct estimation of *in situ* egg production

Low salinity and oxygen conditions may affect the reproductive output of the copepod. The video images recorded by the VPR were used

to calculate an index of *in situ* egg-production of *P. acuspes* females for both sampling dates representing different reproductive conditions.

The egg sac and six eggs within each egg sac, of each individual recorded dorso-ventrally or laterally were measured using the freely available software ImageJ (2004). The formula for ellipsoid spheres was used to compute the volume (V) of the egg sac:

$$V = \frac{4}{3} \pi a b b' \quad (2-2)$$

with a , b and b' being the length, width and depth of the measured object (Fig. 2-3). Width and depth were considered equal as only one dimension could be measured. The diameter of the eggs (c , Fig. 2-3) was measured and the volume was calculated using the equation for spheres.

Using the arithmetic mean of the six measured eggs, and assuming a random loose packing of spheres (Weitz 2004), the number of eggs per egg sac were calculated. With the results, a daily egg production was calculated for the area using the temperature dependent development time for *P. acuspes* eggs taken from McLaren *et al.* (1989):

$$D = 1949(T+12.59)^{-2.05} \quad (2-3)$$

2.4 Results

2.4.1 Hydrography

The two studied periods differed greatly in their hydrographic characteristics. The vertical temperature structure in April 2002 showed a marked stratification with cold water ($\sim 4^\circ\text{C}$) from the surface down to 60 m and constantly increasing temperatures from there to the bottom up to 8.5°C (Fig. 2-4). In May 2002, the surface water began to heaten showing temperatures up to 6°C from the surface down to 40 m. The cold water mass was still present in 40 to 60 m depth and beneath the temperature increased to 8.5°C at the bottom (Fig. 2-4). In 2003, the situation was very different. In April the whole water mass showed a temperature of about 3°C (Fig. 2-4). Warmer

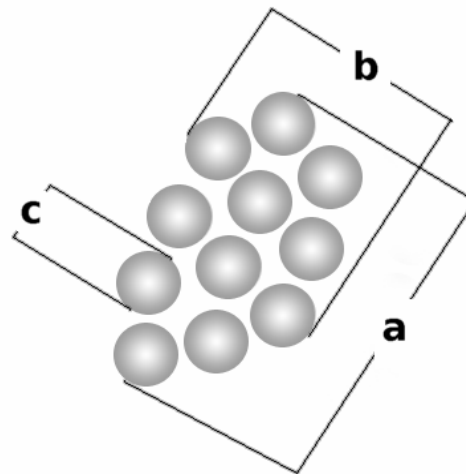


Fig. 2-3 Scheme of an egg clutch of *P. acuspes*; a - length measurement; b - width measurement; c - egg measurement

and the basin wide abundance of female *P. acuspes* calculated with the objective analysis (Bretherton *et al.* 1976) using the abundances derived from bongo sampling. Temperature was taken from CTD measurements and a Basin wide average was calculated.

water masses were only detected at the southern edge of the basin 10 m above the bottom (6°C maximum, Fig. 2-4). In May 2003, again a warming of the upper water mass could be seen with highest temperatures of nearly 10°C at the surface, decreasing to $3-4^\circ\text{C}$ at 40 m depth. From 40 m to the bottom the water mass had a temperature of 3°C (Fig. 2-4). The vertical salinity structure in 2002 showed a homogeneous upper water body from the surface down to 50 m with a salinity of 8.5. Beneath this water mass the salinity increased continuously to the bottom where it reached a value of 15.5 (Fig. 2-4). In May 2002 this pattern did not changed (Fig. 2-4). However, in

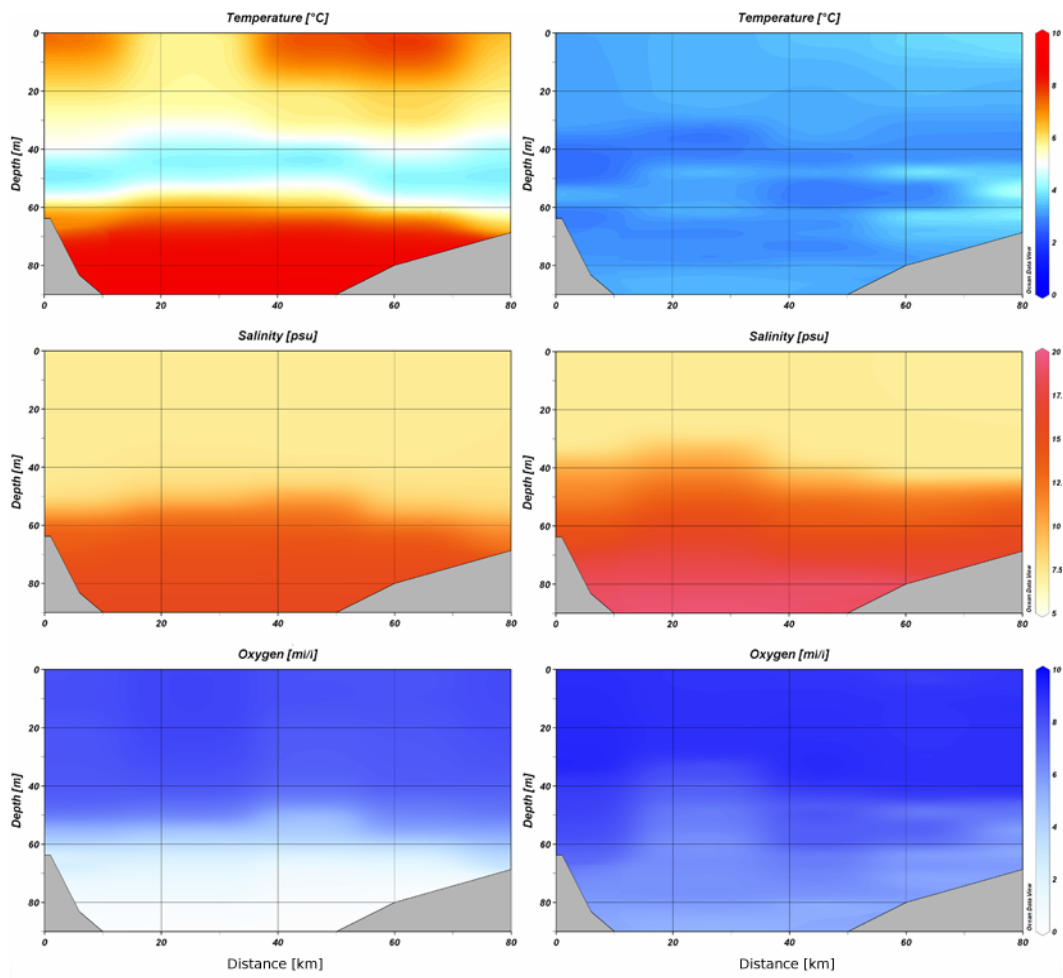


Fig. 2-4 Hydrography on the VPR-transect in 2002 (left column) and 2003 (right column); interpolated with Kriging from CTD casts on stations on the transects

2003 both in April and in May the stratification in salinity was similar, but differed in the total value and the thickness of the homogenous upper water body. The salinity was about 7.5 in the upper 40 m and beneath it increased up to 19.5 near the bottom (Fig. 2-4). The halocline in 2002 was in about 70 m depth where it was in a water depth of 60 m in 2003. A strong difference between the years could also be seen in the oxygen content. In 2002 in April as well as in May the upper water layer

from the surface down to 40-50 m depth was well oxygenated with values around 8.5 ml/l. Beneath the oxygen content decreased to a value of 0 ml/l oxygen 10 m above the ground in the centre of the basin (St. 23, see Fig. 2-1 and Fig. 2-4). In 2003 similar to 2002 the saturated upper water mass reached from the surface down to 40 m. In contrast to 2002, the oxygen content did not decrease to 0 ml/l, but was erratic with lowest values of 5 ml/l in April 2003 and 3 ml/l in May 2003 (Fig. 2-4).

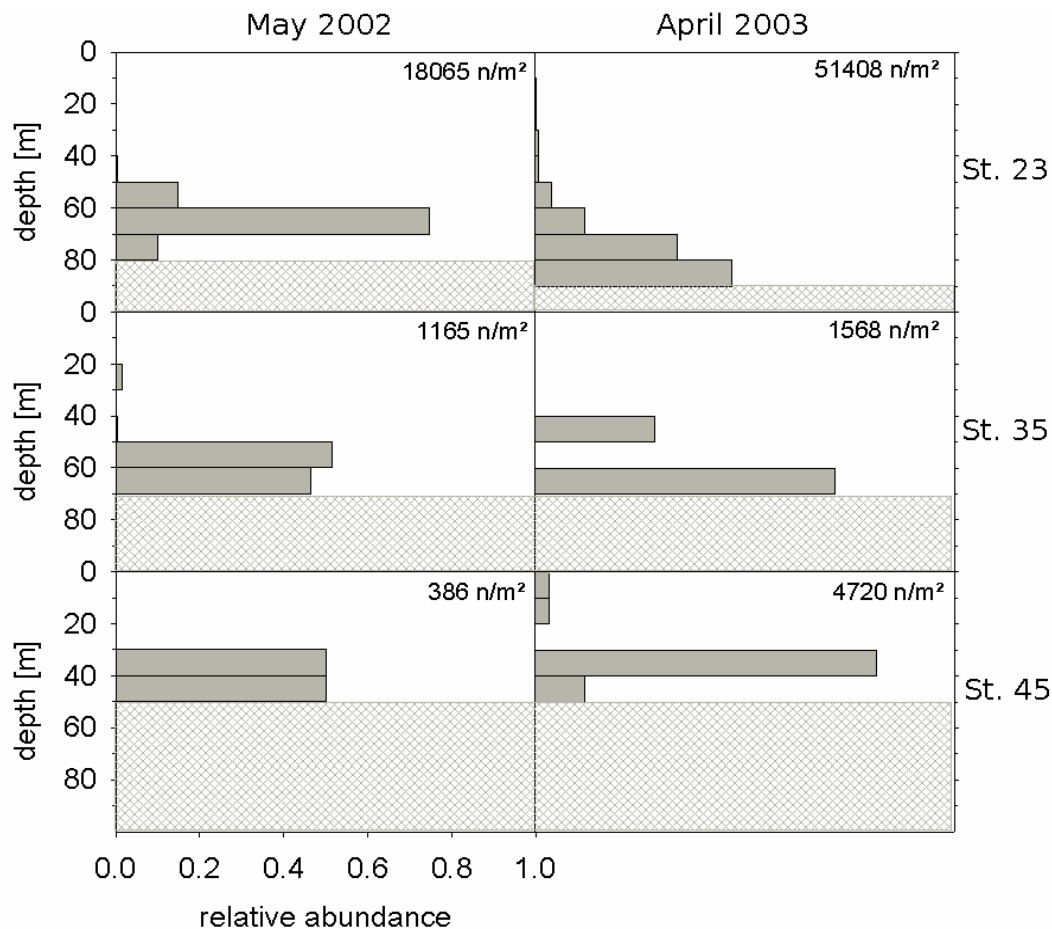


Fig. 2-5 Depth distribution of female *P. acuspes* from multinet sampling on three stations on the north south transect; the abundances on each station are given in the upper right corner of each graph

2.4.2 Vertical distribution of female *P. acuspes*

Results from the vertically resolving net samples show that female *P. acuspes* generally inhabited the water masses underneath the halocline (Fig. 2-5). The vertical distribution in May 2002 and April 2003 were different only on station 23 in the centre of the basin, with the females being significantly deeper distributed as seen in the weighted mean depth. In generally female *P. acuspes* were observed to have inhabited a wider range of the water column in April 2003 when compared to the previous year. The VPR was used to record only the reproductively active, i.e. egg-carrying female *P. acuspes*.

Observations in May 2002 revealed egg-carrying female *P. acuspes* to be distributed between 50 and 79m, with the median depth being 69m (Tab. 2-1).

Tab. 2-1 Weighted mean depth of female *P. acuspes* sampled in May 2002 and April 2003, *H =15.19115, p =0.0001

		2002	2003
VPR		69.3*	74.4*
	St. 23	64.4	69.0
Multinet	St. 35	59.1	59.3
	St. 45	40.0	34.5

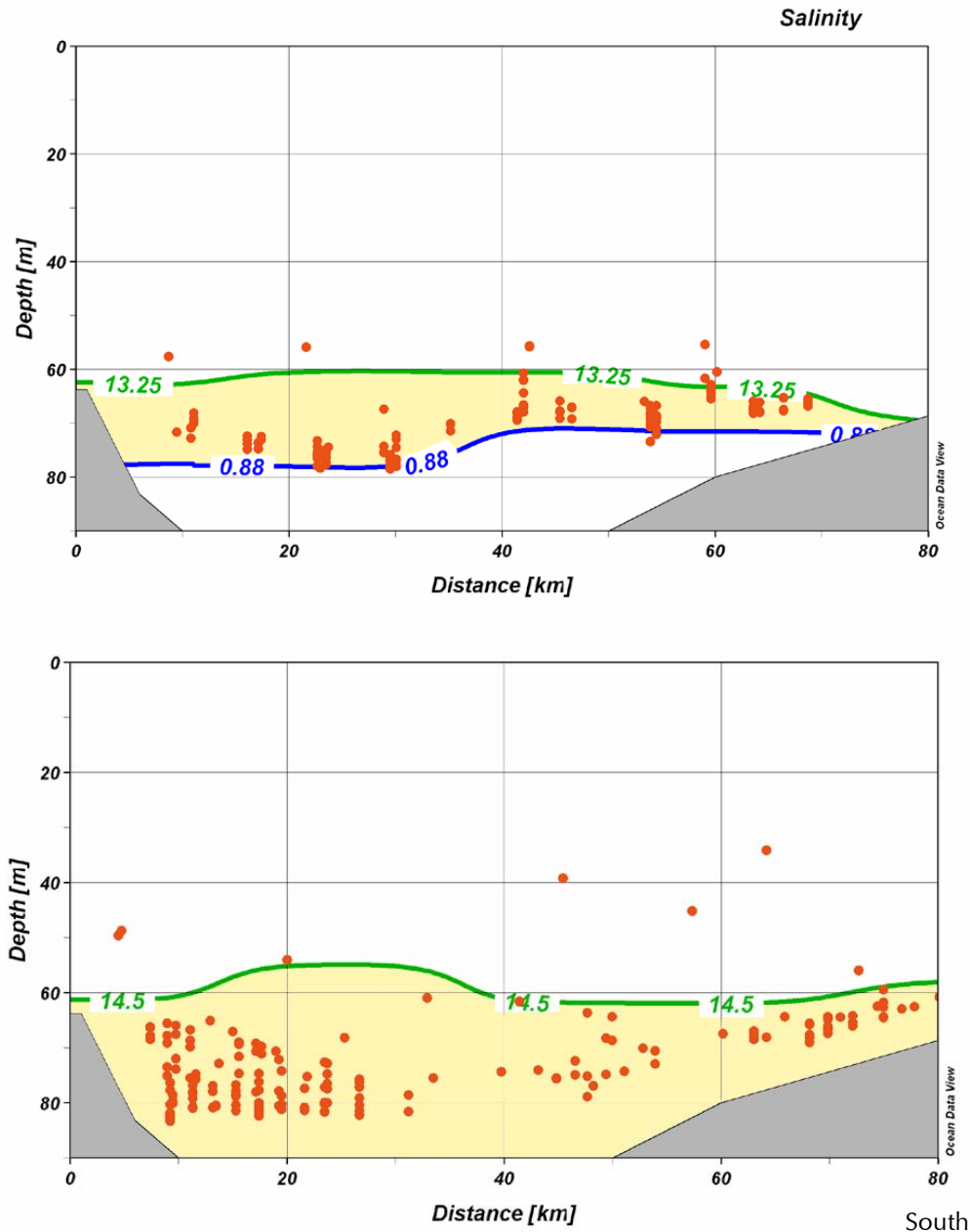


Fig. 2-6 Distribution of female *P. acuspes* carrying egg-sacs from VPR recordings in 2002 (upper panel) and 2003 (lower panel); red dots represent single individuals on VPR image; green line indicates salinity level above which 95% of individuals were found; blue line indicates oxygen level above which 95% of individuals were found. The Volume of reproductive habitat (VRH) is indicated in light yellow

Most of the population was distributed in the permanent halocline in a narrow band of about 10m thickness, with the maximum depth limited by the oxygen conditions, i.e. the 0.88 ml/l oxycline. In the central part of the basin this oxycline was found deeper in the water column

allowing the animals to dwell deeper than in the southern part (at the margins of the basin), where the oxycline was found in significantly shallower depth. An upper limit was found at a salinity value of 13.25.

Tab. 2-2 Basin wide abundance of *P. acuspes* females and nauplii calculated with an objective analysis (Bretherton *et al.* 1976) using abundance measurements from Bongo net samples (for females; 150 μm mesh) and multinet samples (for nauplii; 50 μm mesh)

Month and Year	<i>P. acuspes</i> females [n/m ³]	<i>P. acuspes</i> nauplii [n/m ³]	nauplii to female ratio
May 2002	0.952×10^{14}	2.632×10^{15}	27.6
April 2003	1.273×10^{14}	6.765×10^{15}	53.1

2.4.3 Reproduction volume

Our indices for the volume and the quality of the reproductive habitat, i.e. VRH and QRH, showed clearly how the ambient environmental conditions improved for of *P. acuspes* females

after the inflow in winter 2003 (Tab. 2-3). We found VRH to be 4 times larger after the inflow event, and QRH, defined as the mean oxygen content, more than doubled.

2.4.4 In situ egg production measurements

The measurement of about 30 egg sacs per cruise showed a slight difference in individual egg number per clutch between May 2002 and April 2003. In May 2002 the females carried in average 18.9 eggs and in April 2003 22.3 eggs. However, the calculation of the daily egg production revealed a slightly higher production in 2002 (411.1×10^{12} eggs produced within the 60 metre depth isoline). The reason was the higher temperature in May

2002 (7°C) compared to April 2003 (3°C and 407.4×10^{12}). Therefore, the development time of the eggs was much shorter in May 2002 with 4.4 days compared to April 2003 with 7 days. The ratio of nauplii to female abundance was calculated to get an idea of the production/survival ratio. The nauplii to female ratio was 27.6 in 2002 and 53.1 in 2003 being nearly twice as high (Tab. 2-2).

Tab. 2-3 Reproduction volume for the Bornholm Basin calculated with an objective analysis (Bretherton *et al.* 1976) using CTD measurements on each of the stations covering the whole basin (Fig. 2-1); Limits were set by salinity (13.25) and the oxygen content (0.88 ml/l), take from the 2002 95% distribution interval of female *P. acuspes* carrying egg sacs

Month and Year	extend of the reproduction volume [km ³]	mean oxygen content [ml/l]
May 2002	51.4	2.11
April 2003	208.6	4.41

2.5 Discussion

The aim of this investigation was to observe the distribution of reproducing female *P. acuspes* with the goal to identify potential mechanisms behind the observed salinity related decline in the population size of the copepod. To this end, an *in situ* sampling was performed using a VPR and conventional net sampling during contrasting hydrographic conditions before and after the major Baltic inflow in early 2003 (Feistel *et al.* 2003). Our hydrographic measurements documented the change in the physical conditions, characterized mainly by higher post-inflow salinity and oxygen conditions in the deep water, the main habitat of our target species. A further result of the inflow was considerable lower deep-water temperatures.

Our observations, both with the VPR and nets, clearly demonstrated the influence of the altered hydrographic conditions on the distribution of the female *P. acuspes*. Comparing vertical distributions from the two contrasting hydrographic situations showed the animals to have been dwelling deeper after the inflow in 2003. This deeper distribution points towards the crucial importance of high salinity levels for the reproduction of this species of marine origin (Corkett and McLaren 1978). Suboptimal salinity conditions are known to increase respiration rates in copepods (Farmer and Reeve 1978, Gaudy *et al.* 2000, Gyllenberg and Lundqvist 1979, Pagano and Gaudy 1986) which results in a need of supplementary energy for osmoregulation (Kinne 1964). The result of the influence of suboptimal low salinity can be decreased egg production (Uriarte and Villate 2005) and/or lower survival (Devreker *et al.* 2004). Our study showed that Baltic female *P. acuspes* maximize ambient salinity conditions by descending as deep as possible into the deep basins. This mechanism is displayed by the very narrow distribution in the stagnation situation, where the animals find only a small layer with sufficiently high salinities, and are

restricted from below by low oxygen contents. After the inflow, no restriction in distribution existed from below due to improved oxygen conditions. Rather the high salinity level allowed the copepods to occupy a much wider layer of the water column.

A comparison of the results from the different gears in use, revealed the VPR to more clearly pick up the signal of the difference in vertical distribution compared to the conventional net sampling. Statistically significant different WMDs between the two sampling dates could only be found by using the small-scale observations with the VPR (Tab. 2-1). One reason behind this may be different vertical distributions between reproductively active and non-active females. These cannot be distinguished from the conventional net sampling, as the egg sacs are destroyed during the sampling process. This point towards another strength of the VPR beside the ability to resolve a smaller scale of distribution, i.e. the non-invasive nature of the sampling with this gear. However, results from both gears confirm earlier studies showing the permanent Baltic halocline to be the reproductive habitat of female *P. acuspes* and the positive correlation of salinity and dwelling depth (Hansen *et al.* 2006, Renz and Hirche 2005).

The risk of the strategy applied by *P. acuspes* to migrate into the high saline layer of the deep Baltic basins, is the danger of suboptimal oxygen conditions. Recent investigations exemplified this effect for *Acartia* spp. and showed that suboptimal oxygen conditions reduce egg production (Marcus *et al.* 2004, Sedlacek and Marcus 2005, Richmond *et al.* 2006) and survival (Stalder and Marcus 1997, Marcus *et al.* 2004, Richmond *et al.* 2006). Our indices of size and quality of the reproductive habitat for female *P. acuspes*, with VRH being in 2003 four times and QRH two times the values of 2002, display the degradation of reproductive conditions during stagnation

periods in the Baltic. To evaluate the potential effect of low oxygen on the recruitment of new generations, daily egg production rates were estimated from VPR recordings, which were however very similar in both hydrographic regimes. This confirms concurrent measurements of *in situ* egg production (Renz pers. commun.) excluding recruitment as the mechanisms leading to the difference in observed nauplii abundance. Consequently, lowered survival of eggs and nauplii may be the reason for enhanced recruitment. The ratio of nauplii to females was used as an index of the combined survival of eggs and nauplii, which

indicates 2 times higher survival after the inflow. Based on this result it was concluded that a major mechanism leading to the long-term decline of *P. acuspes* (Möllmann *et al.* 2000, 2003b) is low egg and nauplii survival due to lethal oxygen concentrations during stagnation periods. The correlation of the population reduction with salinity is thus caused by the parallel degradation of oxygen and salinity conditions, because lowered salinity forces the animals to descend into increasingly low oxygen conditions affecting the survival of the offspring.

3 Simulating the interaction of *Pseudocalanus acuspes* with the physical environment in the Central Baltic Sea

3.1 Abstract

In this study the influence of drift on retention or dispersion of *Pseudocalanus acuspes* in the Central Baltic Sea was investigated. A biological model of *P. acuspes* development was coupled with a circulation model of the Baltic Sea. Drift studies were performed for 1980 to 2000 from 1st of April to the 31st of October. The results showed a change in circulation patterns in the 1990s, resulting in a larger proportion of *P. acuspes* being transported in the eastern part (Gdansk Deep and Gotland Basin). However, *vice versa* the transport was very limited. Therefore, drift was suspected to be a concurrent factor of biomass change between the years. Transport to near shore waters, however, reduces the biomass due to potential unfavourable conditions and death of the animals.

3.2 Introduction

Transport is one of the prevailing features of plankton in the sea. However, besides the relevance for distribution of larval stages of meroplankton it is suspected to sometimes exhibit negative consequences (Davis 1984a, Aksnes and Blindheim 1996, Reiss *et al.* 2003, Zakardjian *et al.* 1999). The transport out of areas with favourable conditions into less favourable areas will have a severe impact on the biomass development. In the last decades, the development of circulation models yielded a valuable tool to investigate the distribution pattern of plankton, besides mere field sampling (Hinrichsen *et al.* 1997, Hinrichsen *et al.* 2001). The coupling of biological models to the circulation models was the next step (Fennel 2001).

*Pseudocalanus acuspes*¹ is a key species in the

Central Baltic Sea and a major food organism for many fish larvae, juvenile and adult fish (Voss *et al.* 2003, Möllmann and Köster 2002). This species lives at the margin of its distribution in the Baltic with respect to salinity (Möllmann *et al.* 2000), which led to large interannual fluctuations (Fig. 3-1) (Möllmann *et al.* 2000, Möllmann *et al.* 2003b). The hydrography of the Baltic Sea and the circulation patterns are mainly driven by the NAO (Matthäus and Schinke 1994, Schinke and Matthäus 1998) or rather the Baltic Sea Index (BSI), which depicts the difference of normalised sea level pressure anomalies between Oslo (Norway) and Szczecin (Poland) (Lehmann *et al.* 2002). Changes in the atmospheric forcing resulted in changes of the general circulation pattern in the Central Baltic deep basins (Schrum 2001, Hinrichsen *et al.* 2003a). A simple stage-based Individual-based Model (IBM) was coupled to a General

¹ Formerly termed as *Pseudocalanus elongatus* or *Pseudocalanus minutus* (Renz and Hirche 2005)

Circulation Model (GCM) of the Baltic Sea to simulate the interaction of *P. acuspes* with the physical environment for years 1980 to 2000. Drift and development of individual copepods were investigated with respect to (i) the exchange of animals between the Bornholm Basin (the major spawning area for the commercially important species cod and sprat) and the more eastern Gdansk Deep and Gotland Basin, and (ii) advection in low salinity habitats potentially impacting interannual dynamics of *P. acuspes*.

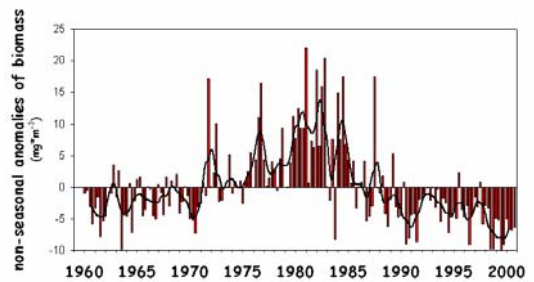


Fig. 3-1 Non-seasonal biomass anomalies of *P. acuspes* in the last four decades in the Gotland Basin in mg/m^3 ; the black line shows a three-point running mean

3.3 Material and Methods

3.3.1 General Circulation Model (GCM)

The hydrodynamic model is based on the free-surface Bryan–Cox–Semtner model (Killworth *et al.* 1991), which is a special version of the Cox numerical ocean general circulation model (Bryan 1969; Semtner 1974; Cox 1984). A detailed description of the equations and modifications made, necessary to adapt the model to the Baltic Sea, can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000a). The model domain consists of the entire Baltic Sea with a horizontal resolution of 5 km and 41 vertical levels. Simulated three-dimensional velocity fields were extracted to develop a database for a Lagrangian particle tracking exercise on larval cod. This data set offers the possibility to derive Lagrangian drift

routes by calculating the advection of “marked” water particles representing individual larvae. Vertical velocities were calculated from the divergence of the horizontal velocity fields. Three-dimensional trajectories of the simulated drifters were computed using a 4th-order Runge–Kutta scheme (Hinrichsen *et al.* 1997). The drifters were allowed to leave the layers from which they were initially released. The positions of the drifters varied over time as a result of the three-dimensional velocities that they experienced. Furthermore, the data contain information on the temporal evolution of experienced hydrographic property fields (temperature, salinity, oxygen, current velocity, etc.) along the trajectories.

3.3.2 Individual based model (IBM)

Information on biological processes such as diapause, egg production, growth and mortality were not available, thus the intention was not to realistically simulate the seasonal life-cycle of the copepod. A simple stage-structured, temperature-dependent and food independent IBM with no mortality was coupled to the physical model. The IBM traces a population of individuals as they move and develop in a three

dimensional flow field. Simulations were performed for the years 1980 to 2000. For every year, the model was initiated with an artificial resting stock ($C5_{\text{rest}}$) of 10390 individuals, emerging from diapause at every grid point of the GCM in five weekly intervals starting at the 1st of May. Release depth of the particles was 60m depths, which reflects current knowledge on the vertical distribution

(Möllmann and Köster 2002). After release, C5 developed in the model to C6 and all individuals were assigned to be females and produce eggs and die afterwards. Eggs developed at depth of their production to the first nauplii stage (N) which ascends to 30m depth (Fig. 3-2).

Individuals developed through copepodites C1 to C5. C4 and C5 descend again to 60m and after completing their stage duration enter again the resting stage C5_{rest}. When individuals drifted into waters with depths less than their assigned idealized depth, they were put to one metre above the bottom.

Model simulations were performed for every year until end of October. During each time-step of the physical model, i.e. six hours, model copepods developed in dependence of the temperature experienced along their trajectories in the GCM. Stage durations of the different life-stages were related to temperature through Behlehradek's function (Corkett and McLaren 1978):

3.4 Results

The cumulative final distribution of the C5_{rest} stage showed a large fraction of the Bornholm Basin population to be advected into the more eastern basins, while only a very small percentage of the Gdansk Deep/Gotland Basin population is able to reach the Bornholm Basin

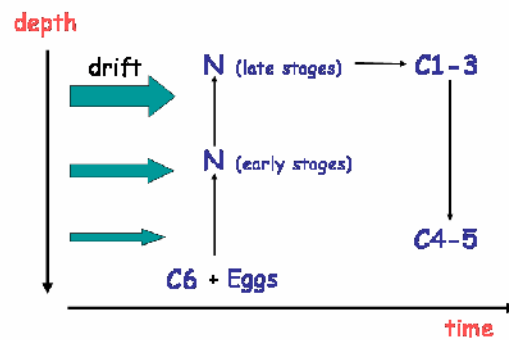


Fig. 3-2 Scheme of spatial distribution of different developmental stages of *P. acuspes* and the strength of drift influence in different depth strata

$$D_i = a_i(T-\alpha)b \quad (3-1)$$

where D_i is the mean duration of stage i in days, T is temperature ($^{\circ}\text{C}$), and b and α (-2.05 and -13.87 respectively) were taken from (Corkett and McLaren 1978). Values of a_i for each life-stage were derived from Davis (1984b).

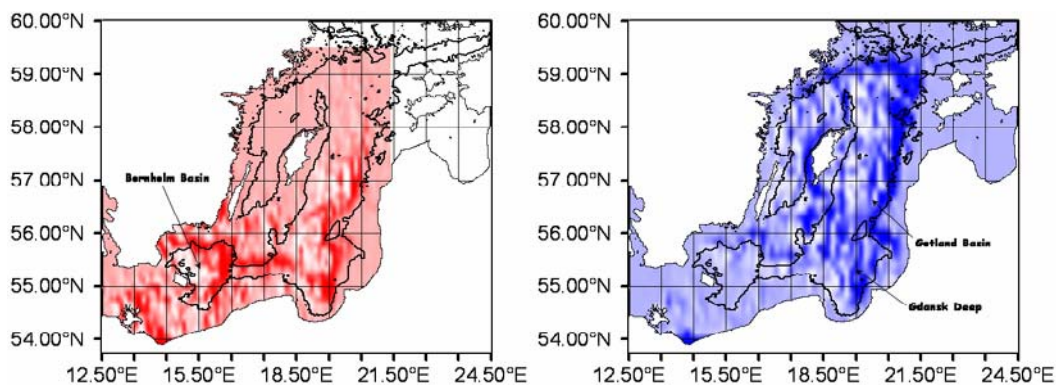


Fig. 3-3 Sum (1980-2000) of the final distributions of C5_{rest} (October 15th) originating from areas >60m in the Bornholm Basin [left] and the Gdansk Deep and Gotland Basin [right]; relative abundance

decreasing percentages in salinities greater than 7 were observed, the proportions in low salinity waters increased during the 1990's.

3.5 Discussion

The influence of drift on the population dynamics of calanoid copepods has been shown in the past (Davis 1984a, Aksnes and Blindheim 1996, Miller *et al.* 1998). This study exhibits the first attempt to couple simple individual based models for a zooplankton species to a circulation model for the Baltic Sea. Although the results are preliminary they showed clear differences of the drift pattern during the 1980's compared to the 1990's. In our case, the transport out of the Basin mainly ended in the easterly basins (Gotland Basin, Gdansk Deep) or the shallow coastal waters. This decreased the biomass in the Bornholm Basin, while increased the biomass in the other Basins, thus having an effect on the food availability for adult and larval fish in the different areas of the Baltic Sea. A similar transport between distant regions was shown by Miller *et al.* for *Calanus finmarchicus* in the Georges Bank Region. The biomass of the Georges Bank originated from production in the gulf and the Scotian Shelf. However, the transport from easterly basins back to the Bornholm Basin was very low. Therefore, the biomass in the Bornholm Basin must originate from autochthonal production or allochthonal insertion from westerly parts, probably coupled to North Sea water inflow. Dynamic exchange processes between the Baltic and the North Sea were shown from an inflow in 1972 (Radziejewska *et al.* 1973). Another drift pattern was the transport into shallow coastal areas. The consequences might be detrimental effects

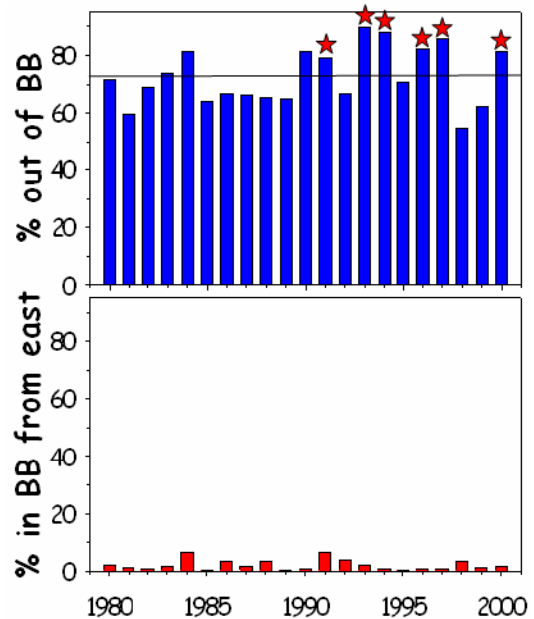


Fig. 3-4 Annual proportions of the final distributions of $C5_{rest}$ advected out of the Bornholm Basin [above], as well as reaching the Bornholm Basin from the eastern Basin [below]; line in upper panel indicates the mean, red stars indicate years during the 1990's with above average proportions

on survival and/or reproduction due to low salinity and high temperature as *P. acuspes* is supposed to be physiologically restrained to higher salinity and lower temperatures (Hansen *et al.* 2006). However Corkett and McLaren (1978) reviewed the physiological preferences for this genus, derived from field sampling, showing, that the environmental limits could be broader. Consequently, laboratory studies might help to reveal physiological limits related to mortality and reproduction, improving the interpretation.

4 Dependency of larval fish survival on retention/dispersion and spatial overlap with prey in a food limited environment: cod in the Baltic Sea

This chapter comprises two already published manuscripts following this short summary.

4.1 Manuscript Summary

The hypothesis of a critical life stage in the development of fishes by Hjort (1914) was specified by Cushing (1973), describing a match-mismatch between fish larvae and their prey as a key process driving the recruitment success. In the original context, it was a fixed spawning time assumed and the variable peak production of zooplankton led to success or failure of recruitment via larval starvation. However, through transport mechanisms of both larva and plankton this temporal overlap is biased. The drift of larva may therefore be beneficial or obstructive for growth and survival (Sinclair 1988, Heath and Gallego 1998, Hinrichsen *et al.* 2002). This was tested for cod (*Gadus morhua* L.) in the Baltic Sea in the following two manuscripts.

In the first manuscript (Hinrichsen *et al.* 2003b) we used a hydrodynamic model to analyse temporally and spatially resolved circulation patterns of the Baltic Sea with special emphasis on drifting particles representing larval cod. The main purpose of this study was i) to investigate potential drift patterns, ii) to identify its intra- and interannual variability for time periods based on the timing of spawning of cod, and (iii) to analyse its seasonal and spatial variability in dependence of the atmospheric forcing conditions. Temporally and spatially resolved simulated flow fields of larval cod for the period 1979-1998 were used to describe the potential

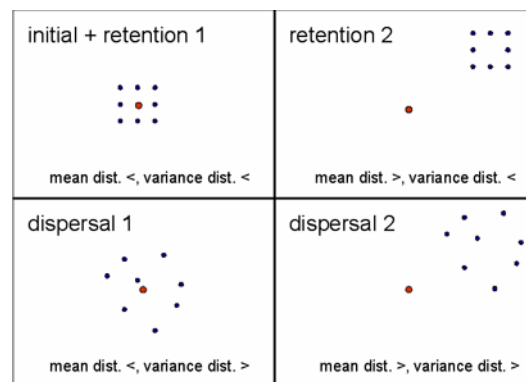


Fig. 4-1 Examples of drift patterns, large red dot indicates center of spawning area, small blue dots larval drifter

drift from the centre of main reproductive success. The results of the model runs demonstrated a general change in circulation patterns from retention during a first decade (1979-1988) to dispersion in a second decade (1989-1998) (Fig. 4-1). The advantage and accordingly the disadvantage were discussed based on idealized prey distribution of the main copepod species in the area *Pseudocalanus* sp., *Acartia* spp., *Temora longicornis* and *Centropages hamatus* (Fig. 4-2) In the second manuscript (Hinrichsen *et al.* 2005) an overlap coefficient was calculated for larval cod and their prey on the basis of drift trajectories of larval cod in the spawning time for the time period 1979 - 1998. The basis for the prey field

again were idealized seasonal development schemes for the main copepod species (Fig. 4-2). The overlap was calculated indirectly calculating first the initial distribution of larval cod and the final distribution after drift (Eq. 4-1). A value of 1 indicates an identical distribution and therefore retention in the area of spawning. Zero indicates no overlap at all. The comparison with the idealized prey field distribution revealed a spatial or temporal match or mismatch.

$$C = 2 \sum_{i=1}^n (A_i \times B_i) / \left(\sum_{i=1}^n A_i^2 + \sum_{i=1}^n B_i^2 \right) \quad (4-1)$$

The overlap has decreased since the mid-1980's. However, the 1990's showed a high variability. Seasonally the overlap was highest in summer and to the end of the spawning time in the early autumn. The results from the overlap calculations were related to the variability of Baltic cod recruitment success.

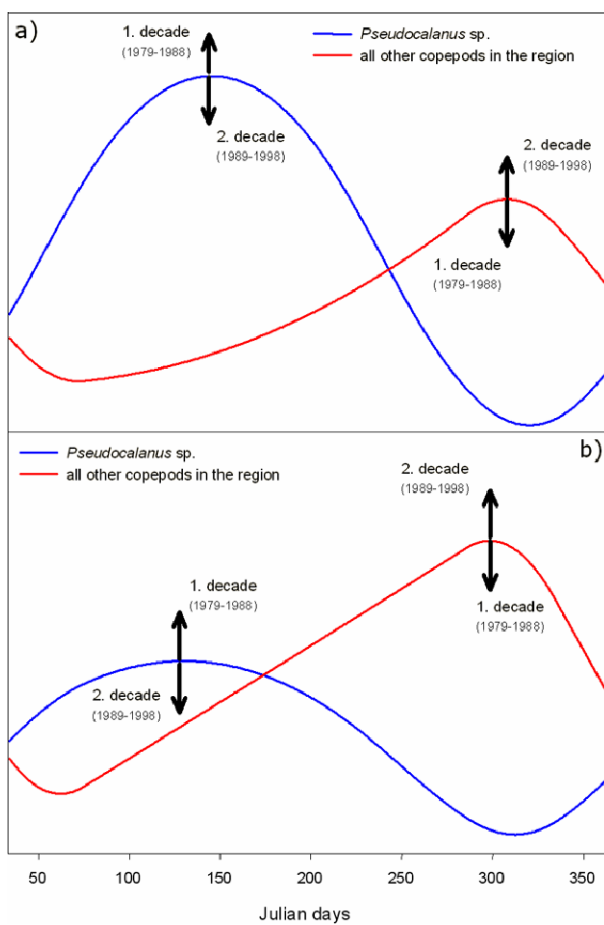


Fig. 4-2 Scheme of seasonal copepod abundances in the Central Baltic (a) deep water areas, and (b) shallow water areas. Arrows indicate abundance change between decades

Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study

Hans-Harald Hinrichsen, Andreas Lehmann, Christian Möllmann and Jörn Oliver Schmidt
This Manuscript is already published in Fisheries Oceanography 12(4-5):425-433 in 2003

Abstract

A three-dimensional hydrodynamic model has been used to analyse temporally and spatially resolved circulation patterns in the Baltic Sea with special emphasis on drifting particles representing larval fish. The main purpose of this study was (i) to investigate potential drift patterns of larval fish, (ii) to identify its intra- and inter-annual variability for time periods based on the timing of spawning and (iii) to analyse its seasonal and spatial variability in dependence of the atmospheric forcing conditions. For the time period 1979-1998 temporally and spatially resolved simulated flow fields were used to describe the potential drift from the centre of main reproductive effort of Baltic cod (*Gadus morhua*). The results of the model runs demonstrate a general change in circulation pattern from retention during a first decade (1979-1988) to dispersion in the following decade (1989-1998). This increase in dispersion was related to an increase in the variability of the local wind forcing conditions over the Baltic. The more frequent occurrence of dispersion in spring of the recent decade was accompanied by a strong decay in biomass of one of the main larval fish feeding component in the central basin, the calanoid copepod *Pseudocalanus elongatus*. Larger dispersion of this prey organism may have affected the spatial overlap and thus the contact rates between predator and prey. Hence, this may have resulted in a food limitation for early life stages of Baltic cod and potentially contributed to the pronounced shift in cod peak spawning time from spring to late summer. Early life stages of cod originating from late spawning fish, benefited from a stronger dispersion in late summer and autumn, into shallow coastal areas with higher calanoid abundance.

Introduction

Eastern Baltic cod (*Gadus morhua*) spawn in the deep basin areas of the Central Baltic Sea (Bagge *et al.* 1994). Since the mid 1980s, the Bornholm Basin is the only spawning ground for cod in the area providing successful spawning conditions. Recruitment of Baltic cod critically depends on egg mortality caused by ambient oxygen level (Köster *et al.* 2001) and egg predation by clupeids (Köster and Möllmann 2000). A few days after hatch, Baltic cod larvae

start to migrate vertically through the halocline into the low saline surface layers for feeding (Grønkjær and Wieland 1997). Historically, the peak abundance of feeding larvae is found at middepth (e.g. 1994 and 1995 between 30 and 40 m; Grønkjær *et al.* 1997). Further survival of larval and juvenile cod is affected by the spatio-temporal variability in size and composition of the mesozooplankton community (MacKenzie *et al.* 1996), identified as their dominant food

(Voss *et al.*, 2003). Thus, retention or dispersion of cod early life stages from their spawning area, the Bornholm Basin (Fig. 1), into optimal feeding environments (Sinclair, 1988; Heath and Gallego 1998) is critical to the recruitment success of this species. Owing to the ephemeral nature of the atmospheric conditions over the Baltic Sea observations show high fluctuations. The transport of cod larvae is mainly determined by the wind driven circulation of the Baltic Sea (Voss *et al.* 1999). Wind stress acting at the sea surface results in Ekman transport in cross direction to the wind in the near surface layers, with coastal jets produced in the direction of the wind along both coasts of the basin. The Ekman flow is compensated by a mainly topographically steered return flow in the central interior of the basin (Krauss and Brüggel 1991, Lehmann *et al.* 2002), which generally is opposite in direction to the prevailing winds. Results of the analysis of the vertical distribution of cod larvae suggest that larval drift mainly occurs in the depth range of this compensating return flow (Grønkjær *et al.* 1997).

Results from simulations with a coupled hydrodynamical/trophodynamical individual-based model (IBM) on survival and growth of cod larvae revealed the occurrence of non-optimal feeding conditions for first-feeding larval stages in the Baltic Sea from 1993 onwards (Hinrichsen *et al.* 2002). For this larval stage exclusively feeding on nauplii stages of calanoid copepods, pronounced differences in nutritional condition and survival were observed because of variability in ambient temperature and the encountered feeding environment. The biomass of *Pseudocalanus elongatus* was found to be especially critical for cod larvae (Hinrichsen *et al.* 2002).

Hinrichsen *et al.* (2002) constructed idealized mean spatially and seasonally resolved prey fields for cod larvae based on long-term data sets of the Latvian Fisheries Research Institute (LATFRI) in Riga, published in Möllmann *et al.*

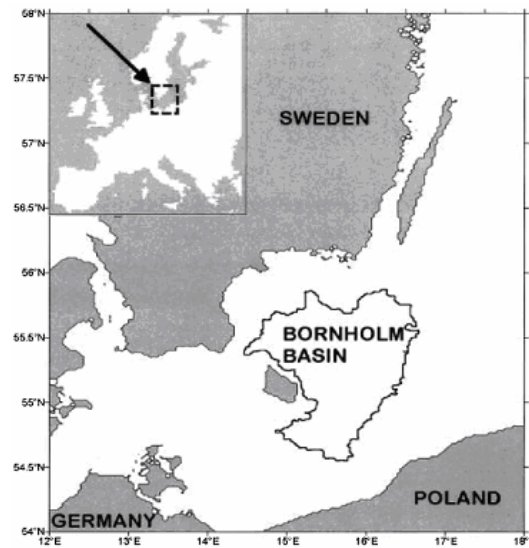


Fig. 1 Horizontal map of the Bornholm Basin, Baltic Sea

(2000). The prey fields include nauplii of the dominant calanoids in the area, i.e. *P. elongatus*, *Temora longicornis*, *Acartia* spp. and *Centropages hamatus*. Based on these prey fields, Fig. 2 displays idealized seasonal developments of the main copepod species. In deep water areas, where *P. elongatus* prevails because of the deeper vertical distribution compared with the other calanoid species (Möllmann and Köster 2002), mean nauplii abundance strongly increases in February/March with peak abundance between April and May (Fig. 2a). In late summer and autumn *P. elongatus* abundance decreases whereas the abundance of all other species peaks later in the year. Shallow areas on the margins of the Baltic deep basins show similar trends as the deep water areas with the maximum in late summer of the 'other' copepods being significantly higher than the *P. elongatus* maximum (Fig. 2b). Additionally decadal variability of meso-zooplankton dynamics in the Baltic Sea has been observed with the 1980's characterized of high biomass of *P. elongatus*, and the 1990s, dominated by the other calanoid copepods (Fig. 2; Möllmann

et al. 2000).

The paper is structured as follows: first, the circulation model, the experimental design and also a description of the characteristics of different drift patterns are given. Secondly, the parameterization of atmospheric forcing conditions over the Baltic Sea is described. In

Material and Methods

Baltic Sea circulation and transport model

In order to calculate the advection of larval Baltic cod, numerical simulations of the circulation of the Baltic Sea were performed by application of a three-dimensional, eddy-resolving baroclinic model of the Baltic Sea (Lehmann 1995, Lehmann and Hinrichsen 2000b). The model is a version of the Bryan-Cox-Semtner general circulation model with a free surface (Killworth et al. 1991). The model is based on primitive equations derived from the Navier-Stokes equations, applying the shallow water, the traditional and the hydrostatic approximation. The model is implemented with a 5-km vertical resolution. Sixty vertical levels with a resolution of 3-m intervals are used. The model comprises the entire Baltic Sea. At the western boundary, an idealized North Sea basin is attached to the model domain. This is used to take up sea-surface elevations in the area of the Skagerrak and to provide the water masses necessary for the water mass exchange, which have the typical characteristics of the North Sea. The model is forced by realistic atmospheric conditions taken from the Swedish Meteorological and Hydrological Institute (SMHI, Norrköping, Sweden) meteorological data base and by river runoff taken from a monthly mean runoff data set (Bergstrom and Carlsson, 1994). The meteorological data base covers the entire Baltic Sea drainage basin, with its parameters stored at a temporal increment of 3 hours.

Design of the numerical experiment

Simulated three-dimensional velocity fields were

the following section larval drift patterns and their relation to atmospheric forcing conditions are analyzed. Finally, these findings are discussed in the context of the long-term dynamics of the main larval cod feeding component *P. elongatus* and also recruitment of Eastern Baltic cod.

extracted in order to develop a data base for a Lagrangian particle tracking exercise on Baltic larval cod, which was utilized to calculate larval drift routes. Three-dimensional trajectories of the simulated drifters were computed using a fourth order Runge-Kutta scheme (Hinrichsen et

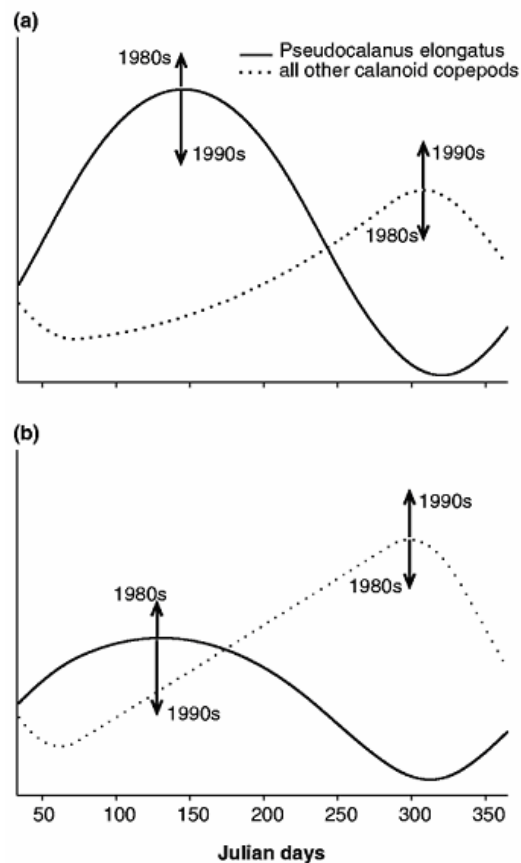


Fig. 2 Schematic of seasonal copepod abundances in the Central Baltic (a) deep water areas, and (b) shallow water areas. Arrows indicate abundance change between decades

al. 1997). The drifters were allowed to leave the layers from which they were initially released. The positions of the drifters varied over time as a result of the three-dimensional velocities that they experienced. These trajectories of passive drifting particles released into the flow fields were tracked with a fixed time step of 3 hours. Within and between year variations in drift patterns were simulated for April to September 1979-1998. Therefore, a total of 720 Lagrangian drifters have been released at depths between 25 and 35m on a regular spaced grid enclosed by the 60m isobath, encompassing the historical peak egg and larval abundance in the Bornholm Basin (Wieland 1995). Estimates of larval drift patterns can be made knowing the spatially and temporally oceanographic flow field as well as the length of time larvae spend in the plankton before they become developmentally and physiologically capable of settling. In order to temporally resolve the larval drift patterns, in the simulations, every 10 days a new batch of larval drifters was released into the modeled flow fields. These drifters were tracked for a period of 65 days, as the feeding larval stages of Baltic cod are susceptible to drift for approximately 60-70 days until reaching the demersal life stage (Possum 1986).

Identification of larval fish drift patterns

Retention and dispersion of larval fish were estimated by calculation of simple statistical parameters of larval drift patterns. First, the distances of drift trajectories from the center of main spawning activity in the Bornholm Basin were ensemble averaged for 65-day periods. Ensemble averaging over many individual trajectories enables calculation of dispersion scales in terms of variances of mean drift distances. Thus, as a second step the variability of each of the ensembles has been estimated by calculating the root mean square (rms)-values of the mean drift distances from the center of spawning activity. This method is aimed at approximating the mechanics for larval transport.

In order to demonstrate the latter, Fig. 3 shows examples of how retention and dispersion can be derived from the model output. Fig. 3a illustrates a first case of retention and also an example for the initial start of larval drifters. Here, drifters are located around a center position, which for instance can be assigned to the center of a fish spawning ground. Retention appears, if after a specific time period the larvae remained in the area where they initially started their drift, and shows low rms-values. If the larval drift endpoints also exhibit only low variability although on average are transported a larger distance apart from their initial locations, a second case of retention has been defined (Fig. 3b). The latter potentially represents the movement of eddy-like structures. Most prominent features for dispersion are shown in Fig. 3c and 3d. Both circulation patterns reveal strong variation of larval drift endpoints with a difference in their mean displacements.

Wind forcing conditions over the Baltic Sea

To describe the wind forcing conditions over the Baltic Sea, we made use of the recently developed Baltic Sea Index (BSI, Lehmann *et al.* 2002). This index represents the difference of normalised sea level pressure (SLP) anomalies between Oslo (Norway) and Szczecin (Poland). The SLPs have been obtained from the SMHI

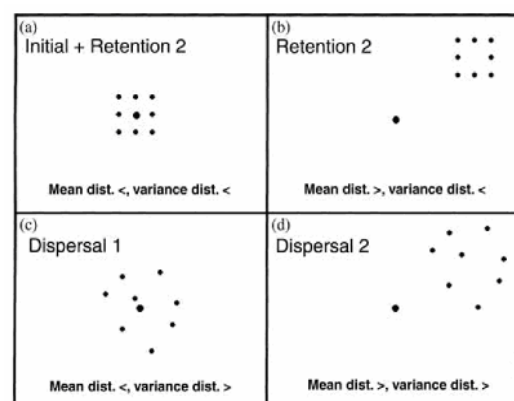


Fig. 3 Examples of drift patterns, large dot indicates center of spawning area, small dots larval drifter

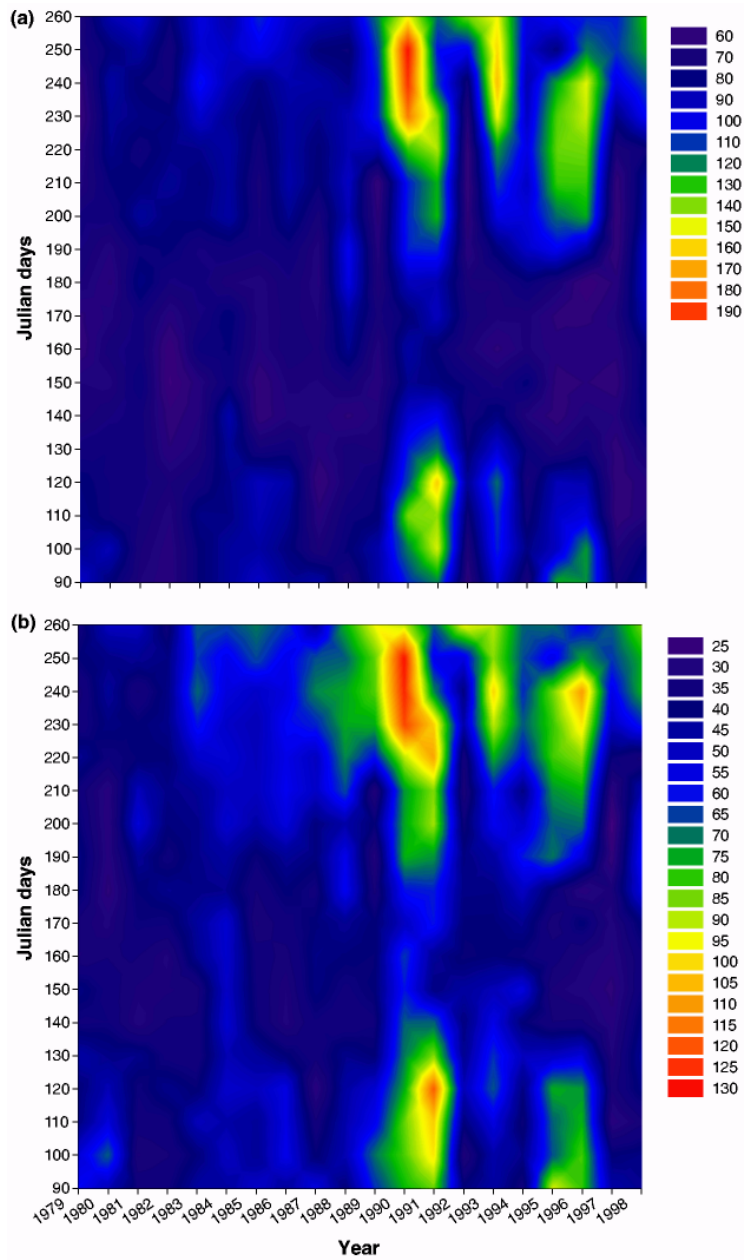


Fig. 4 Long-term 65 days (a) mean drift distances (km), and (b) corresponding standard deviations (km)

meteorological data base in which SLPs are stored every 3 h. In analogy with the definition of the NAO index, SLP anomalies at each position were normalized by dividing each SLP by the long-term mean (1979-1998) standard deviation. A positive BSI corresponds to an anomalous SLP difference, with westerly winds over the Western Baltic Sea, whereas a

negative BSI corresponds to easterly winds. To identify historic variations of retention/dispersion owing to variations in wind forcing between and within years, BSI averages for each 65-day period (representing the pelagic phase of larval cod) were calculated commencing at 10-day intervals from April to September.

Results

Figure 4a displays mean drift distances of Baltic cod larvae from the centre of spawning activity in the Bornholm Basin. The mean drift distances lie in the range of 60-190 km. Comparisons of within- and between-year variability of larval drift show large differences between 1980's and 1990's. As can be seen, highest variability of mean drift distances occur during the 1990's. Compared with the 1980's, the drift distances were larger especially late in the spawning season, i.e. larvae were typically found more than 100 km from their source. Generally, the simulations for the 1990's indicated a high probability of larval transport towards coastal regions early and late in the spawning season (Hinrichsen *et al.* 2003), whereas the corresponding simulations for the 1980's as well as for the summer periods of the 1990's yield that much higher numbers of larvae were retained in the deep water areas. A similar pattern was observed for the variability of the mean drift distances represented as rms-values (Fig. 4b). The large differences in spatial scale of variabilities occurred at the end of the 1980's. This indicates that during the 1980's dispersal scales were almost homogeneous and relatively low, while larval drifters initially released in the 1990's ended up widely dispersed over the whole Bornholm Basin. Typical scales for the 1980's are 25-65 km, whereas for the 1990's more than 120 km were found.

In correspondence with the results of the 65-day drift periods of larval cod, mean wind forcing conditions were calculated for the same duration and with respect to the release dates of the simulated drifters. Figure 5a represents the mean seasonal development of the wind forcing conditions for the last two decades expressed by means of the BSI. The time periods, which were chosen for the simulations, differ significantly in their overall atmospheric conditions. During spring of the first decade (1979-1988), winds of mainly eastern directions were registered, while later in the spawning

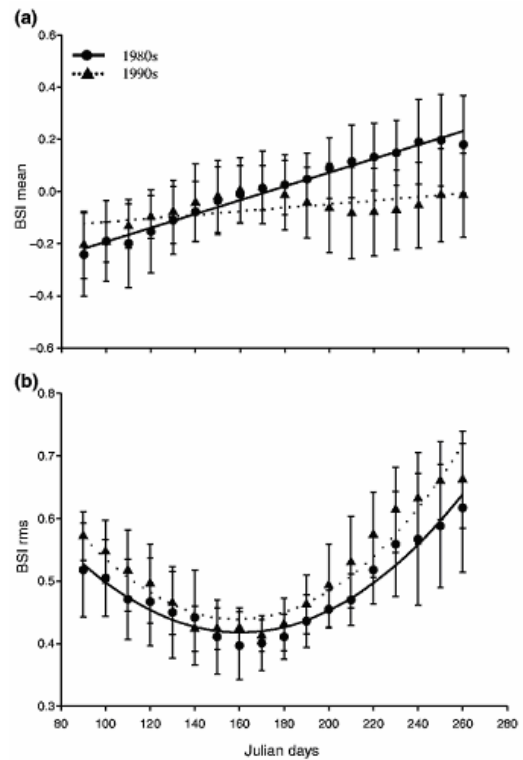


Fig. 5 Long-term (decadal) averages of (a) seasonal mean wind conditions expressed by the Baltic Sea Index (dimensionless), and (b) corresponding standard deviations

season winds changed gradually from eastern to western direction. Seasonal mean BSI values for the spawning season strongly differed in the following decade (1989-1998). Although highly variable, this decade showed on average low wind forcing conditions throughout the spawning season. The variability (rms-values) of the seasonal mean BSI values exhibits a strong seasonal signature (Fig. 5b). Early and late in the spawning season the variance of the wind forcing conditions was relatively high, whereas in summer the variance was low, indicating winds to be more persistent in time. However, this analysis also reveals rms-values of the BSI to be significantly higher during the 1990's compared with the decade before.

To obtain a general impression of meteorological impacts on larval transport, we related the statistical parameters of larval drift

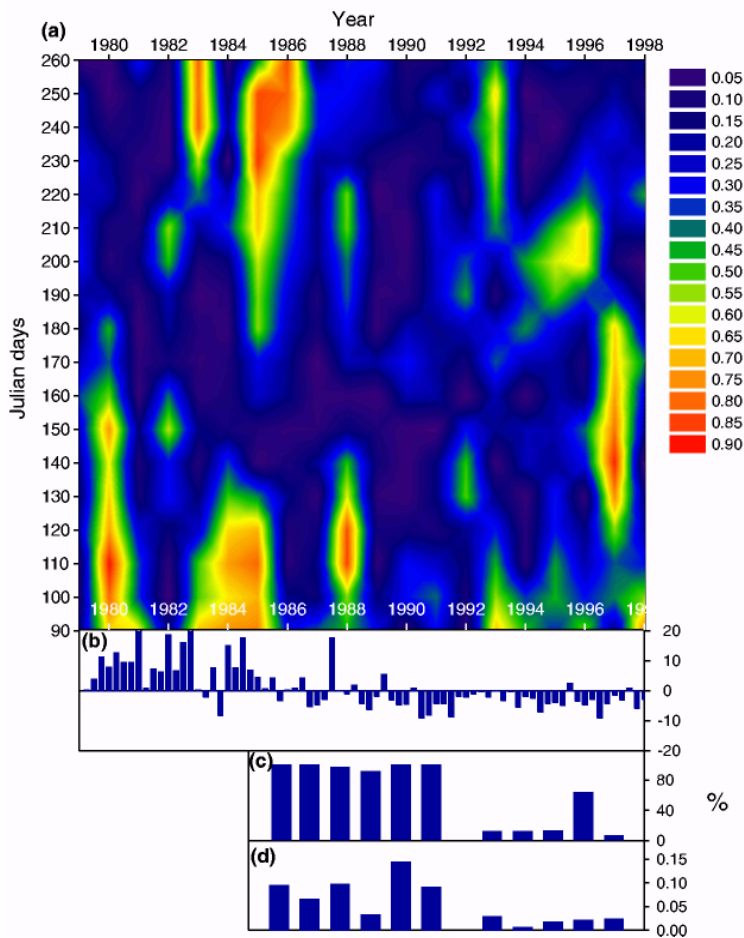


Fig. 6 Combination of long-term 65 days averages of (a) atmospheric forcing condition as the ratio of Baltic Sea Index (BSI) mean (dimensionless) and BSI root mean square, (b) long-term bio-mass anomaly of *Pseudocalanus elongatus*, (c) Baltic cod larval survival rates (%), and (d) Baltic cod recruitment per egg production stage III (x1000, dimensionless)

patterns to atmospheric conditions. Linear correlation analysis between the mean BSI values and the averaged mean drift distances revealed only weak correlation ($r = 0.26$). However, it was found that the rms-values of the BSI accounts for 94% of the variance of the mean drift distances. Thus, the variability of the atmospheric conditions expressed by rms-values of ensemble averaged BSI values, has a strong impact on the dispersal scales of larval drift patterns, e.g. high dispersal rates during the 1990's corresponded to high variability of atmospheric conditions.

Figure 6 provides a combination of data on physical forcing conditions with the temporal development of observed zooplankton abundances and recruitment data on Baltic cod. Physical forcing is represented by the ratio of mean and rms-values of the BSI (Fig. 6a). As

obtained from this study, low values of this ratio can be related to dispersion and high values to retention. Highest values occurred until the middle of the 1980's. During the same time period the biomass of *P. elongatus* (Fig. 6b) showed positive non-seasonal anomalies in the Central Baltic Sea, followed by a decline until the end of the 1990's (Möllmann *et al.* 2000). High abundances in *P. elongatus* were accompanied by a period of retention, while negative anomalies of this copepod species could be related to dispersion.

A spatially-explicit coupled biophysical model was utilized to analyse the influence of abiotic and biotic environmental variability on the larval and juvenile survival success of Baltic cod. The model combines a three-dimensional eddy-resolving hydrodynamic model of the Baltic Sea (Lehmann 1995, Lehmann and Hinrichsen

2000a) with a trophodynamic IBM for larval cod. The results of the model runs indicate that the strong decay in abundance of the calanoid copepod *P. elongatus* had a strong impact on cod larval survival. The model predicts relatively high levels of larval survival from 1986 to 1991 as well as the strong decay in survival for late spawners from 1993 onwards (Fig. 6c; Hinrichsen *et al.* 2002). Consequently, in the latter time period variability in the abundance of *P. elongatus* has had most likely only a limited impact on larval survival, depending to a

Discussion

In order to understand better the effects of physical forcing on the distribution of early life stages of cod, physical modelling activities have been focussed on the description of the circulation of the Baltic Sea and its influence on the seasonal and inter-annual distribution and transport of larvae originating in the Bornholm Basin (the centre of the stock's spawning activity). Our simulation represents an examination of the optimal timing of spawning with respect to the probability of getting into optimal feeding environments at the right time. Several generalizable results emerge from the Lagrangian approach utilized in this study. First, regime shifts of the Baltic Sea ecosystem can be detected by simple time integrated measures of the physical environment. Secondly, characteristics of larval drift can be developed from knowledge of the mean and fluctuating components of the winds over the Baltic Sea. Finally, larval drift distances range from only 40 to 200 km. Although these distances are in general low, the resulting final destination areas of larvae might have an impact on their feeding success. The retention and dispersion from the main spawning ground may be one of the key processes influencing recruitment success of the Eastern Baltic cod stock (Hinrichsen *et al.* 2002). When *P. elongatus* was available in the prey, high survival occurred in spring and early summer if larvae were retained in the deep

higher extent on the availability of juvenile stages of other copepods (Hinrichsen *et al.* 2002). Comparing the ratio of observed recruitment and egg production at stage III of Baltic cod (Fig. 6d; Hinrichsen *et al.* 2002) with the simulated larval potential revealed a similar trend. Although, e.g. late cod egg or early larval stages were highly abundant in the field, from 1993 onwards the recruitment remained on a relatively low level.

basins. In contrast, when *P. elongatus* was not available, cod larvae only could benefit from dispersion later in the spawning season, i.e. only those larvae had high survival probabilities which were transported into shallower regions with relatively high food abundance of calanoid copepods other than *P. elongatus*.

Correlation analyses with the combined biomass of all life-stages showed *P. elongatus* to be positively dependent on salinity in all seasons. First, this dependence on salinity is reflected in the positive development of *P. elongatus* in the 1970's and the early 1980's as a possible result of increased salinities because of the 1971 and 1975/76 major inflows of saline water from the North Sea (Möllmann *et al.* 2000). Since the early 1980s salinity decreased as a result of lacking inflow events (Matthäus and Schinke 1994) in combination with high precipitation and river runoff (Bergstrom and Carlsson 1994). The positive correlations with biomass indicate the need of *P. elongatus* for a relatively high salinity level for processes such as maturation, reproduction and growth to occur (Möllmann *et al.* 2003a). A further explanation yields transport of juvenile *P. elongatus* stages to potentially contribute to the decline in biomass. The calanoid shows a ontogenic vertical distribution with adult females reproducing in the permanent halocline and nauplii as well as early copepodites

dwelling in upper water layers were they are transported with the surface drift (Möllmann and Köster 2002). Similar to fish larvae, during the 1980's most of the juvenile stages of this copepod species were retained in the central part of the basins. This might have had positive effects on the population dynamics of *P. elongatus*, as most life stages of this species finally remained in their reproduction area under optimal haline conditions for production and development. The second decade exhibits dispersion of nauplii and copepodites more frequently. As a consequence, during dispersive periods the juvenile copepod stages of *P. elongatus* have higher probabilities to be more widely distributed and thus might end up within the low salinity regimes of shallower coastal regions, detrimental for reproduction. Larger dispersion of this prey organism may have affected the spatial overlap and thus the contact rates between prey and predator. Hence, this may together with the general decline in biomass have resulted in a food limitation for early life stages of Baltic cod and potentially contributed to the pronounced shift in their peak spawning time from spring to late

summer. Recruitment during the last decade mainly depended on the production of late-hatched larvae as the main spawning season has successively changed from late spring to summer months (Wieland *et al.* 2000). The shift in peak spawning time of Baltic cod obviously accounts for the decline in *P. elongatus*. Larvae are now born later in the season, thus profiting from the increasing abundances of juveniles of the remaining copepod species accumulating at this time of the year. It is not clear yet if spawning in general is delayed or if late spawners are the only surviving part of the eastern Baltic cod stock (Hinrichsen *et al.* 2002).

From the numerical simulations, it appears that utilization of simple statistical parameters allows the identification of changes in transport regimes of larval fish within their spawning seasons. Examining the different transport regimes with respect to spawning or hatch date may help to identify the favourable physical conditions leading to enhanced survival. These could then be useful indicators for prognosis of growth and developmental success of commercially important fish species.

Acknowledgements

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Survival probability of Baltic larval cod in relation to spatial overlap patterns with their prey obtained from drift model studies

Hans-Harald Hinrichsen, Jörn O. Schmidt, Christoph Petereit, and Christian Möllmann

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Abstract

Temporal mismatch between the occurrence of larvae and their prey potentially affects the spatial overlap and thus the contact rates between predator and prey. This might have important consequences for growth and survival. We performed a case study investigating the influence of circulation patterns on the overlap of Baltic cod larvae with their prey. A three-dimensional hydrodynamic model was used to analyse spatio-temporally resolved drift patterns of larval Baltic cod. A coefficient of overlap between modeled larval and idealized prey distributions indicated the probability of predator-prey overlap, dependent on the hatching time of cod larvae. By performing model runs for the years 1979-1998 investigated the intra- and interannual variability of potential spatial overlap between predator and prey. Assuming uniform prey distributions, we generally found the overlap to have decreased since the mid-1980's, but with the highest variability during the 1990's. Seasonally, predator-prey overlap on the Baltic cod spawning grounds was highest in summer and lowest at the end of the cod spawning season. Horizontally variable prey distributions generally resulted in decreased overlap coefficients. Finally, we related variations in overlap patterns to the variability of Baltic cod recruitment success.

Introduction

Recruitment success of marine fish stocks can to a large degree be related to the feeding success of their early life stages, i.e. larvae and juveniles (Mullin 1993). The survival of fish larvae and juveniles depends on their ability to encounter, capture, and ingest a sufficient quantity of appropriate prey in order to avoid starvation and assure growth. According to the "match-mismatch" hypothesis, variability in recruitment depends on the temporal match/mismatch of the annual reproductive cycle of fish and the prey of their larvae (Cushing 1973). Differences in the match between larvae and their prey may thus generate variability in larval

feeding success, including both interannual (Cushing 1996) and spatial variability. Thus, the transport of eggs and larvae into sub-optimal feeding environments may influence recruitment success (e.g. Sinclair 1988, Heath and Gallego 1998, Hinrichsen *et al.* 2002).

The deepwater area off the island of Bornholm (Baltic Sea) is the major spawning ground of Baltic cod (Figure 1). Larval cod prey mainly on nauplii of the dominant calanoid copepods in the area, i.e. *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia* spp., and *Centropages hamatus* (Voss *et al.* 2003). Based on long-term data sets (Möllmann *et al.* 2000), idealized

spatio-temporal distributions of the seasonal abundance of nauplii of the main copepod species have been constructed (Figure 2). In deepwater areas, where *P. elongatus* is most abundant owing to its deeper vertical distribution compared with the other calanoid species (Möllmann and Köster 2002), mean nauplii abundance strongly increases during late winter, with peak abundance between April and May (Figure 2a). In late summer and autumn, *P. elongatus* abundance decreases whereas the abundance of all other species peaks later in the year. Shallow areas at the margins of the deep basin show a similar temporal trend to the deepwater areas, with the maximum of the "other" copepods in late summer being significantly higher than the *P. elongatus* maximum (Figure 2b).

The described spatio-temporal variability in occurrence of food for larval cod indicates the possibility of a spatial mismatch between the appearance of larval predators and their planktonic prey, depending on the hatching time of larvae. It can be assumed that the degree of this spatial mismatch strongly depends on the intra- and interannual variability in circulation patterns. In the present study we use data on the location and timing of spawning of Baltic cod as input into a particle-

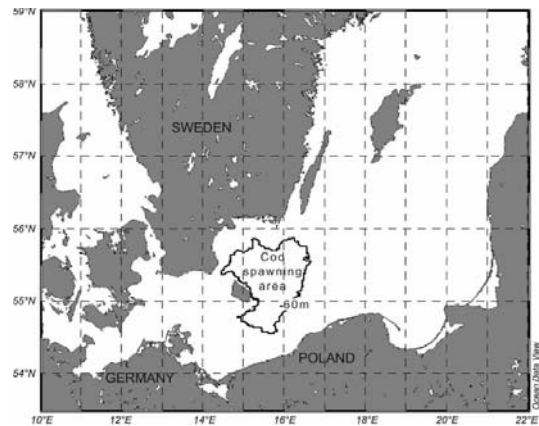


Fig. 1 Map of the Bornholm Basin (Baltic Sea) and statistical rectangles. Thick line represents the spawning area of Baltic cod (60-m isobath)

tracking model (Hinrichsen *et al.* 1997). Utilizing currents from a three-dimensional circulation model of the Baltic Sea (Lehmann 1995), cod larvae were tracked through space and time. Modelled distributions of larvae were then compared with assumed distributions of prey, reflecting the spatio-temporal variability in occurrence of copepod species. The utilization of an overlap coefficient (Horn 1966) provided an integrative view, indicating the probability of the simultaneous spatial occurrence of cod larvae and their prey.

Material and Methods

Hydrodynamic model and particle tracking

The hydrodynamic model is based on the free surface Bryan-Cox-Semtner model (Killworth *et al.* 1991), which is a special version of the Cox numerical ocean general circulation model (Bryan 1969, Semtner 1974, Cox 1984). A detailed description of the equations and the modifications made to adapt the model to the Baltic Sea can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000a). A detailed analysis of the Baltic Sea circulation has been performed by Lehmann and Hinrichsen (2000b) and by Lehmann *et al.* (2002). Physical

properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann 1995, Hinrichsen *et al.* 1997, Lehmann and Hinrichsen 2000a).

The model domain comprises the entire Baltic Sea including the gulfs of Bothnia, Finland and Riga, as well as the Belt Sea, Kattegat, and Skagerrak. The horizontal resolution is 5 km, with 60 vertical levels specified. The thickness of the different levels is chosen to best account for the different sill depths in the Baltic. The

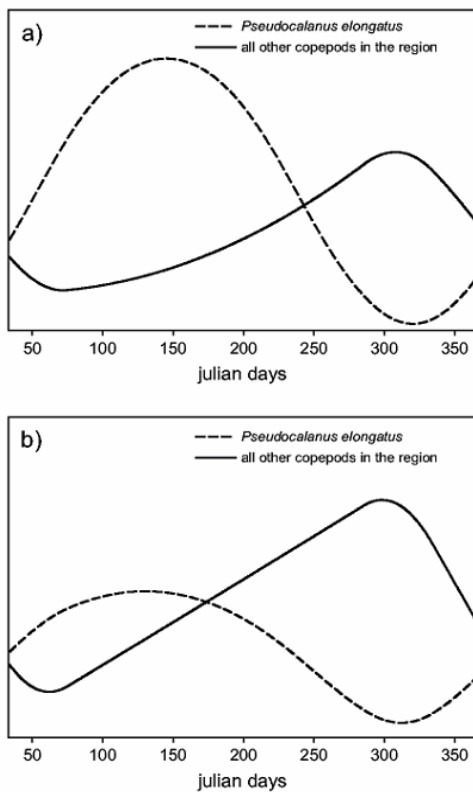


Fig. 2 Schematic of seasonal copepod abundances in the Central Baltic (a) deepwater areas, and (b) shallow-water areas

Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and river run-off taken from a mean runoff database (Bergstrom and Carlsson 1994). The meteorological database covers the whole Baltic Sea drainage basin with a grid of $1^\circ \times 1^\circ$ squares. Meteorological parameters such as geostrophic wind, 2m air temperature, 2-m relative humidity, surface pressure, cloudiness, and precipitation are stored with a temporal increment of 3 h. Simulated three-dimensional velocity fields were extracted (at a 6-h interval) in order to develop a database for a Lagrangian particle-tracking exercise for larval cod. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of "marked" water particles. Vertical velocities were calculated from the divergence

of the horizontal velocity fields. The drifters were allowed to leave the layers where they were launched. The positions of the drifters varied over time as a result of the three-dimensional velocities that they experienced.

In order to establish a Lagrangian view of the simulated circulation, drifters can be placed in the modeled flow fields at every location within the model domain. Moreover, the initial launch positions can be chosen independently from the vertical resolution of the model's grid. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were computed using a fourth order Runge-Kutta scheme (Hinrichsen *et al.* 1997).

First, the hydrodynamic model on Baltic cod larval drift was utilized for the time period 1979-1998 in order to obtain means of intra-annual variability in distribution and transport patterns. In order to consider seasonal variability in relation to spatial and temporal variations in larval transports, 720 Lagrangian drifters were released at depths between 25 and 35 m (depths at which feeding larvae occur after vertical feeding migration) on a regularly spaced grid enclosed by the 60m isobath, representing the main spawning area of the Bornholm Basin (Fig. 1). The main spawning area of Baltic cod is also known as one of the main reproductive areas of the calanoid copepod *P. elongatus* (Möllmann *et al.* 2000). Drifters, at their release representing first-feeding larvae, were inserted into the modelled flow fields at 10-day intervals, and were tracked for certain time periods. The release dates commenced on 1 April and ended on 20 September, thereby encompassing the historic as well as the present peak spawning period of eastern Baltic cod (Wieland *et al.* 2000).

Overlap calculation

Our main goal was to estimate the overlap between successively released batches of larval cod and their prey (Fig. 2). To determine how

many larvae and prey were simultaneously present in the specified subareas of the central Baltic Sea (Fig. 1), a coefficient of overlap (C) was calculated (Horn 1966), which is 0 when there is no overlap, and 1 when two distributions are identical:

$$C = 2 \sum_{i=1}^n (A_i \times B_i) / \left(\sum_{i=1}^n A_i^2 + \sum_{i=1}^n B_i^2 \right)$$

where n is the number of statistical rectangles (Fig. 1) covering the main spawning area as well as the whole Bornholm Basin. The latter is the area of most likely larval and juvenile appearance (Hinrichsen *et al.* 2003a). The statistical rectangles have an approximate size of 15 nautical miles in both latitudinal and longitudinal direction. For our analysis, A and B are the proportions of larvae found in each rectangle at hatch (A) and after a given time period of larval drift (B), respectively. High values of this coefficient indicate retention of larvae in the region of initial larval release (water depth > 60m). Low values indicate dispersal and hence transport of larvae out of the area where they originally hatched. In order to generate temporal mismatches between larval predators and prey, the delayed time periods for which final larval drift locations were calculated have also been assumed to be the dates of peak prey occurrence. Hence, owing to the intra- and interannual variability of drift patterns, considerable spatial mismatches between larvae and their potential prey might have occurred. According to the mean seasonal evolution of prey fields (Fig. 2), during spring and early summer retention in the deep area can be related to optimum encounter rates between predator and its predominant prey (*P. elongatus*), whereas low values might indicate low survival success and growth of larvae. On the other hand, a low spatial overlap coefficient obtained for the late spawning period (late summer and autumn) might lead to higher prey encounter only in shallower coastal regions outside the main spawning area. There, at the same time of year, the abundances of "other"

copepods are significantly higher than those of *P. elongatus* (Fig. 2b).

In order to obtain measures for maximum accepted temporal mismatches between larval fish and zooplankton species/stages as their potential prey, we performed laboratory rearing experiments on starvation mortality of Baltic cod first-feeding larvae (Petereit 2004). Parts of these experiments were conducted to determine the time until death of starved cod larvae. The results revealed a significantly high dependence of the maximum duration of survival on temperature. At a temperature of about 2°C larvae survived for about 39 days (Fig. 3), while larvae under warmer temperature conditions survived for a shorter time (e.g. 13 days at 10°C). The experiments showed a significant impact of temperature on the maximum survival duration of non-fed larvae; however, larval fish usually die before reaching this age at the so-called "point of no return". This "point of no return" is defined as the larval age after which a restart of feeding and subsequent recovery is impossible. For North Sea cod, the "point of no return" has been identified to be 11 days at 7°C and 10 days at 9°C (Yin and Blaxter 1987). Ellertsen *et al.* (1980) found in their experiments a "point of no return" of 11 days at 5°C. In order to account for the average prevailing temperature conditions within the larval Baltic cod habitat,

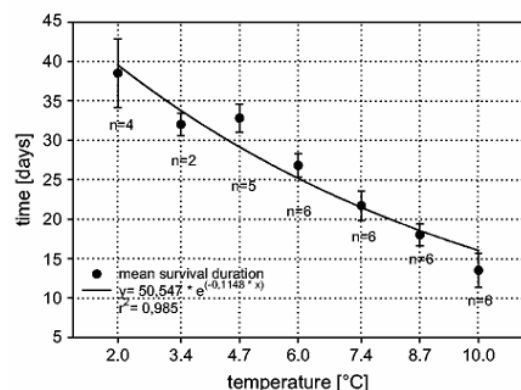


Fig. 3 Temperature-dependent average maximum survival duration of non-fed Baltic cod larval

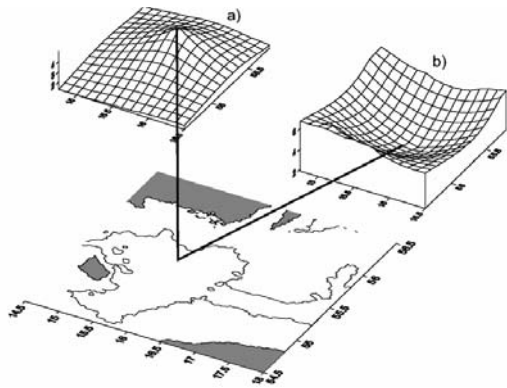


Fig. 4 Horizontal distribution patterns used for the calculation of the coefficients of overlap of (a) maximum abundance in the centre area, and (b) at the margins of the main spawning ground of Baltic cod

Results

Generally, results of the overlap probability between larval cod predators and their prey focused on the analysis of the within- and between-year variations of larval drift. To obtain a general impression of the magnitude of the coefficient of overlap, examples of two contrasting years are displayed in Figure 5. The temporal evolution of the spatial overlap patterns between prey and predator caused by a temporal delay in peak prey abundance is

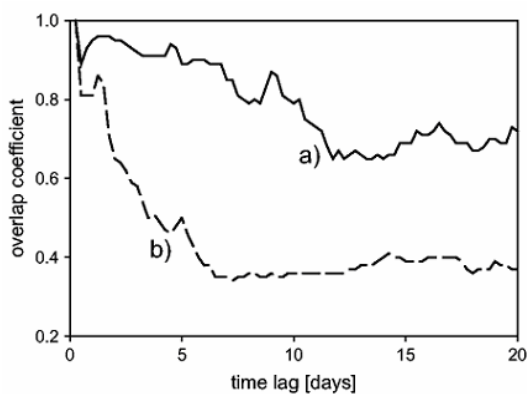


Fig. 5 Temporal evolution of the coefficients of spatial overlap (a) May 1981 and (b) May 1995

for our numerical model simulations we decided to chose temporal mismatches between the occurrence of larvae and their prey not to exceed 15 days, which is in good accord with the observed "points of no return" of non-fed or less optimal fed larvae.

In order to analyse how geographically variable larval cod distributions impact the spatial overlap between larvae and their prey, we performed three case studies with different horizontal distributions of larvae; i.e. (i) basin-wide (water depth > 60m) mean abundance, as well as peak abundance (ii) within the basin centre area, and (iii) at the margins (approximately in the area of 60-80m water depth) of the spawning area of cod (Fig. 4).

considered here. At the beginning of the spawning period in 1981, the probability of a high overlap between a predator cohort released as larval drifters at Julian day 111 and its larval drift endpoints obtained for specific drift periods remained high for a time period of about 15 days. This indicates good retention of larvae in the spawning ground area (water depth > 60m). During the spawning season of Baltic cod, retention leads to a high overlap between predator and prey, which at this time of the year is most likely concentrated in the deep basin area (Fig. 2a). The opposite was observed for the early spawning period in 1995, when the spatial overlap was significantly lower than in 1981. The coefficient rapidly decreased to values below 0.4 within less than one week, which can be related to strong dispersal and high transport of larvae out of the spawning ground caused by strong wind forcing. Analyses of the intra- and interannual variability of the spatial overlap coefficient between initial larval release locations and the final larval drift endpoints, showed large differences if a drift period of 10 days was considered (Fig. 6).

The coefficient of overlap ranged from 0.29 to 0.87 with the highest variability observed during the 1990's. The lowest value was obtained for autumn 1993, whereas the highest spatial overlap was in late spring 1995. Compared with the early 1980's, spatial overlap was lower from the mid-1980's, especially early and late in the spawning season. Only for the late 1980's and early 1990's, throughout the seasons, anomalously high coefficients of overlap were found. Generally, the overlap coefficient remained at a relatively high level during summer months. The latter is confirmed by seasonally averaged overlap coefficients obtained for the 20-year simulation period, (Fig. 7). If a delay of peak prey abundance of 10 days compared with the occurrence of larval cod has been considered, an uniform horizontal distribution of larvae resulted in higher spatial overlap in summer than in spring and autumn. However, on average the overlap during the late spawning period was lowest. Assuming horizontal variability in prey abundance with maximum occurrence either in the centre or at the margins of the basin yielded generally a strong decrease in spatial overlap. However, during the early spawning period, larval growth, survival, and subsequent recruitment benefits from retention. Hence, the best survival rates of larvae could be expected where a uniform horizontal larval distribution dominates. Because high larval prey concentrations usually occur in shallow-water areas only late in the spawning season (third quarter), optimal late spawner survivorship might result during periods of dispersal if larvae originally hatched at the margins of the spawning area.

Recruitment as obtained from Multispecies Virtual Population Analyses (MSVPA) runs and the overlap coefficients calculated for the early and late spawning period showed generally declining trends towards the end of the 1990's ($r = 0.55$, $p < 0.015$), with extraordinarily high values from 1979 to 1983 (Fig. 8). An overestimation of recruitment at age 0 was

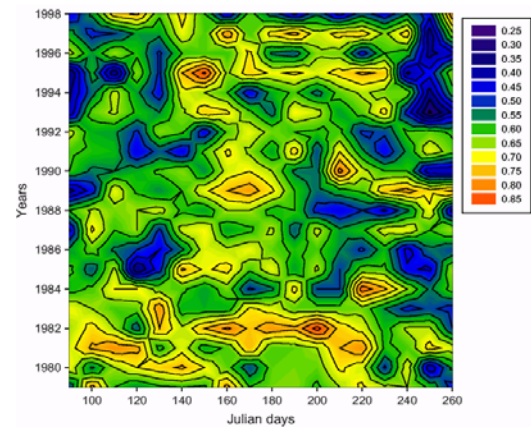


Fig. 6 Coefficients of overlap between larval cod and their potential prey (time-lag 10 days)

potentially encountered for 1979 (Köster *et al.* 2001). Although the potential egg production was lower than in preceding years and the reproductive volume (habitat of successful egg development) of Baltic cod was well below average conditions (MacKenzie *et al.* 2000), recruitment at age 0 as determined by MSVPA was highest. 0-group abundance indices from trawl surveys in 1980 were above average but not extraordinarily high (ICES Baltic trawl survey database). Excluding the 1979 data from the model fitting increased the explained variance

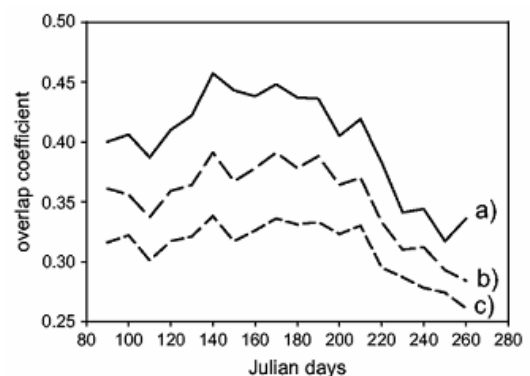


Fig. 7 Seasonally averaged coefficients of overlap between larval cod and their prey (time-lag 10 days) (a) uniform even distribution, (b) maximum distribution in the centre, and (c) at the margins of the cod spawning area

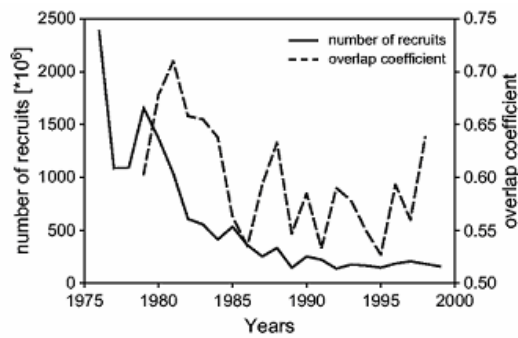


Fig. 8 Baltic cod recruitment obtained from Multispecies Virtual Population Analysis (solid line) and averaged overlap coefficients after 10 days of larval drift during the early spawning season (dashed line)

Discussion

Hinrichsen *et al.* (2002) utilized a spatially explicit coupled biophysical model to analyse the influence of abiotic and biotic environmental variability on the larval and juvenile survival success of Baltic cod. It turned out that variations of the feeding conditions (temporal and spatial variations of suitable prey availability) had a strong impact on survival of first-feeding larval stages. Their study suggests that food limitation for first-feeding larvae during the last two decades was caused by a pronounced decline of the copepod *P. elongatus*, the main food of larval cod. In the absence of this copepod, larvae hatched only at the outer edges of the Bornholm Basin at the end of the spawning period had good survival probability, because of their short drift distances towards the optimal feeding environments in more shallow coastal areas. In contrast, larvae hatched within the deep part of the Bornholm Basin required more prey to survive along their drift routes than was available.

In this study, information on temporally and spatially resolved larval drift patterns can be applied in determining larval prey encounter, by

to 52% ($p < 0.001$). Accompanied by changes in the timing of spawning of Baltic cod (Wieland *et al.* 2000), the slight recovery of recruitment at the end of the 1990s might be due to a high spatial overlap between peak abundance of larvae and prey late in the spawning season in shallower and coastal areas of the basin.

coupling transport regimes to temporal and spatial differences of the feeding environment. The model results suggest, for Baltic cod spawning seasons during the last 20 years, strong variability in the potential co-occurrence of peak prey and larval abundance, which allowed us to re-address the question of food limitation in larval Baltic cod. Thus, this spatial predator-prey overlap might be considered to be a key process and a candidate parameter for reducing uncertainty in the prediction of recruitment. From numerical simulations it appeared that variation in larval transport and hence in horizontal distribution are mainly controlled by the local atmospheric conditions over the Baltic Sea (Hinrichsen *et al.* 2001, 2003a). We investigated the influence of retention/dispersal of Baltic larval cod in the Bornholm Basin on overlap with their prey, dependent on the time of hatching. High overlap values could be related to periods in which larvae are retained on the spawning ground, so suggesting beneficial feeding conditions with a positive effect on growth, survival, and subsequent recruitment for spring

and early summer spawners. Those time periods are characterized by weak wind forcing conditions and occur mainly in summer. On the other hand, relatively strong wind forcing results in limited spatial overlap and was highest late in the cod spawning season. Thus, larvae hatched within the spawning area are transported to shallower coastal areas and potentially could only contribute to recruitment if they are in contact with good food abundance late in the spawning season.

The coefficients of overlap have been calculated with respect to some simplifications. Detailed information on spatial and temporal variability in availability of larval cod and prey in combination with variation in ambient physical conditions was lacking. Although transport patterns of water layers where post-yolk-sac larvae mainly occur (Grønkjær and Wieland 1997) are relatively well known (Krauss and Brugge 1991, Voss *et al.* 1999, Hinrichsen *et al.* 2003a), validation of the modelling results is

difficult. Transport patterns of larvae are influenced by the initial spawning location, assumed here to be an even horizontal distribution, their initial vertical position in the water column, and their behaviour. These processes and factors were not incorporated in our study. Furthermore, resolving the importance of co-occurrence of larvae and the peak abundance of their prey requires the analysis of growth characteristics of larvae and juveniles over the range of potential prey abundance available to them during the season. Grønkjær *et al.* (1997) clearly identified the importance of prey abundance for the successful growth of larval cod. As obtained from a comparative analysis of simulated coefficients of spatial overlap and observed recruitment, temporal and the corresponding spatial mismatches between predator and prey potentially have an impact on the reproductive success of Baltic cod.

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5 Modelling the impact of differences in the abundance and diversity of copepod nauplii on the early survival of larval fish: Baltic cod (*Gadus morhua* L.) as a theoretical case study

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5.1 Abstract

Existing coupled biophysical models for Baltic larval cod drift, growth and survival use idealised constructed mean prey fields of nauplii distributions. These simulations revealed best feeding conditions for Baltic cod larvae larger than 6 mm. For smaller, first feeding larvae (> 4.5 mm) pronounced differences in growth and survival were observed, which depend on food availability and to a lesser degree on ambient temperature. We performed runs with an Individual Based Model (IBM) for Baltic cod larvae in order to demonstrate how natural variability in prey abundance influences survival success of first feeding larvae. In the Baltic this larval stage dwells mainly between 20 and 40 m depth and feed exclusively on nauplii of different calanoid copepods (*Acartia* spp., *Pseudocalanus acuspes*, *Temora longicornis* and *Centropages hamatus*). Prey data obtained from vertically stratified samples in the Bornholm Basin (Baltic Sea) in 2001 and 2002 revealed strong variabilities on spatial and temporal scales. We calculated larval survival and growth in relation to natural variation of prey fields, i.e. species-specific nauplii abundance. The results of the model runs revealed larval survival rates from 60 to 100 % if a mean size of nauplii species was taken and lower survival if prey consisted of early nauplii stages only.

5.2 Introduction

During fish development Hjort (1914) hypothesized that a critical period affects the recruitment. This period is often stated as the first-feeding stage of fish larvae when larvae shift from endogenous to exogenous feeding (Hewitt *et al.* 1985, Houde 1989). Opinions

diverge whether the susceptibility is due to high starvation or high predation (Leggett and Deblois 1994). However, as Bailey and Houde (1989) stated, the answer to the question whether starvation or predation is the major cause of mortality could depend on the species,

the area, the year and which developmental stage is mostly affected. For Baltic cod predation from sprat and herring substantially affect the egg stage while predation on the larvae is negligible due to missing spatial overlap with the predators (Köster and Schnack 1994).

The reason for starvation of early life stages of fish was hypothesized from different authors covering different temporal and spatial scales (Cushing 1990). The main reason is a temporal (seasonal Cushing 1974) or a spatial (dispersion or retention, Parrish *et al.* 1981) mismatch between larvae and their prey. Laboratory experiments seemed to show the importance of patchiness of prey organisms for larval fish to find food (Gamble *et al.* 1981). An increasingly used tool to study fish larval growth and survival are individual based models (Letcher *et al.* 1996, Hinckley *et al.* 1996, Hinrichsen *et al.* 2002, Lough *et al.* 2005). They can be imbedded within realistically simulated flow fields to explore the roles of growth, starvation, mortality and of advective losses. Coupled hydrodynamic/trophodynamic modelling studies on growth and survival of Baltic larval cod highlighted the dependence of feeding and survival success on the availability of calanoid copepod nauplii (Hinrichsen *et al.* 2002). Hinrichsen *et al.* (2002) using idealized constructed mean prey fields with a relatively coarse horizontal resolution, suggested the necessity of the co-occurrence of peak prey and larval abundance and

favourable oceanographic conditions for high larval survival rates. All simulations revealed optimal feeding conditions for larger larvae, but for small first feeding larvae, exclusively preying on copepod nauplii (Voss *et al.* 2003), pronounced differences in growth and survival were obtained that depend on food availability as well as on ambient temperature. However even though Hinrichsen *et al.* (2002) and others (Werner *et al.* 1996, Lough *et al.* 2005) are aware of the patchiness of larval prey, prey fields are averaged over large scales. In this paper we investigated firstly the influence of prey field variability on cod larval survival in the Bornholm Basin (Baltic Sea) with field data obtained from a small spatial and temporal sampling in 2001 and from a basin wide, monthly sampling, i.e. mesoscale, in 2002. Secondly, we investigated the influence of ambient temperature on the amount of food necessary for a larva to survive. Finally, we compared model outputs obtained from literature-based sizes of nauplii with a measured size distribution from samples obtained in June 2001 in the Baltic Sea.

5.3 Material and Methods

5.3.1 Zooplankton sampling

Copepod nauplii were sampled on cruises in June 2001 and in April, May and July 2002. In June 2001, six profiles were taken at one station covering day and night in a 48 h period (Fig. 5-1). In 2002, sampling was performed at nine stations (Fig. 5-1) deploying the net only once at each station. In parallel to the

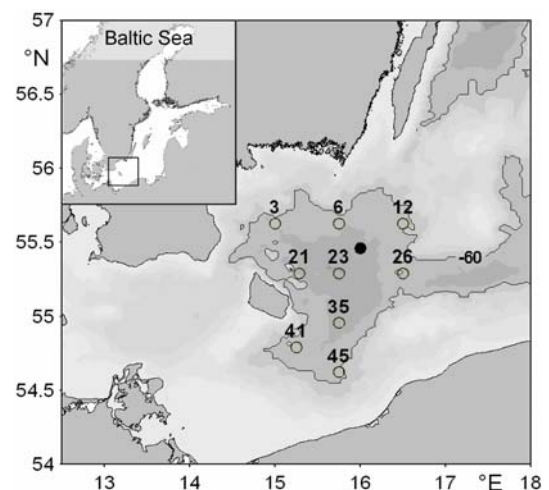


Fig. 5-1 Investigation area Bornholm Basin in the Baltic Sea (overview in the upper left corner); Black dot shows sampled station in June 2001; open dots show the sampled stations in April, May and July 2002

zooplankton sampling, hydrographic parameters (temperature and salinity) were recorded at each station using an ADM-CTD (Analoge und Digitale Meßsysteme GmbH).

Zooplankton samples were collected with a 0.25 m² multi opening/closing net system (Multinet, Hydro-Bios Kiel). The Multinet was equipped with five nets of 50 µm mesh size. The gear was applied vertically with a down-and upward speed of 0.2 m/s, resolving the water column in 10 m intervals from the bottom up to the surface. Nauplii were preserved in 4% borax buffered formalin seawater solution and sorted in the laboratory under a binocular microscope. All nauplii were identified to species except *Acartia* spp. nauplii.

The abundance was calculated as number per cubic meter for each species. The biomass was calculated as dry weight using the length for each nauplii-stage taken from Ogilvie (1953) as a basis for the growth term in the model (Culver *et al.* 1985). In June 2001 the length of *Pseudocalanus acuspes* nauplii was additionally measured irrespective of the stage to obtain real size distributions. The measurements were done using the ImageJ software (2003) with a precision of ± 5µm. For our model calculations, only the nauplii abundances of the depth-strata 20-30 m and 30-40 m were taken, because these are the depth layers where first feeding cod larvae mainly dwell.

5.3.2 Model description and design of simulations

The individual based model (IBM) used in this study was developed by Hinrichsen *et al.* (2002) using a generalized model described by Letcher *et al.* (1996) (Fig. 5-2). This IBM tracks individual cod larvae through all larval phases including first feeding (4.5 - 6 mm). In the IBM, encounter of prey, foraging, growth, survival and nutritional condition in terms of weight at length of larvae is simulated by specific submodels in 6-h time steps.

The basis of this IBM is the standard bioenergetic supply-demand function (Beyer and Laurence 1980, Carloti and Hirche 1997), where growth is represented as difference between the amount of food ingested by a larva and the metabolic costs of its daily activities. Due to missing data for Baltic cod, length-weight relationships from Otterlei *et al.* (1999) were applied to compute the expected weight under superabundant prey concentrations. Deviations of the simulated weight from the bioenergetic model and a maximum weight at length were used to run a starvation model. Larvae were defined to die from starvation if the final weight at a specific length was falling below specific threshold

values, i.e. 75% of the maximum weight-at-length of larvae (Letcher *et al.* 1996).

Larval prey conditions were taken from *in situ* zooplankton measurements as described above. Each sample was assumed to be a “potential prey field” individual larva experienced throughout their first feeding phase. That was for June 2001 six profiles times 2 depth bins resulted in 12 “potential prey fields” and for 2002 nine profiles each month

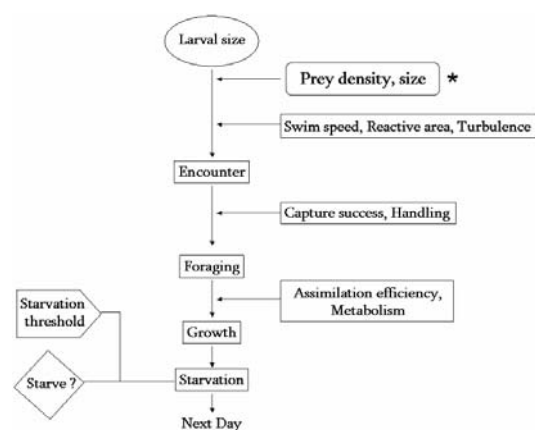


Fig. 5-2 A scheme of the IBM used in this study; investigated parameter marked by an asterisk. Modified after Letcher *et al.* 1996

Tab. 5-1 Length and weight of the different stages of the different species, respectively sibling species where data of the original species was not available (*Pseudocalanus minutus*, *Centropages typicus*, *Acartia clausi*) taken from Ogilvie (1953) and the length-weight relationship given by Culver *et al.* (1985) for naupli dry weight = $a \cdot \text{length}^b$ (with $a = 3.009$ and $b = 1.706$)

species	N1		N2		N3		N4		N5		N6		mean	
	length	weight	length	weight	length	weight	length	weight	length	weight	length	weight	length	weight
<i>P. minutus</i>	0.176	0.155	0.187	0.172	0.26	0.302	0.33	0.454	0.38	0.577	0.44	0.742	0.295	0.400
<i>C. typicus</i>	0.106	0.065	0.15	0.118	0.18	0.161	0.19	0.177	0.22	0.227	0.29	0.364	0.189	0.185
<i>T. longicornis</i>	0.112	0.072	0.16	0.132	0.21	0.210	0.26	0.302	0.32	0.431	0.38	0.577	0.240	0.287
<i>A. clausi</i>	0.12	0.081	0.14	0.105	0.16	0.132	0.19	0.177	0.23	0.245	0.28	0.343	0.187	0.181

times 2 depth strata resulted in 18 “potential prey fields”.

For calculations of larval survival, experiencing prey fields taken in June 2001 the IBM was coupled to a circulation model as described in Hinrichsen *et al.* (2002). This was done to obtain an estimate of small scale temperature variability for this examination period because accompanied temperature measurements and thus a measure for temperature variability was lacking. In the simulation, a cohort of larvae was released and tracked for a period of 15 days. This time span approximately covers the first feeding period of larvae at June temperatures (Hinrichsen *et al.* 2002). 550 larval drifters were released at depths where first feeding larvae mainly dwell (26, 28, 30, 32, and 34 m) on a regular spaced grid with a horizontal resolution of 500 m. At start of the model run (6th of June), all larvae were initially defined to have equal length and weight (4.5 mm). Along the drift trajectories within the coupled model, the larvae experienced specific temperature conditions. For all examination periods in 2002 only a one-dimensional version of the IBM was performed, not considering larval drift. The temperature variability obtained from basin wide measurements from each

sampling period within the depth range of 20-40 m was split in 0.1°C steps for the model. For each “prey field” and each temperature category a model run was performed. We assumed that the nauplii abundances and sizes, with respect to their temporal development, remained uniform for the whole duration of the simulation periods, which were between 12 and 14 days depending exclusively on ambient temperature conditions. Sizes of the different copepod stages for each species were obtained from literature (Ogilvie 1953). Where data for a species was not available we used data for a sibling species.

Another set of model runs was performed using the abundances of *Pseudocalanus* sp. in 2001 samples with the real size distribution obtained from measurements and with an average literature size for *Pseudocalanus* sp. A threshold for nauplii abundance was calculated needed for a 6 mm larva to survive and to gain maximum weight-at-age.

Survival curves for the dependence of prey size and abundance on the temperature were calculated with the IBM for average temperatures of quarter 2 and quarter 3 obtained from a time series from 1966-2002.

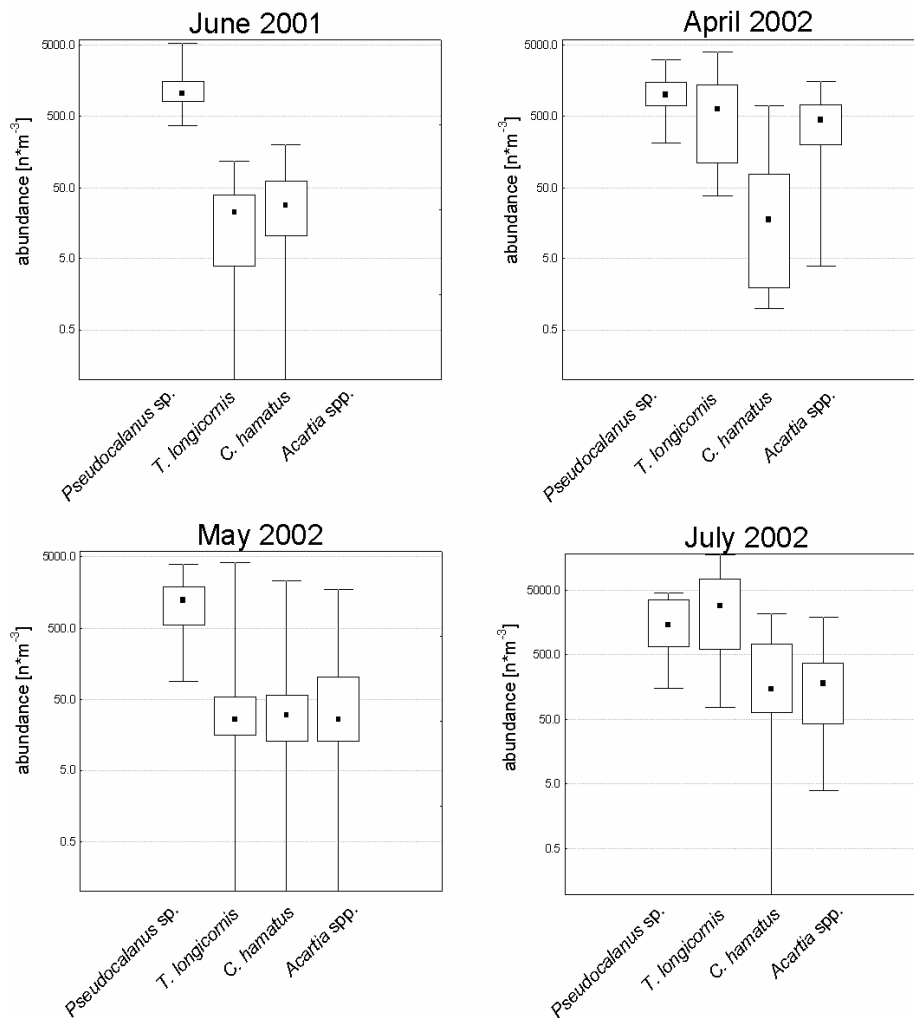


Fig. 5-3 abundances of the four copepod species estimated from multinet samples on a logarithmic scale; ■ - median, box - 25 and 75 percentiles, ⊥ - minimum, T - maximum; note different scaling

5.4 Results

5.4.1 Prey fields

In June 2001 nauplii of *P. acuspes* were predominant within the 20-40m depth stratum. Differences in abundance between samples were more than tenfold from 369 to 5358 individuals per cubic metre (Fig. 5-3). Peak abundance of the other species were only 120 individuals for *T. longicornis*, 200 for *C. hamatus* and 80 for *Acartia spp.*

In 2002 *P. acuspes* was the dominant species in

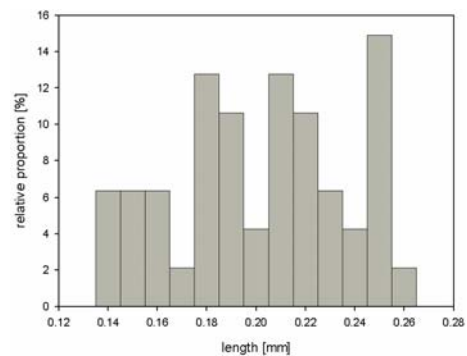


Fig. 5-4 Size distribution of *Pseudocalanus sp.* nauplii in samples from June 2001 (n = 47); Length were measured with an accuracy of ± 5 μm

April and May. The abundance was almost constant in April, May and July. *T. longicornis* was dominant as well in April, nearly absent in May but the predominant species in July. *Acartia* spp. was found in high numbers only in April. *C. hamatus* was the lowest abundant

species in all sampling periods. The size distribution of 47 measured *P. acuspes* nauplii in June 2001 is shown in Fig. 5-4. The length varied between 0.14 mm and 0.26 mm.

5.4.2 Results of the model runs

An average nauplii size obtained from literature allowed survival of the cod larva in 60% to 80% of the prey fields with the lowest value in May 2002 and the highest in July 2002 (Fig. 5-5). Increasing size of the nauplii, expressed as an older stage, resulted in an increase in survival probability for cod larva in all cases. Highest survival for the larva having the three smallest stages (n1 - n3) as prey was found in July 2002 with 22%, 48% and 83% respectively whereas lowest values were found for June 2001 with 0%, 3% and 25%. Highest values with older stages (n4 - n6) as prey were found in April 2002 with 89%, 94% and 100% respectively. The lowest values for nauplii stage 4 and 6 were found in May 2002 with 78% and 94%. The lowest value for nauplii stage 5 was found in June 2001 with 89%. The size distribution pattern was assumed to be equal for all prey fields in June 2001 and served as input parameter for separate model runs with only *P. acuspes* as prey. Another set of model runs was performed with the literature average size of *P. acuspes* nauplii. For both sets of models, a threshold was calculated for survival and for maximum weight at 6 mm length of the cod larvae. In (Fig. 5-7) the minimum amount of *P. acuspes* nauplii necessary for survival and for reaching the maximum weight at 6 mm length are shown for this model run and for comparison the amount using a mean size for prey. The figure shows that for mean sized prey nine potential prey fields were higher than the survival threshold. Four of the 12 prey fields allowed the larvae to reach maximum weight at

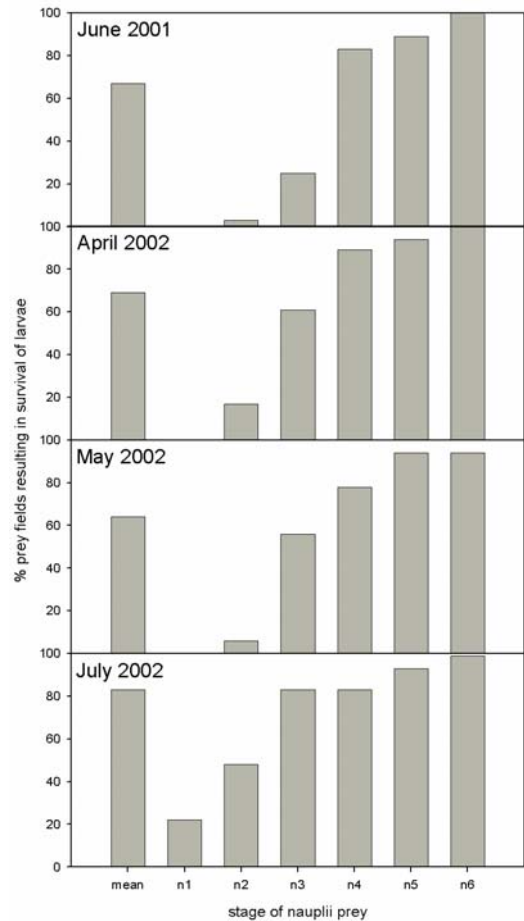


Fig. 5-5 Percentage of prey fields leading to survival of larvae calculated by the model for the four sampled periods; "mean" represents the results using the average size of nauplii stage 1 to 5 of each species derived from literature data

6 mm length. In case the real size distribution was used, only five prey fields led to a survival and three prey fields were sufficient that larvae were able to reach the maximum weight.

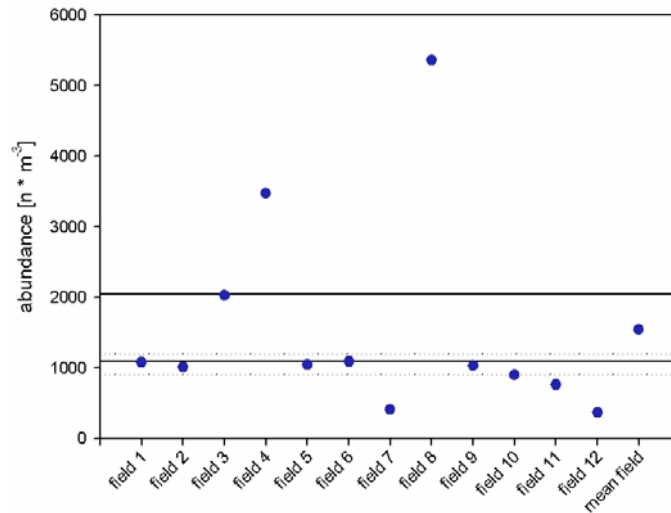


Fig. 5-7 Abundance of *P. acuspis* nauplii in samples from June 2001; each point represents one sample (six stations, samples in 20m-30m and 30m-40m plus an average of all 12 samples). Dotted lines mark the survival threshold (lower line) and the threshold for maximum weight at 6 mm length (upper line) using the average literature size of nauplii, the solid lines mark the same using the real size distribution (shown in Fig. 5-4) for each prey field (lower line indicates the survival threshold, the upper line the maximum weight at 6 mm length)

The calculated mean prey field led in both cases (mean size and real size) to survival, but maximum weight was only reached if mean size derived from literature was assumed. Survival curves, taking into account the seasonal mean temperature of quarter 2 and 3 obtained from long-term measurements (1966-2002), showed only slight differences in the number of prey items that guarantee survival of cod larvae. The number of prey needed increased dramatically with decreasing prey size (Fig. 5-6). The decrease in needed abundance for larger larvae

is mainly due to an increase in reactive distance increasing the contact rate.

5.5 Discussion

Model results from a recent study (Hinrichsen *et al.* 2002) revealed the importance of combined advective and trophodynamic processes on growth and survival of Baltic larval cod populations. Generally, this kind of modelling approach has to cope with sparse temporal and spatial resolutions of zooplankton prey fields (Hermann *et al.* 1996, Werner *et al.* 1996). However, sensitivity studies like this demonstrate that the model is sensitive enough

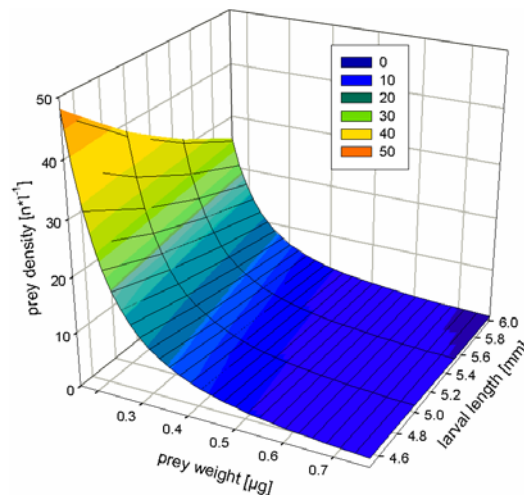


Fig. 5-6 Number of nauplii with a given weight needed for a cod larva of a certain length to survive at a given temperature of 5°C (survival = a minimum weight for a given length of 75% of the maximum weight for that length)

to show the impact of natural perturbations of the number of encountered and ingested prey on growth and survival. The consideration of the development of zooplankton species and stages on different temporally and spatially resolved scales is highly announced, because spatial and temporal variability of zooplankton is not merely noise but an essential feature of food web dynamics (Carlotti 2001), linking larval fish trophodynamics to different patch sizes and dynamic distributions of prey is thus essential. This study does not directly address patchiness of larval prey but attempts to analyse larval survival success in relation to a natural variability in larval prey fields derived from a point sampling in 2001 and a basin wide sampling in 2002. The point sampling in the central Bornholm Basin in June 2001 illustrates that the differences in prey concentration and finally in larval growth and survival could be high on a small temporal and spatial scale, in fact nearly as high as the basin wide variability during a comparable period (Fig. 5-4).

For most of the analysed observation periods, idealized constructed mean prey abundance values (Hinrichsen *et al.* 2002) led to high growth rates, optimum nutritional conditions, and, consequently, high estimated rates of larval survival. Systematic overestimation of survival and nutritional condition can potentially be prevented by taking into account natural variability of the prey fields obtained from spatially resolved zooplankton abundance measurements as well as by considering observed compositions of prey. The model results also stress the necessity to use *in situ* measurements of nauplii sizes instead of literature values. Although this study did not address the real stage specific length of nauplii, especially for the Baltic as a brackish water system, size spectra from the North Sea or the

Atlantic Ocean could lead to overestimation of larval survival and nutritional condition. Neglecting realistic information on stage composition, size and abundance of prey modifies the results of the bioenergetic supply-demand function used to describe Baltic cod larvae growth. It could strongly alter the amount of food ingested by a larva and, hence may lead to inaccurate daily larval growth rates and subsequently might lead to erroneous calculation of larval survival. The field-observed variability in temperature generally has a strong impact on larval growth conditions as well as on survival of larval cod and thus may have contributed to the observed year to year differences in Baltic cod recruitment. In general, the higher temperature in the third quarter of the year, compared to the second quarter, requires higher prey abundance, but the differences are small if the prey consists mainly of late nauplii stages, but could be essential if prey is smaller.

A topic not investigated in this study was how behavioural changes, e.g. swimming speed of larvae, predator avoidance of prey (Titelman and Kiørboe 2003), influence the encounter of larvae and their prey. It has been reported by Munk and Kiørboe (1985) that herring larvae alter their swimming speed after encountering a prey patch, thus increasing the probability of remaining within a patch. Furthermore, although an analysis of small scale variability on feeding success and survival has been performed, dynamics of patches have not been considered, e.g. turbulence or behavioral adaptations of zooplankton to predation in terms of vertical migration. Studies of predator and prey patch dynamics are envisaged in future, whereby models with a high spatial resolution may increase our knowledge of these processes in nature.

II General Conclusions

The prerequisite for a sustainable use of living marine resources is the understanding of the complexity of ecosystems. The detailed knowledge on species, their spatio-temporal distribution and the interactions between them, comprising predator-prey interactions or resource competition are the basis for the valuation of impacts caused by influences like fisheries or on environmental factors. Fisheries has a direct influence on mortality of adult fish that can be regulated. Environmental impact on the development of fishes is manifold and difficult to regulate. Consequently understanding the processes regulating the survival from egg to recruitment, is important to predict stock size development and to derive e.g. sustainable catch levels. In many cases, especially the larval stage has been shown to be of critical importance for recruitment success. This study aims to add knowledge on several aspects of zooplankton distribution and its influence on larval fish survival in the Baltic Sea.

The distribution of key copepod species, investigated in chapter one is not only important to understand their population dynamics, but it also forms the basis to generate prey fields for larval and adult fish. The general food selection of adult sprat and herring in the Baltic Sea has been investigated in the past (Möllmann *et al.* 2004 and references herein, Casini *et al.* 2004 and references herein), however, ignoring detailed daily/seasonal vertical distribution patterns. Data gained in this study have recently been used for this purpose (Bernreuther *et al.* in prep.).

The only copepod in this study that showed a diel vertical migration was *Temora longicornis*. In the summer month it migrated from 10 metre depth at night to 50 metre at day. This behaviour could not be related to predator avoidance as the main predator, sprat, showed a similar migration behaviour staying near the halocline at day and moving to the surface during night. *Pseudocalanus acuspes* showed an ontogenetic migration with the youngest stages dwelling near the surface and the older stages inhabiting deeper water layers. The reason for an ontogenetic migration could be different physiological needs of the different stages. The youngest stages need high temperatures for fast development and the Phytoplankton as food. The older stages need high salinity and feed on detritus and ciliates near the halocline. All species showed seasonal differences in their vertical distribution. The driving force is the temperature development in the upper water layers leading to a seasonal thermocline that structured the water column.

However, the patterns observed in this study showed, that sometimes only slight migrations were performed by the copepods. *Acartia longiremis* showed differences in its vertical distribution between day and night in July between 5 and 15 metre. Those differences could hardly been resolved with the gear in use.

P. acuspes has been shown to serve as important food for sprat, herring (Möllmann and Köster 2002, Möllmann *et al.* 2004) and larval cod (Voss *et al.* 2003). However the population size of *P. acuspes* declined during the last decades influencing growth and condition of Baltic clupeid fish (Möllmann *et al.* 2003a, 2005, Rönkkonen *et al.* 2004) and potentially affecting cod recruitment (Hinrichsen *et al.* 2002). The decline of *P. acuspes* was supposed to be coupled with the salinity (Möllmann *et al.* 2003b). However, the processes driving the short-term biomass fluctuations

remained unclear. The investigation of two hydrographically contrasting years confirmed the dependence of reproducing female *P. acuspes* on high ambient salinity values. Added knowledge on oxygen thresholds allowed the definition of a volume of reproduction habitat (RVH). Images derived with the Video Plankton Recorder (VPR) were used to calculate an *in situ* egg production. Surprisingly the results showed no significant difference in egg production between the years, although the calculation of nauplii to female ratio showed values twice as high in 2003 than in 2002. This led to the hypothesis of increased nauplii mortality during stagnation years. The method further has the potential to be used in studies on egg production besides conventional experiments.

Coupling the biology to the physics has frequently been done by using circulation models to investigate the drift of copepods and larval fish.

First drift studies on plankton species in the Baltic Sea revealed potentially important processes relevant for the copepod population dynamics. Results for the drift of *P. acuspes* showed a switch in the transport between the 1980's and 1990's. Whereas in the first investigated decade the circulation was characterized by retention in the Bornholm Basin, whereas the second decade was marked by transport out of the Basin, mostly in easterly direction. In conclusion, the biomass development in the Gdansk Deep and the Gotland Basin might have been affected by production in the Bornholm Basin. Additionally, the transport to shallow near shore waters with low salinity and high temperatures might have detrimental effects on survival and reproduction, although the physiological constraints remain unclear.

Moreover the switch of the drift pattern between 1980's and 1990's induced to marked changes in overlap of larval fish and their prey and thus decreased survival of larval fish. This switch was related to a climate change indicated by the NAO that had an influence on the barotropic circulation in the Baltic Sea (Matthäus and Schinke 1994).

The variability in the abundance and diversity of nauplii of the key copepod species as obtained from this study has been used to improve an individual based model for larval cod (Hinrichsen *et al.* 2002). Hinrichsen *et al.* (2002) have shown that the two most influencing parts of the model were the prey abundance and size and the metabolism of the larval cod. However, the prey abundance and the size used for the model were averages, ignoring natural variability. A strong dependence of survival of first feeding larval cod on natural variability of nauplii size and abundance is shown in the present study. The assumption of average prey fields overestimated the survival dramatically.

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Description of the individual scientific contribution to the multiple-author paper

The chapters of this thesis are partly already published (chapter four) or written as manuscripts with multiple authorship. This list serves as a clarification of my personal contributions on each publication.

Chapter 1: Vertical distribution and diel vertical migration of main mesozooplankton species in the Bornholm Basin (Baltic Sea)

All statistical analyses, zooplankton analysis for 2001, the text writing and graphical presentation were done by Jörn Schmidt. Project participants from STORE and GLOBEC Germany were instrumental during field sampling. Colleagues provided helpful comments to improve earlier versions of the manuscript. The zooplankton samples from 2002 were analysed by a sorting centre in Poland.

Chapter 2: Small scale distribution of reproducing female *P. acuspes*.

All analyses, the text writing and graphical presentation were done by Jörn Schmidt under supervision of Dr. Christian Möllmann, Prof. Dr. Axel Temming and Prof. Dr. Mike St. John. Other authors were instrumental during field sampling and provided helpful comments to improve earlier versions of the manuscript.

Chapter 3: Simulating the interaction of *P. acuspes* with the physical environment in the Central Baltic Sea

Analysis, and graphical presentation were done by Dr. Christian Möllmann, Jörn Schmidt and Hans-Harald Hinrichsen. Text writing and allocation of biological background information were done by Jörn Schmidt.

Chapter 4: Dependency of larval fish survival on retention/dispersion and spatial overlap with prey in a food limited environment: cod in the Baltic Sea

This chapter comprises two manuscripts. All analysis and text writing were done by Hans-Harald Hinrichsen in close cooperation with Jörn Schmidt. Graphical presentation was done by Jörn Schmidt.

Chapter 6: Modelling the impact of differences in the abundance and diversity of copepod nauplii on the early survival of larval fish: Baltic cod (*Gadus morhua*) as a theoretical case study

All analyses, the text writing and graphical presentation were done by Jörn Schmidt in close cooperation with Hans-Harald Hinrichsen.

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Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation selbständig von mir angefertigt wurde. Die Dissertation ist nach Form und Inhalt meine eigene Arbeit und es wurden keine anderen als die angegebenen Hilfsmittel verwendet. Diese Arbeit wurde weder ganz noch zum Teil einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Fischereibiologie erfolgen. Des Weiteren erkläre ich, dass ich Zuhörer bei der Disputation zulasse.

Kiel, den 22.03.2006

Jörn Schmidt