

**Alfred-Wegener-Institut für Polar und Meeresforschung  
Bremerhaven**

**Life cycle and population dynamics  
of the calanoid copepod *Pseudocalanus* spp.  
in the Baltic Sea and North Sea**

**DISSERTATION**

zur

Erlangung des akademischen Grades  
des Doktors der Naturwissenschaften  
(Dr. rer. nat.)

am Fachbereich 2 (Biologie/Chemie) der  
Universität Bremen

vorgelegt von

**Jasmin Renz**

Bremen, Juni 2006

- 1. Gutachter: Prof. Dr. Wilhelm Hagen, Universität Bremen**
- 2. Gutachter: Prof. Dr. Sigrid Schiel, Alfred-Wegener-Institut Bremerhaven**

## CONTENTS

SUMMARY	III
ZUSAMMENFASSUNG	V
<b>1 INTRODUCTION</b>	<b>1</b>
1.1 Distribution patterns of calanoid copepods	1
1.2 Life cycles of calanoid copepods in different geographical regions	2
1.3 Population dynamics of calanoid copepods	2
1.4 The genus <i>Pseudocalanus</i>	3
<i>Pseudocalanus acuspes</i> and <i>Pseudocalanus elongatus</i>	5
<b>2 THESIS OUTLINE</b>	<b>8</b>
<b>3 MATERIAL AND METHODS</b>	<b>10</b>
3.1 Study sites	10
3.1.1 Baltic Sea	10
3.1.2 North Sea	10
3.2 Sampling	11
3.3 Weighted mean depth (WMD)	13
3.4 Length measurement	13
3.5 Egg production	14
3.6 Moulting and growth rate	14
3.7 Secondary production and productivity	14
3.8 Statistics	14
<b>4 DISCUSSION</b>	<b>16</b>
4.1 The distribution of <i>Pseudocalanus</i> species in the Baltic and North Sea	16
4.1.1 Vertical distribution	18
4.2 Life cycle	19

<b>4.3 Population dynamics</b>	21
4.3.1 Reproduction	21
4.3.2 Development and growth	22
4.3.3 Secondary production	23
4.3.4 Mortality	23
<b>4.4 Climate variability and <i>Pseudocalanus</i> spp.</b>	25
<b>5 CONCLUSIONS</b>	28
<b>6 PUBLICATIONS</b>	29
<b>PUBLICATION I</b>	31
Renz J and Hirche H-J (2006) Life cycle of <i>Pseudocalanus acuspes</i> Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Mar Biol 148: 567-580, DOI 10.1007/s00227-005-0103-5	
<b>PUBLICATION II</b>	47
Renz J, Peters J, Hirche H-J (2006) Life cycle of <i>Pseudocalanus acuspes</i> Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: II. Reproduction, growth and secondary production. Mar Biol submitted	
<b>PUBLICATION III</b>	77
Peters J, Renz J, van Beusekom J, Boersma M, Hagen W (2006) Trophodynamics and seasonal cycle of the copepod <i>Pseudocalanus acuspes</i> in the Central Baltic Sea (Bornholm Basin) – evidence from lipid composition. Mar Biol DOI 10.1007/s00227-006-0290-8	
<b>MANUSCRIPT</b>	93
Renz J and Hirche H-J Life cycle and population dynamics of <i>Pseudocalanus elongatus</i> Boeck in the southern North Sea. Manuscript	
<b>Further publications</b>	
Renz J, Peters J, Hirche H-J, Hagen W (2006) Does the calanoid copepod <i>Pseudocalanus acuspes</i> retain an arctic life cycle in the Central Baltic Sea? GLOBEC International Newsletter 12 (1): 71-73	
Renz J, Hirche H-J (2004) Life cycle of <i>Pseudocalanus acuspes</i> in the Central Baltic Sea. ICES CM L:20	
<b>7 REFERENCES</b>	122
<b>8 ACKNOWLEDGEMENTS</b>	132
<b>ABBREVIATIONS</b>	133

## Summary

Calanoid copepods of the genus *Pseudocalanus* constitute important members of the zooplankton in the northern hemisphere and play a major role in the recruitment and stock dynamics of commercially used fish. This study analyses the population dynamics of the calanoid copepod *Pseudocalanus* spp. in the Baltic and North Sea ecosystems and compares life cycle characteristics, vital rates and secondary production of the two congener species, *P. acuspes* from the Baltic Sea and *P. elongatus* from the North Sea. Reproduction, growth and secondary production of these species are interpreted in the light of the nutritional environment and hydrography. The connected continental shelf areas of the Baltic Sea and the North Sea exhibit pronounced differences in their hydrographic conditions and number of species and were the object of a comparative study in the framework of the GLOBEC Germany Project.

The study on the population dynamics of *P. acuspes* in the Bornholm Basin (central Baltic Sea) was carried out on 17 cruises between March 2002 and July 2003. *P. acuspes* was an important member of the zooplankton throughout the year, with maximum abundances up to  $618 \cdot 10^3$  and  $869 \cdot 10^3$  n m<sup>-2</sup> in May 2002 and April 2003, respectively. Maximum biomass, estimated from prosome length, was 594 (May 2002) and 855 mg C m<sup>-2</sup> (May 2003). A stage specific ontogenetic vertical distribution with youngest stages highest up in the water column and older stages concentrated in deeper layers was governed by physiological requirements and therefore closely related to hydrographic conditions. Copepodite stages V (CV) and adults were distributed in the region of the permanent halocline located in approx. 60 m depth, where they were subjected to higher salinities, while nauplii and younger stages preferred intermediate waters. However, in particular of this high latitude species, all stages avoided the thermocline in summer. The characteristic vertical distribution pattern exposed especially older stages to their main predators, herring and sprat, which are known to feed in the region of the halocline. All stages of *P. acuspes* were present year round, with a stage shift from nauplii in April/May to CIV and CV in November indicating a slow seasonal development. This was confirmed by extremely long stage durations of 15-25 days at 4°C in May and July 2003, determined from moulting experiments. Maximum growth rates based on stage durations amounted to 0.03-0.05 d<sup>-1</sup> in CI-CIV. The mean egg production rate (EPR) showed a seasonal course with highest rates in April 2002 (3.6 eggs f<sup>-1</sup> d<sup>-1</sup>) and 2003 (2.1 eggs f<sup>-1</sup> d<sup>-1</sup>), corresponding to a mean specific egg production rate (SEPR) of 0.13 and 0.04 d<sup>-1</sup>. Mean secondary production was 9.1 mg C m<sup>-2</sup> d<sup>-1</sup> (max. 16 mg C m<sup>-2</sup> d<sup>-1</sup>), corresponding to a mean productivity of 0.031. Based on lipid composition of CV and females, stage structure data and a slow seasonal development there was evidence, that the life cycle of *P. acuspes* resembles those of high latitude species with a reproductive peak in spring and a successive accumulation of overwintering copepodite stages during summer. However, a potential interposition of minor generations might occur during summer.

The population dynamics of *P. elongatus* were studied in the southern North Sea between February 2004 and May 2005. Maximum abundance was in the range of *P. acuspes* from the

Baltic Sea and reached up to  $564 \cdot 10^3 \text{ n m}^{-2}$  in June 2004. Spatial distribution showed highest abundance of nauplii and youngest stages in the southern and central part of the study area, while older stages and adults concentrated in the central and westerly part. Stage durations derived from moulting experiments ranged from 1 d for CII in February up to 9.2 d for CV in April, with highest stage durations generally observed at lowest temperatures. Weight specific growth rates were highest in youngest stages in April and August ( $0.31 \text{ d}^{-1}$ ), while growth rate of females peaked in February/March and May ( $0.12\text{-}0.13 \text{ d}^{-1}$ ). Maximum EPR of females reached  $9.1 \text{ eggs f}^{-1} \text{ d}^{-1}$  in April 2004, while SEPR was highest in June ( $0.13 \text{ d}^{-1}$ ). Mean secondary production of *P. elongatus* was  $19 \text{ mg C m}^{-2}$  (max.  $110 \text{ mg C m}^{-2}$ ) in May and June, corresponding to a mean productivity of  $0.15 \text{ d}^{-1}$ . At least 3 generations were identified in the southern North Sea between February and October 2004, distinguished by changes in prosome length of females.

The comparison of *P. acuspes* from the Baltic Sea and *P. elongatus* from the North Sea revealed strong differences in the population dynamics of this morphologically similar congener species. The highly stratified Baltic Sea makes high demands on the distribution of the glacial relict *P. acuspes*, which is adapted to a life at high latitudes. To reach optimal temperature conditions, a vertical distribution below the summer thermocline is compellent. This vertical innidation prevents utilisation of food from the euphotic zone by this primarily herbivorous species. The food limitation, the low salinity and the low temperatures in the Baltic Sea lead to diminished growth rates of all stages of *P. acuspes*, which is indicated by the stage structure and the slow development in May and July. Compared to that, the growth of *P. elongatus* seemed to be unlimited by food particularly during spring and summer, which is indicated by lower stage durations and higher growth rates and results in a higher max. secondary production. These differences emphasise the importance of careful identification and studies of key species for an understanding of their role in the marine ecosystem.

## Zusammenfassung

Calanoide Copepoden der Gattung *Pseudocalanus* stellen eine wichtige Gruppe des Zooplanktons in der nördlichen Hemisphäre dar und spielen eine bedeutende Rolle in der Rekrutierung und der Bestandsdynamik kommerziell genutzter Fische. Diese Arbeit analysiert die Populationsdynamik des calanoiden Copepoden *Pseudocalanus* spp. in den Ökosystemen Ost- und Nordsee und vergleicht Charakteristika in Lebenszyklus und -raten und Sekundärproduktion der verwandten Arten *P. acuspes* aus der Ostsee und *P. elongatus* aus der Nordsee. Die Parameter Reproduktion, Wachstum und Sekundärproduktion dieser Arten werden auf dem Hintergrund der Nahrungsbedingungen und der Hydrographie interpretiert. Die miteinander verbundenen kontinentalen Schelfmeere von Ost- und Nordsee weisen ausgeprägte Unterschiede in ihren hydrographischen Bedingungen und der Artenanzahl auf und sind Objekt einer vergleichenden Studie im Rahmen des Projektes GLOBEC Deutschland. Die Populationsdynamik von *P. acuspes* wurde auf 17 Ausfahrten ins Bornholm Becken (zentrale Ostsee) zwischen März 2002 und July 2003 untersucht. *P. acuspes* stellte über das ganze Jahr einen wichtigen Bestandteil des Zooplanktons dar und erreichte eine max. Abundanz von  $618 \cdot 10^3$  und  $869 \cdot 10^3$  ind.  $m^{-2}$  im Mai 2002 und April 2003. Die max. Biomasse, welche über die Prosomenlänge ermittelt wurde, erreichte 597 (Mai 2002) und 855 (Mai 2003) mg Kohlenstoff  $m^{-2}$ . Die stadienspezifische ontogenetische Vertikalverteilung zeichnete sich durch eine flache Verteilung der jungen Stadien und eine tiefe Verteilung der älteren Stadien aus. Sie war durch physiologische Anforderungen bestimmt und daher eng an die hydrographischen Bedingungen geknüpft. Copepodite des Stadiums V (CV) und Adulte verteilten sich im Bereich der Salzgehaltssprungschicht in ca. 60 m Tiefe, wo sie einem hohen Salzgehalt ausgesetzt waren, während Nauplien und jüngere Stadien mittlere Wassertiefen bevorzugten. Als spezielle Eigenschaft dieser aus höheren Breiten stammenden Art vermieden alle Stadien den warmen Bereich über der Sommersprungschicht. Das charakteristische Muster in der Vertikalverteilung setzte speziell ältere Stadien ihren Hauptprädatoren Hering und Sprotte aus, welche dafür bekannt sind, im Bereich der Salzgehaltssprungschicht zu fressen. Alle Stadien von *P. acuspes* waren ganzjährig vorhanden. Die Verlagerung von Nauplien im April/Mai zu CIV und CV im November deutete eine langsame Entwicklung an, was durch die langen Stadiendauern aus Häutungsexperimenten von 15-25 Tagen bei 4°C im Mai und Juli bestätigt wurde. Die auf Stadiendauer basierenden max. Wachstumsraten beliefen sich bei CI-CIV auf 3-5% pro Tag. Die mittlere Eiproduktionsrate (EPR) zeigte einen saisonalen Verlauf mit höchsten Raten im April 2002 (3,6 Eier pro Weibchen und Tag) und 2003 (2,1 Eier pro Weibchen und Tag), was einer spezifischen EPR von 13 und 4% entsprach. Die mittleren Sekundärproduktion lag bei  $9,1$  mg Kohlenstoff  $m^{-2} \text{ Tag}^{-1}$  (Max.  $16$  mg Kohlenstoff  $m^{-2} \text{ Tag}^{-1}$ ), was einer Produktivität von 0,031 entsprach. Basierend auf der Lipidzusammensetzung, der Stadienstruktur und der langsamen Entwicklung gab es Hinweise darauf, dass der Lebenszyklus von *P. acuspes* mit einem Reproduktionsmaximum im Frühjahr und einer sukzessiven Akkumulation von Überwinterungsstadien im Sommer dem Lebenszyklus von

Arten aus höheren Breiten ähnelt. Während des Sommers tritt möglicherweise eine Zwischenschaltung kleinerer Generationen auf.

Die Populationsdynamik von *P. elongatus* wurde von Februar 2004 bis Mai 2005 in der südlichen Nordsee untersucht. Die max. Abundanz lag im Bereich der Abundanz von *P. acuspes* in der Ostsee und erreichte Werte bis zu  $564 \cdot 10^3$  ind.  $m^{-2}$ . Die räumliche Verteilung zeigte, dass die Abundanz der Nauplien und jüngere Stadien im südlichen und zentralen Teil des Untersuchungsgebietes am höchsten war, während ältere und adulte Stadien sich im zentralen und westlichen Teil anreicherten. Die aus Häutungsexperimenten errechnete Stadiendauer lag im Bereich von 1 Tag für CII im Februar bis zu 9 Tagen für CV im April, wobei die längsten Stadiendauern generell bei den niedrigsten Temperaturen beobachtet wurden. Die gewichtsspezifischen Wachstumsraten waren in den jüngsten Stadien im April und August am höchsten (31%). Die max. EPR erreichte 9,1 Eier pro Weibchen und Tag im April 2004, während die spezifische EPR im Juni am höchsten war (13%). Die mittlere Sekundärproduktion lag bei  $19 \text{ mg Kohlenstoff } m^{-2} \text{ Tag}^{-1}$  (Max.  $110 \text{ mg Kohlenstoff } m^{-2} \text{ Tag}^{-1}$ ), was einer Produktivität von 0,15 entsprach.

Der Vergleich von *P. acuspes* aus der Ostsee und *P. elongatus* aus der Nordsee zeigte deutliche Unterschiede in der Populationsdynamik der beiden morphologisch ähnlichen, verwandten Arten. Die geschichteten Verhältnisse der Ostsee stellen hohe Anforderungen an die Verteilung der glazialen Reliktart *P. acuspes*, welche an ein Leben in höheren Breitengraden angepasst ist. Um optimale Temperaturbedingungen zu erreichen, ist eine Vertikalverteilung unterhalb der Sommersprungschicht zwingend erforderlich. Diese vertikale Einnischung hindert diese Art an der Nutzung von Futter aus der euphotischen Zone. Die Futterlimitierung, der geringe Salzgehalt und die geringen Temperaturen in der Ostsee führen zu verringerten Wachstumsraten aller Stadien, was durch die Stadienstruktur und die geringen Wachstumsraten angezeigt wird. Im Vergleich dazu scheint das Wachstum von *P. elongatus* in der Nordsee speziell während des Frühjahrs und Sommers nicht durch Nahrungsverfügbarkeit limitiert zu sein, was sich in geringeren Stadiendauern und höheren Wachstumsraten bemerkbar macht und in einer höheren max. Sekundärproduktion resultiert. Diese Unterschiede verdeutlichen die Wichtigkeit einer sorgfältigen Identifizierung und Untersuchung von Schlüsselarten, um ihre Rolle im marinen Ökosystem zu verstehen.

## 1 Introduction

Calanoid copepods constitute the most abundant mesozooplankton group of the world (Kinne 1978) and serve as an important link for energy transfer between primary producers and higher trophic levels. They are a principal food source for commercially important fishes and the knowledge on their distribution patterns and population dynamics is essential for modelling carbon flux and marine food webs.

### 1.1 Distribution patterns of calanoid copepods

The environmental conditions inhabited by copepods in tropical, temperate and high latitudes cover a wide range of different biotic and abiotic conditions and result in different life history patterns. Conditions in marine areas range from saline to brackish water, from shallow to deep and from temperatures between -1.9 and 40°C, including coastal and estuarine areas (Lalli and Parsons 1993). The geographical distribution of a species depends on abiotic and biotic factors. A species is subject to the prevailing hydrographic situation and circulation patterns and disperses from its place of origin to other regions and habitats, where it has to establish itself continuously (Mauchline 1998). This implies that the physical environment is adequate for reproduction, growth, survival and interactions with other organisms and thus allows maintenance of an autochthonous population (e.g. Kinne 1963, Mauchline 1998, Miller 2004). Populations have developed a variety of life history patterns enabling them to survive in broad or restricted geographical regions.

Distribution patterns of congener copepods often differ considerably, either in spatial or temporal scale. Spatial separation of species may occur latitudinally, as shown for *Calanus* species (e.g. Conover 1988), vertically in the water column as in *Paraeuchaeta* congeners (e.g. Mauchline 1995, Auel and Hagen 2005) or by topographic regions, e.g. shelf or shore areas, as observed for *Centropages* species (Grant 1988). Temporal separation has been noticed as a seasonal succession in different regions and species, where 'colder' species precede 'warmer' ones (Eriksson 1973, Fransz and van Arkel 1983).

The global distribution patterns of several *Clausocalanus* species are characterised by a latitudinal gradient and therefore by temperature limits (Frost 1969). The circumglobal, warm-water species *C. parapergens* and *C. furcatus* inhabit the regions between 45° north and south of the equator with only small differences in the exact southern and northern limits. *C. ingens* shows a circumglobal, subantarctic pattern of distribution, while *C. lividus* is known to occur in temperate (or central gyre) regions. Some species, like *C. farrani* and *C. minor* are restricted to the Indo-Pacific, temperate-tropical region. Miller (2004) summarised the distribution patterns as follows: Species can vary in the width of the latitudinal belt they inhabit. While some show a broadly tolerant distribution, others require a very specific hydrographic regime. If this hydrographic regime is found in several places around the globe, the species will be found in many or all of them. As the three major oceans show very different habitat characteristics, they share some, but not all species.

## **1.2 Life cycles of calanoid copepods in different geographical regions**

The life cycle of copepods in tropical and subtropical regions is characterised by continuous and irregular breeding throughout the year without any seasonality. This, together with lacking seasonal variation in prosome length (Chisholm and Roff 1990a) makes it difficult to identify successive broods or generations. Generation times might be comparable to those in temperate regions (Chisholm and Roff 1990b) without reflecting the higher temperatures. Longevity of individuals has been shown to decrease with increasing temperature and has been reported to take from a few days to several weeks (e.g. Ianora et al. 1996, Vuorinen 1987, Paffenhöfer 1991). In temperate regions copepods are larger in body size and have longer generation times. They show a marked seasonality in breeding, with occasional very protracted breeding periods of higher and lower activity. They often have successive broods and 4-6 or more generations per year. Species producing diapause eggs, resting copepodids and resting adults are common. In high latitudes growth rates are slowed down, developmental times extended and breeding periods restricted seasonally. Overwintering occurs as a certain developmental stage, often coupled with an ontogenetic seasonal vertical migration or production of diapause or resting eggs sinking to the bottom and residing at the sea bed. The low temperatures enable individuals to live one year and longer (Conover 1967).

## **1.3 Population dynamics of calanoid copepods**

In temperate ecosystems, zooplankton biomass and abundance typically undergo seasonal changes with a unimodal distribution and a peak during late spring and summer (Colebrook 1979). The seasonal cycle of zooplankton in spring lags considerably behind the seasonal distribution of primary production and concentration of phytoplankton, while in summer the zooplankton cycle appears to be largely unrelated to either primary production or phytoplankton concentration. Abundance and biomass changes are mainly caused by variation in productivity and mortality (Kjørboe and Nielsen 1994).

Precise and frequent measurements of the abundance and age structure of copepod populations, over a suitably long time period, enable estimates of birth, growth and death rates, which are fundamental to descriptions of population dynamics (Hay et al. 1988). Abundance is the basic parameter when describing development of zooplankton populations and reconstructing life cycles. Weight specific fecundity, development and growth are key parameters, as they are descriptors of the rates at which copepods process material. These terms also relate to their potential to supply energy and matter to higher trophic levels. They are primarily dependent on food quality and availability, predation and temperature (e.g. Hirst and Bunker 2003). Salinity also plays an important role particularly in brackish water systems. The relationship between copepod development and environmental factors is often studied by cohort analysis from time series of samples collected in the field. However, estimating the rate of development from population data is not easy due to variation in birth rate, development and mortality and continuous reproduction (Hairstone and Twombly 1985). The biological effects of given environmental conditions may differ between populations of the same species, between

different life stages and sexes and may reflect the history of an individual. Moreover, present and past effects may interact with each other. Owing to predation in the field, mortality may be size or stage specific and must be considered for a proper estimate of the developmental rate (Hairstone and Twombly 1985, Ohman et al. 1996). Moreover, ambient conditions may change rapidly and in long-term observations it is difficult to determine the causal relationship between the rate of development and environmental conditions (Klein Breteler and Gonzalez 1982). When field data are lacking, laboratory studies are often used to observe cohorts of simultaneously hatched eggs under controlled environmental conditions (e.g. Corkett and McLaren 1970, Klein Breteler and Gonzalez 1982, Klein Breteler et al. 1995, Koski et al. 1998), which give precise estimates, but accuracy may be low when transferred to field conditions due to of the non natural surroundings (Hay et al. 1988).

Over the last few decades, productivity has become a central and extensively studied aspect of marine plankton research (e.g. Runge and Roff 2000). Estimating production is of paramount importance as the biomass produced per unit time by a population is the most important parameter for estimating the total productivity in the sea. The highest production rates occur in small animals such as cladocerans, appendicularians and copepods (Greze 1978). Measuring productivity in the ocean and understanding the factors controlling it makes it possible to estimate total production on the basis of biomass and species composition (Greze 1978).

Biological production is based on metabolism, growth and reproduction of organisms. However, total rates of production cannot be estimated solely from information obtained from single individuals. Organisms always exist as populations and the performance of individuals for a given population is affected by variations in abiotic and biotic environmental factors. They determine functions and structures of populations, which are considered to represent basic biological elements in the overall flow of energy and matter in the ecosystem (Greze 1978). Temperature plays an important role, directly influencing growth and production of copepods. Many metabolic processes are temperature limited and do not allow development beyond the species specific temperature range, which defines zoogeographic boundaries. Salinity might be of major importance especially in brackish water areas where species diversity is lowest.

Most copepod production in the oceans is associated with net phytoplankton blooms (e.g. Kiørboe and Nielsen 1994). The frequent observation that copepod reproduction (Durbin et al. 1983, Kiørboe et al. 1988, Niehoff et al. 1999) as well as growth and development (Landry 1978, Kimmerer and McKinnon 1987, Hirche et al. 2001) is less than optimal and limited by food availability most of the year is controversial and several authors suggest that quantity of food very seldom limits development times (Corkett and McLaren 1978, Davis 1984a). Especially instar development in copepod populations appears mostly to proceed at maximum rates limited only by temperature (Corkett and McLaren 1978, Huntley and Lopez 1992).

#### **1.4 The genus *Pseudocalanus***

The lack of the interspecific morphological differentiation and a potential co-occurrence of species have confused the scientific study of this genus.

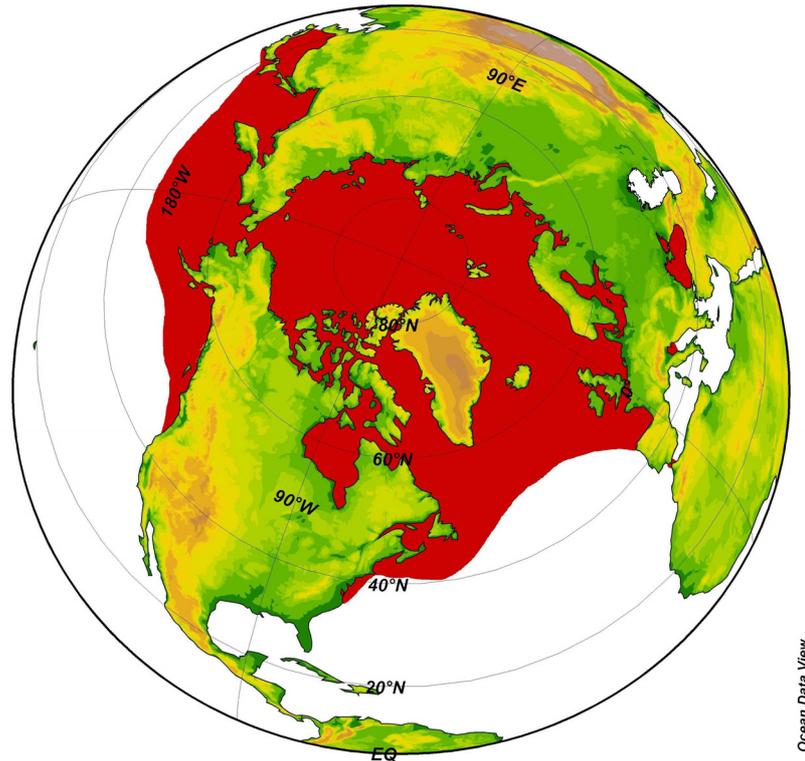


Fig. 1: Distribution of the genus *Pseudocalanus* in the northern hemisphere (after Corkett and McLaren 1978)

Frost (1989) reviewed the taxonomy based on morphological differences, which was supported by biochemical evidence (Bucklin et al. 2003). The genus *Pseudocalanus* is now represented by 7 species.

Taxonomic hierarchy of the genus *Pseudocalanus* (Frost 1989):

Calanoida

Clausocalanoidea

Clausocalanidae

*Pseudocalanus*

*Pseudocalanus acuspes* (Giesbrecht 1881)

*Pseudocalanus elongatus* (Boeck 1865)

*Pseudocalanus major* (Sars 1900)

*Pseudocalanus mimus* (Frost 1989)

*Pseudocalanus minutus* (Krøyer 1845)

*Pseudocalanus moultoni* (Frost 1989)

*Pseudocalanus newmani* (Frost 1989)

Among the calanoid copepods the genus *Pseudocalanus* often dominates the zooplankton in temperate seas of the northern hemisphere (Corkett and McLaren 1978). The genus is considered basically neritic and is found in Arctic Seas extending southward along cooler coasts and even beyond in deeper oceanic waters (Sewell 1948). Its distribution ranges from Chesapeake Bay (eastern USA) to the North Atlantic Drift south of Iceland and in European waters to the south of Portugal and the Mediterranean. In the North Pacific it has been recorded down to the south of Japan and Vancouver Island (Fig. 1).

Species of the genus *Pseudocalanus* show a wide distribution in temperate and boreal pelagic ecosystems all over the northern hemisphere (Fig. 1). They comprise a suite of sibling species that exhibit exceptional morphological and ecological similarity. The considerable lack of easily recognisable distinguishing characters for different *Pseudocalanus* species accounts for the incomplete knowledge of fundamental aspects of their life histories. Though some *Pseudocalanus* species differ in size distribution, individual size is not categorically a diagnostic character for different species. Based on a number of studies, it is clear that there is a considerable taxonomic and geographic variation in the life histories of *Pseudocalanus* species (Corkett and McLaren 1978). Frost (1989) found *P. moultoni* to dominate the zooplankton fauna of Puget Sound (Vancouver Island, Pacific) during late winter and early spring, while *P. newmani* was more abundant during late spring and summer and experienced completely different biotic and abiotic conditions. In the same region, Jónasdóttir (1989) observed *P. newmani* year round. In the Gulf of Alaska *P. mimus* females dominated during late winter and early autumn and *P. newmani* was present in almost all occasions and most relevant in spring samples, while Napp et al. (2005) found a numerical increase during the warm water season. In Bedford Basin (Nova Scotia), *P. newmani* diminishes during the warm water season (McLaren et al. 1989a). McLaren et al. (1989a) concluded that 'To some extent the species partition themselves among the seasons'.

#### ***Pseudocalanus acuspes* and *Pseudocalanus elongatus***

*Pseudocalanus acuspes* mainly inhabits high latitudes and is distributed throughout the neritic part of the Arctic region. The southern limits of its range extend to the Baltic Sea and Bedford Basin (Nova Scotia, Canada) in the North Atlantic Ocean and into the eastern Bering Sea in the North Pacific Ocean (Frost 1989)(Fig. 2). In the Baltic Sea it occurs e.g. in the Kiel Bight (Frost 1989), the Arkona Basin (Bucklin et al. 2003), the Bornholm Basin (Renz and Hirche 2006, PUBLICATION I) and in the Gotland Basin (Frost 1989).

*Pseudocalanus elongatus* is a neritic species (Hansen 1969), and its distribution ranges from the temperate eastern North Atlantic Ocean to the south of the English Channel and the North Sea. It is found in the western Mediterranean and probably isolated populations occur in the Adriatic and Black Seas (Frost 1989) (Fig. 2). In the North Sea it is observed in the south-western part (e.g. Künné 1952), the west coast of Sweden (Eriksson 1973) and the English Channel (Digby 1950) throughout the year. Particular high numbers of *P. elongatus* were found

in the central part of the North Sea (Farran 1920, Wimpenny 1933) and the Fladen Ground (Krause and Trahms 1983, Fransz et al. 1984).

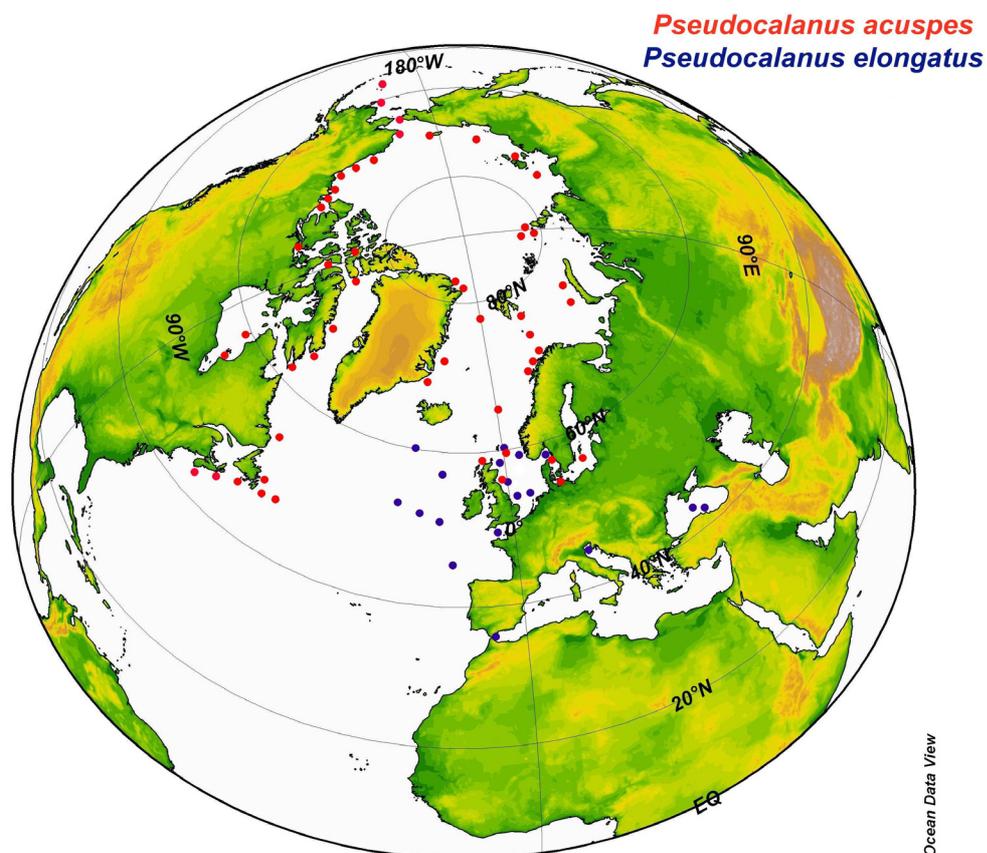


Fig. 2: Distribution of *Pseudocalanus acuspes* and *P. elongatus* in the northern hemisphere (after Frost 1989)

Different life cycles were described for *Pseudocalanus* species: from biennial (Cairns 1967) and annual cycles (Davis 1976, Conover and Siferd 1993, Lischka and Hagen 2005) in polar regions, up to cycles with two or more generations per year (Pertsova 1981, McLaren et al. 1989a, Norrbin 1992). In temperate regions a life cycle with several generations per year is commonly observed (Marshall 1949, Digby 1950). Stage structure or size is often used as a critical parameter to distinguish between successive generations. However, constant environmental conditions or opposing interactions between temperature and food effects might lead to difficulties in the identification of different generations.

*Pseudocalanus* exhibits a mainly herbivorous feeding behaviour (e.g. Corkett and McLaren 1978, Fraser et al. 1989, Cottonnec et al. 2001), though the classical concept that copepods depend primarily on diatoms for their nutrition has been challenged repeatedly over the last decade and several studies suggest a more omnivorous food spectrum for *Pseudocalanus*,

especially in less diatom-characterised habitats and seasons (Båmstedt et al. 1990, Norrbin et al. 1990).

Reproducing females of *Pseudocalanus* carry their eggs in sacs or masses attached to the female genital opening until the nauplii hatch. Depending on size of females, temperature and food conditions, females are able to produce >40 eggs per sac with a potential production of around 9 clutches per female (Thompson 1976, Paffenhöfer and Harris 1976). The variability concerning measurements of fecundity in the literature is high due to the different *Pseudocalanus* species, localities and environmental conditions. After hatching, the nauplii pass through 6 naupliar and 5 copepodite stages until they mature and reach the adult copepodite stage VI (CVI). During their development from instars to adulthood, individuals of this genus store energy in the form of lipid reserves, most important in periods of food shortage during winter times. *Pseudocalanus* is known to overwinter in late copepodite stages (CIV and/or CV), characterised by a phase of slowed down or arrested development. When conditions become favourable, the overwintering stages start to moult and develop into females and males. While females are known to have a lifespan of several weeks to months, males of this genus are relatively short lived as they have reduced mandibles and do not feed (Corkett and McLaren 1978).

*Pseudocalanus* shows a tendency for younger stages to occur nearer to the surface than older stages (Ackefors 1969, Hernroth and Ackefors 1979). This ontogenetic vertical distribution often has been interpreted as a result of physiological preferences (Corkett and McLaren 1978). Seasonal vertical migrations with a deep distribution of overwintering stages in colder waters below 600 m have commonly been observed in the Norwegian Sea (Øvstedt 1955, Hansen 1969).

## 2 Thesis outline

This work was conducted in the framework of the German GLOBEC (Global Ocean Ecosystem Dynamics) Project. The project aims for a better understanding of the interaction between zooplankton and fish under the influence of physical processes in order to elucidate the principle mechanisms accounting for the high variability of copepod production and reproductive success of fish.

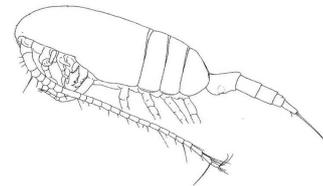
The stocks of copepods and several commercially important fish species in the Baltic Sea and North Sea have undergone a large fluctuation during the last decades. The stock size of cod, one of the most important predator fish, has significantly decreased. During the same period, a decreasing individual weight of sprat and herring in the Baltic Sea was accompanied by high stock densities, a relationship which was not detected in the North Sea (Köster et al. 2001). The observed phenomenon of the Baltic Sea was suggested to be a result of food limitation of fish by their main prey: the copepods, *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes*, which constitute the most important members of the copepod community in the central Baltic Sea. Long term dynamics of these species have shown that they to a large extent depend on hydrographic conditions (Ojaveer et al. 1998, Viitasalo 1992, Vuorinen et al. 1998, Möllmann et al. 2000). Especially *Acartia* spp. showed an increase in biomass with increasing temperatures in the 1990s (Möllmann et al. 2000). During the same period the decreasing salinities caused by increased river run-off (Bergström and Carlsson 1994) and the lack of pulses of saline water intrusions from the North Sea and the Skagerrak (Matthäus and Schinke 1994) caused a decline in the biomass of *Pseudocalanus* sp. (Dippner et al. 2000, Möllmann et al. 2000). However, it is not clear, whether the observed changes in the stock dynamics of several fish species is due to a direct effect of trophic interactions or whether the decrease of the *Pseudocalanus* population is a reaction to physical processes, as especially females of *Pseudocalanus* were suggested to depend on higher salinity during maturation and reproduction (Möllmann et al. 2003).

In the North Sea, many species of zooplankton have exhibited pronounced changes in abundance since the late 1980s. Increasing numbers of warm water species such as *Calanus helgolandicus* were accompanied by decreasing concentrations of cold water species such as *C. finmarchicus* (Beaugrand 2003, 2004). The most important copepod species in the North Sea are *Paracalanus parvus*, *Microcalanus pusillus*, *Acartia* spp., *Temora longicornis*, *Calanus finmarchicus*, *C. helgolandicus* and *Pseudocalanus elongatus* (e.g. Franz et al. 1991, Krause et al. 1995). A decreasing trend of many zooplankton species was already observed between the 1950s and the 1980s (Cushing 1982) either in stock size or in their seasonal cycles. The reproduction period of *Pseudocalanus elongatus* e.g. in the Southern North Sea continuously decreased by more than 6 weeks in the period between 1948 and 1979 (Glover et al. 1972). Recent publications relate the long term changes in zooplankton composition to climatic phenomena such as the North Atlantic Oscillation (NAO) or the location of the Gulf stream (e.g.

Hays et al. 1993, Taylor 1995, Planque and Fromentin 1996, Reid et al. 1998), though there is no direct evidence of the mode of operation between climate and the pelagic system.

The present work aimed to investigate the population dynamics and production of the calanoid copepod *Pseudocalanus* spp. in the Baltic Sea and North Sea, as this genus is assumed to play an important role in the recruitment and stock dynamics of commercially important fish and could serve as a mediator between climate and fish (Möllmann et al. 2003). Seasonally and spatially intensive field sampling programs were carried out to investigate the life cycle, biomass and vital rates of *Pseudocalanus* spp. The horizontal and vertical distribution patterns were measured to determine the abundance and biomass of *Pseudocalanus* spp. as prey for higher trophic levels. The estimation of population dynamics is based on high resolution measurements of reproductive parameters in both study areas in almost monthly in-situ incubations on board ship. Furthermore moulting experiments were conducted in short term incubations during several cruises to estimate growth and secondary production in the field. The results are discussed on the background of the nutritional environment and hydrographic conditions.

Despite the review of Frost (1989), the determination of the *Pseudocalanus* species occurring in the central Baltic Sea was inconsistent. A special focus in the discussion will therefore be put on the identification of this species in our investigation area. A comparison between the two congener species of the Baltic and North Sea is made in order to demonstrate the importance of the knowledge on species-specific life history patterns when determining secondary production.



### 3 Material and Methods

#### 3.1 Study sites

The North Sea and Baltic Sea are relatively shallow continental shelf seas. The water of these marginal seas emanates from adjacent open oceans, with renewal largely dependent on sill depth and dimension of the connection between these seas (Dietrich et al. 1975). The hydrographic conditions are strongly dependent on regional wind conditions, heat balances, tides and riverine input. Changes in temperature and salinity gradients influence the stability of the water column, which in turn affects the distribution of phyto- and zooplankton organisms due to their physiological tolerances, ability to migrate, habitat preferences and feeding ecology.

##### 3.1.1 Baltic Sea

The Baltic Sea is one of the largest brackish water areas of the world, covering an area of about 412 560 km<sup>2</sup>. Several basins of different depths (mean 52 m) are connected by shallow sills, influencing circulation and advection in the Baltic Sea ([www.io-warnemuende.de](http://www.io-warnemuende.de)). Water exchange with the North Sea occurs via Kattegat and Skagerrak, while the eastern part is affected by high amounts of river run-off. As a result, salinity decreases from west to east. The hydrography in the central Baltic Sea is characterised by a permanent halocline, located in ca. 60 m depth, preventing vertical mixing and restricting water exchange with upper layers. Renewal of bottom water is dependent on lateral advection of highly saline water from the North Sea. This occurs relatively rarely and results in depletion of oxygen in the region of the halocline (Matthäus and Schinke 1994). From May onwards warming of the upper water layers causes the development of a summer thermocline. The hydrographic conditions in the central Baltic Sea are mainly controlled by climatic factors, with the NAO an important factor driving water temperatures in the central Baltic Sea. A period of relatively warm water temperature in the 1990s was mainly caused by mild winters during the phase of high NAO (Dippner et al. 2000).

##### 3.1.2 North Sea

The North Sea covers an area of 575.000 km<sup>2</sup> (Banner et al. 1980) with a mean depth of 100 m. The southern North Sea and the German Bight are characterised by depths of 20 to 40 m. Atlantic water enters the southern North Sea through the Strait of Dover and continues towards the German Bight. The two water masses found in the German Bight are the Continental Coastal Water (CCW) and the Central (Southern) North Sea Water (Becker et al. 1983). The CCW is a mixture of Atlantic water and water from the English Channel, together with river waters from e.g. Rhine, Meuse and Elbe. A river plume front in the south-east originates from the inflow of fresh water from the river Elbe. The mean North Sea circulation shows a moderate transport of water from the Southern German Bight into the north-east of the German Bight. The northern continuation of this current is the Jutland Current, which flows into the Skagerrak. In the German Bight circulation is mainly cyclonic and strongly dependent on wind direction. Mesoscale variability in the German Bight is high in both, spatially and temporally.

Strong tides cause turbulent horizontal and vertical exchanges. A tidal mixing front, which reaches from the surface to the ground, is advected as a whole by the tides (Becker and Prahm-Rodewald 1980).

### 3.2 Sampling

Sampling of zooplankton was conducted between March 2002 and May 2003 in the central Baltic Sea and between February and October 2004 in the southern North Sea (Table 1) (Fig. 3a).

Cruises Baltic Sea	Rep	Moult	Cruises North Sea	Rep	Moult
<b>2002</b>			<b>2004</b>		
12.03. - 22.03	+		16.02. - 05.03	+	+
02.04. - 16.04	+		06.04. - 27.04	+	+
16.04. - 30.04	+		07.05. - 26.05	+	+
05.05. - 24.05	+		17.06. - 06.07	+	+
15.05. - 30.05	+		04.08. - 23.08	+	+
11.06. - 23.06	+		06.09. - 12.09	+	
22.07. - 07.08	+		11.10. - 16.10	+	
12.08. - 21.08	+		<b>2005</b>		
03.09. - 13.09	+		17.05. - 28.05	+	
30.09. - 10.10	+				
11.11. - 29.11	+				
<b>2003</b>					
13.01. - 24.01	+				
10.02. - 21.02	+				
03.03. - 22.03	+				
17.04. - 28.04	+				
15.05. - 03.06	+	+			
01.07. - 19.07	+	+			

Table 1: Cruises during German GLOBEC to the Baltic Sea and North Sea; experiments performed are marked by +, *Rep* reproduction experiments, *Moult* experiments on moulting rates

In both areas (Fig. 3b, c) on every station double oblique bongo net hauls (mouth opening 0.2 m<sup>2</sup>, mesh size 150 µm, towing speed 3 kn) (Fig. 4) were taken from above the sea bottom to the surface. On 9 focus stations (Fig. 3b, c, squares) additional sampling was performed using a multinet (Hydrobios, mouth opening 0.25 m<sup>2</sup>, mesh size 50 µm, towing speed 0.2 m s<sup>-1</sup>) (Fig. 5)

towed vertically with a 10 m resolution from the bottom to the surface. Bongo and multinet samples were immediately preserved in a 4% borax-buffered formaldehyde-seawater solution. For experimental studies at the focus stations, further samples were taken with a WP-2 net (UNESCO 1968, mouth opening 0.26 cm<sup>2</sup>, mesh size 200 µm, towing speed 0.2 m s<sup>-1</sup>) towed vertically from above the bottom to the surface.

In the laboratory of a polish sorting centre, sub samples of the multinet hauls were analysed for developmental stages until at least 150 individuals of *Pseudocalanus* spp. were counted. Individuals were identified to nauplii, copepodite stages I-V and adult males (AM) and females (AF).

Concurrent to the zooplankton sampling, vertical profiles of temperature, salinity and oxygen were recorded using a CTD-probe (SBE 911+, ME).

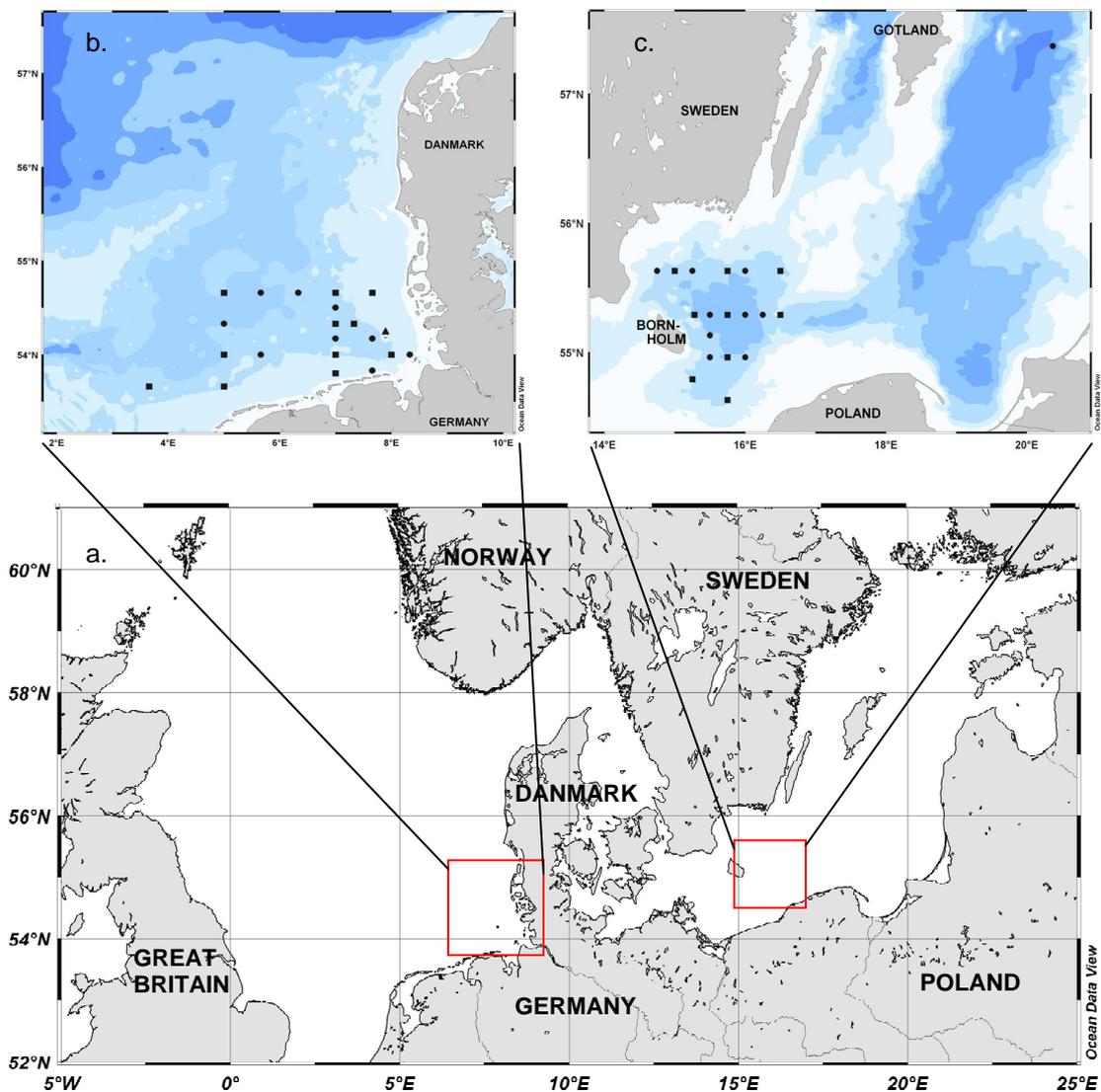


Fig. 3: Sampling sites in the Baltic Sea and North Sea (a) as well as grid stations in the North Sea (b) and Baltic Sea (c)

### 3.3 Weighted mean depth (WMD)

As an index of vertical distribution of different stages in the central Baltic Sea, weighted mean depth (WMD) of copepodids and adults was calculated according to Bollens and Frost (1989) (for details see PUBLICATION I).

### 3.4 Length measurement

For almost each cruise, prosome length of 30-90 preserved CI-CV and adult males (AM) and females (AF) from either bongo net, multinet or WP-2 net hauls was measured using a stereo microscope (Leica MZ 16) with a resolution of 80x. During time of highest egg production rate in the Baltic Sea, the total length of nauplii stages I-VI (NI-NVI) was measured with a resolution of 200x.

Total biomass for every focus station and cruise was calculated using length-weight relationships for *Pseudocalanus* spp. from the literature (for details see PUBLICATION II and III).

No correction was made for shrinkage of individuals by fixation as studies on possible changes in prosome length of preserved copepods are diversely discussed. While some authors assumed only small changes in length after preservation with formalin (e.g. Williams and Robins 1982, Böttger and Schnack 1986), Kaipris et al. (1997) reported significant reduction of length after preservation of 4.43-15.11%, depending on sex and temperature. Halliday (2001) considered a general reduction of 8%. Assuming a reduction of 8% for all stages would lead to up to 25% higher biomass values during our studies.



Fig. 4: Bongo net



Fig. 5: Multi net

### 3.5 Egg production

For measurement of in-situ egg production in the Baltic Sea and the North Sea at the focus stations the first 30 females from the WP-2 net hauls were randomly sorted immediately after capture under ambient temperature conditions. As it has been demonstrated that incubation in small volumes does not affect egg production (Niehoff et al. 1999, Harris et al. 2000) and egg cannibalism of an egg carrying species can almost be excluded, females were incubated individually in 15 ml cell wells for 24-48h under *in-situ* temperature using 50 µm prefiltered water from the upper halocline. Clutch size and number of reproducing females were recorded. In the Baltic Sea females were preserved in a 4% borax-buffered formaldehyde-seawater solution for later length measurement, while in the North Sea females were measured immediately after incubation.

### 3.6 Moulting and growth rate

Moulting rates (MR) of copepodids were measured on 2 cruises in the Baltic Sea and 4 cruises in the North Sea in short-term incubations (Klein Breteler et al. 1998). Copepodids were incubated at ambient temperature conditions in 50 µm prefiltered water. For each experiment, 2-4 subsamples containing altogether 100-150 CI-CV each were taken from a WP-2 haul. After removing old exuviae of *Pseudocalanus* spp., subsamples were incubated for 2-4 days in 1 l Kautex bottles. Every 24h one subsample was preserved in a 4% borax-buffered formaldehyde-seawater solution for later enumeration of moults by counting of exuviae. The moulting rate and growth rate of each stage were calculated (for more details regarding conversion factors, shrinkage and formulas used see PUBLICATION II and III). For nauplii, an isochronal development was assumed in the Baltic Sea. In the North Sea, nauplii were excluded from further calculations.

### 3.7 Secondary production and productivity

Secondary production was calculated by 2 methods: 1. A standard method for continuously reproducing populations (Rigler and Downing 1984), 2. The increment summation method according to Rigler and Downing (1984, modified in Hirche et al. 2001) for populations where cohorts can be followed. In the Baltic Sea a comparison between method 1 and 2 was made to estimate production. In the North Sea only method 1 was used to calculate secondary production (for more details see PUBLICATION II and III).

Productivity (P/B) was calculated for both the Baltic and the North Sea.

### 3.8 Statistics

To test for similarity between the vertical distribution of different stations in the central Baltic Sea, an overall distribution analysis of the WMD of all the focus stations was performed by nonmetric multi dimensional scaling (MDS) using the PRIMER package (Clarke 1993; Clarke and Warwick 1994). The method is based on the Bray-Curtis Similarity calculated between the WMD of each developmental stage, station and cruise (for details see PUBLICATION I).

For the statistical analysis of vertical distribution in relation to hydrographic conditions in the central Baltic Sea, the population density of each developmental stage as a proportion of this stage per 10 m depth layer and station was used to calculate Spearman rank correlations between stage abundances and mean temperature and the salinity of each depth stratum.

Differences in prosome length of copepodids between sampling dates as well as differences in prosome length of AF between stations in the Baltic Sea and the North Sea were tested with one-way ANOVA using Tukey's honestly significant difference (HSD) as the post-hoc test.

## 4 Discussion

### 4.1 The distribution of *Pseudocalanus* species in the Baltic and North Sea

Two species of the genus *Pseudocalanus* occurred at the study sites investigated during German GLOBEC. *P. acuspes*, an inhabitant of high latitudes, originates from arctic regions and is distributed all around the Arctic Ocean and adjacent waters. It is found in the North Pacific Ocean as well as in the North Atlantic Ocean down to Nova Scotia, Canada, where it is considered to be a relict species in the waters of Bedford Basin (McLaren et al. 1989a). Problems in the identification of *Pseudocalanus* species have led to some confusion about the species inhabiting the Baltic Sea. In earlier publications the species was often considered to be *P. elongatus* (e.g. Möllmann and Köster 1999, Walve and Larsson 1999, Möllmann et al. 2000, Dippner et al. 2001, Kornilovs et al. 2001, Viitasalo 2001, Hinrichsen et al. 2002, Möllmann and Köster 2002, Möllmann et al. 2003, Hinrichsen et al. 2003), *P. minutus* (e.g. Dahmen 1995) or *P. minutus elongatus* (e.g. Hernroth 1985). A review of Frost (1989) enlightened the situation. Investigating material from the Kiel Bight (western Baltic Sea) and the Gotland Deep (northern Baltic Sea), he found only specimens of *P. acuspes* in the samples. A more recent genetic identification by Bucklin et al. (2003) confirmed these results and identified *P. acuspes* in the Arkona Sea (Baltic Sea). During our study an intensive genetic study on the identification of *Pseudocalanus* occurring in the Bornholm Basin was performed concurrent to the sampling program between August 2002 and July 2003. With the exception of a small number of individuals of *P. elongatus*, occurring directly after the Major Baltic Inflow (MBI) in the Bornholm Basin (BB), only *P. acuspes* was identified (Grabbert et al. in preparation). The occurrence of *P. elongatus* is normally restricted to Atlantic waters, with single populations even reported from the Mediterranean and from the Black Sea. *P. elongatus* is the main *Pseudocalanus* species inhabiting North Sea waters, though the occurrence of at least 2 species of *Pseudocalanus* (*P. acuspes* and *P. elongatus*) was suggested (Frost 1989). The invasion of *P. elongatus* into the Baltic Sea with inflowing North Sea water is not astonishing as the large amount of inflowing North Sea water carried some 'marine species' such as *Calanus* sp., *Paracalanus parvus* into the central Baltic Sea (GLOBEC Germany, unpublished). Apparently *Pseudocalanus elongatus* was not able to adapt to conditions and maintain a population in the central Baltic Sea, as no further individuals of *P. elongatus* could be detected by genetic identification between February and July 2003 (Grabbert et al. in preparation). We therefore consider the marine species *P. elongatus* to be less adaptable to changes in abiotic conditions, as its congener *P. acuspes* in the Central Baltic tolerates a much wider range of salinity fluctuations. This explains the specific geographical distribution of *P. elongatus*, which is limited to Atlantic waters between 45 and 60°N. A spatial overlap of both species in the Baltic Sea therefore seems to be possible only in the region of the Skagerrak and Kattegat, where physiological requirements, i.e. low temperatures for the high latitude species *P. acuspes* and higher salinities for the marine species *P. elongatus*, are optimal. The only localities where both species co-occur are the northern North Sea and Oslo Fjord. At both localities, adults of *P. acuspes* were somewhat

larger than those of *P. elongatus*, though they considerably overlap in size (Frost 1989). We confirm this, as a comparison between the species from both study sites showed *P. elongatus* females to be larger than *P. acuspes* only during April, when mean prosome length of *P. elongatus* was >1 mm (Renz and Hirche 2006, PUBLICATION I, manuscript).

Historically, the Baltic is a very young sea. Only 12000 years ago large parts of the Baltic Sea were still covered by the continental ice sheet of the last glaciation. Since the ice age the Baltic Sea basin has undergone through several changes in shape and salinity. The current morphological and physico-chemical conditions have developed during the last 8000 years. There have been phases of higher salinity when there has been a more open connection to the North Sea than at present; thus only a few true brackish water species had the chance to evolve. Likewise, the marine species did not have the time to adapt to the lower salinities. On the other hand, the glacial history of the Baltic Sea has left behind relict species that originate from the Arctic Ocean and have lived in glacial lakes formed during the ice age. Populations within species might vary in their propensity to brackish water because of differences in physiological traits among populations. This variation might result from variation in acclimation or selection regime among habitats. Brackish water invaders might originate more readily from habitats that have wide temporal or spatial ranges in salinity, where broad salinity tolerances can exist. The timescale of salinity fluctuations (diel or seasonal) in a habitat could be an important factor because such timescales can affect rates of acclimation response. The occurrence of the arctic *P. acuspes* in the Baltic and the apparent lack of this species in the adjacent North Sea indicate that *P. acuspes* is part of the Baltic relict fauna, together with the fourhorn sculpin (*Triglopsis quadricornis*), *Saduria entomon*, the smelt *Osmerus eperlanus*, the seasnail *Liparis liparis* and the lumpsucker *Cyclopterus lumpus*.

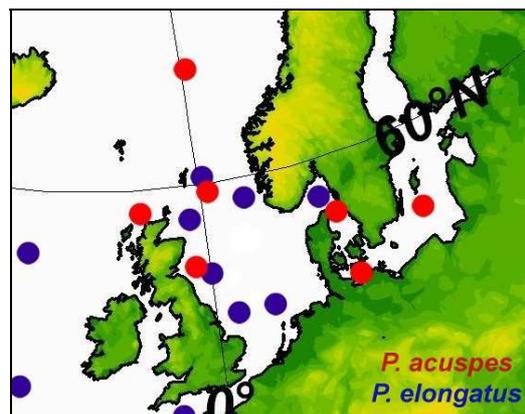


Fig. 6: Distribution of *Pseudocalanus acuspes* and *P. elongatus* in the Baltic Sea and North Sea (after Frost 1989)

Relict species of *Pseudocalanus* are also reported from Prince William Sound, where the arctic species *P. minutus* is found (Napp et al. 2005) and in Bedford Basin, where *P. acuspes* represents a main part of the *Pseudocalanus* population (McLaren et al. 1989a).

#### 4.1.1 Vertical distribution

Vertical distribution is a result of physiological requirements, food availability and predator avoidance (Bollens and Frost 1989, Hattori and Saito 1997, Saito and Hattori 1997). In general, *Pseudocalanus* is found in the upper water layers of the sea (Minoda 1971, Afrikova 1975), though it is capable of living in very deep waters. Studies of vertical distribution in shallow, inshore waters provided insight into the physical, chemical and biological factors that control such a distribution (Corkett and McLaren 1978). In the Landsort deep (Northern Baltic Sea) *Pseudocalanus* sp. was most abundant at 50-100 m, just below the thermal minimum, absent above 30 m, where the temperature raised sharply, but present even in 300-400 m, where oxygen was absent (Ackefors 1966). Near Stockholm, *Pseudocalanus* sp. occurred always below the thermocline in spring and autumn (Ackefors 1969). In a semi-landlocked bay on the island of Split (Croatia) *Pseudocalanus* sp. (probably *elongatus*) occurred at the surface only in January and November, when the water temperature was below 13°C. In the Black Sea *P. elongatus* inhabits all depths in winter, while during summer they are found in greater depth of the water column (Vinogradov et al. 1985). It performs a pronounced diel vertical distribution and inhabits deeper layers during day time. In general, *Pseudocalanus* was observed to leave the surface by day, which could help in avoiding visual predators. However, this was not always a sufficient explanation for its migratory behaviour and it was suggested, that the role of diel migration is at times over-ridden by other factors (Corkett and McLaren 1978), such as the energy-bonus hypothesis, which states that vertical migration in thermally stratified waters might be advantageous to the migrating individual because of enhanced fecundity and conserving energy (McLaren 1963).

In the central Baltic Sea, *P. acuspes* showed a pronounced ontogenetic vertical distribution pattern during our investigation period between March 2002 and May 2003. Nauplii and youngest stages were distributed in the upper layers of the water column, while older stages inhabited intermediate waters. Adults concentrated near the halocline the whole year round, with females showing a clear descent deep below the halocline during times of highest reproduction in spring in both years (Renz and Hirche 2006, PUBLICATION I). As *Pseudocalanus* females carry an egg sac, nauplii have to perform a pronounced upward migration after hatching to reach the upper water layers, most likely resulting from the demand of suitable food in the euphotic zone. Older stages and adults, which are capable of using a diet from detritus and mikrozooplankton, favour inhabiting deeper layers with higher salinities (Renz and Hirche 2006, PUBLICATION I, Peters et al. 2006, PUBLICATION III).

A tendency for younger stages to occur nearer to the surface has been reported by several authors for a variety of places (e.g. Kraefft 1910, Marshall 1949, Ackefors 1969, Wiborg 1954, Hernroth and Ackefors 1979, Renz and Hirche 2006, PUBLICATION I). A descent of stages beginning with CIII was observed in Ogac Lake (Baffin Island, McLaren 1969). This downward migration of older stages was generally interpreted as a 'seeking' for colder waters despite a few findings of deeper distribution at higher food levels. The southern North Sea is a very

shallow area, characterised by strong vertical mixing. An ontogenetic vertical distribution of this species in the North Sea might therefore be excluded.

A number of arctic species are reported to perform seasonal vertical migrations in order to withstand unfavourable food conditions during winter. Several species of the Calanidae can rest in one or more of the older copepodite stages termed a copepodite diapause (Hirche 1998). If a generation is going to include a diapause, the specific stage or stages feed near the surface and accumulate a large mass of storage lipids as a reserve of organic matter and energy. Then they descend to a considerable depth and remain there during the resting phase (e.g. Hirche 1996, Miller 2004). Feeding usually does not take place, respiration is strongly suppressed and activity is nil. In the Norwegian Sea, Østvedt (1955) observed *Calanus finmarchicus* and *C. hyperboreus* to be almost absent from the upper 50 m from September to March and the majority of all stages were concentrated between 1000 and 2000 m. Overwintering *Pseudocalanus* sp. was found below 600 m (mostly 1000-1200 m), consisting almost of CV (Østvedt 1955, Hansen 1969). Marshall (1949) described a descent of the major part of the *Pseudocalanus* population in Loch Striven (Scotland) after the end of June when overwintering stages accumulated. Corkett and McLaren (1978) suggested that a seasonal descent of 'resting' overwintering stages may be the rule among *Pseudocalanus* populations in temperate waters to conserve their energy stores in the cool depths.

In our investigation period we did not observe a seasonal descent of overwintering stages when food conditions became adverse in either the Baltic Sea species *P. acuspes* or in the North Sea species *P. elongatus*. (Renz and Hirche 2006, PUBLICATION I and manuscript). Both study areas are located in shallow shelf seas with maximum depths of ca. 45 m and 100 m in the in the Central Baltic and southern North Sea, respectively. The low depth together with a homogeneous temperature distribution in the water column during winter months might therefore prevent even the arctic relict *P. acuspes* from a seasonal descent during winter.

The characteristic vertical distribution pattern of *P. acuspes* in the Baltic Sea seems to be mainly governed by physiological requirements, as all stages avoided the region of the thermocline from May onwards (Renz and Hirche 2006, PUBLICATION I). They were thus restricted from direct utilisation of food in the euphotic zone (Renz and Hirche 2006, PUBLICATION I and II, Peters et al. 2006, PUBLICATION III). This specific vertical distribution pattern is suggested to put strong constraints on the life cycle of *P. acuspes* and ends in strong limitation of growth processes, which will be discussed in the next paragraphs.

## 4.2 Life cycle

The interaction of planktonic population dynamics with ocean circulation can create enormously complex patterns in abundance. Even an ocean at rest could accommodate significant spatial and temporal inhomogeneity through geographic variations in environmental parameters, time-dependent forcing mechanisms and organism behaviour (McGillicuddy et al. 1998). In the North Sea and the Baltic Sea, both *Pseudocalanus* species occurred in the zooplankton in high numbers year round (Renz and Hirche 2006, PUBLICATION I and manuscript) with a maximum

cumulative abundance in April/May in the Baltic Sea and between June and August in the North Sea resulting from high concentrations of nauplii. While in the Baltic Sea the high nauplii abundance directly followed the early reproductive peak in April, maximum nauplii abundance in the North Sea occurred 2 months after the reproductive peak and coincided with highest concentration of adults (Renz and Hirche 2006, PUBLICATION I, manuscript). Stage structure in the Baltic Sea was characterised by a slow shift from nauplii dominating in spring to younger copepodite stages in summer. Older stages showed highest proportion from autumn onwards, usually indicating an annual life cycle (Renz and Hirche 2006, PUBLICATION I).

In general, *Pseudocalanus* is characterised by females carrying masses of attached eggs and may produce numerous broods of young. The productive season varies; however, the copepods suspend development during the winter in polar regions and may enter resting stages during the summer (Corkett and McLaren 1978), with overwintering usually taking place as CIV or CV. The resting phase is usually preceded by an accumulation of storage lipids, in order to survive periods of food shortage. During the following winter-spring transition, when biotic and abiotic conditions become favourable, the overwintering stages start maturing and produce a new generation. This overwintering strategy of *Pseudocalanus* differs to the strategy of many other neritic calanoid copepod species in temperate regions. They produce resting eggs which sink to the bottom and the first generation in the next year develops from these resting eggs (Marcus 1984). In the Baltic Sea, the life cycle of *P. acuspes* largely resembled those of high latitude species. Most of the population was in a resting stage for several months of the year and only a minor part of the population was growing and maturing at rates determined by prevailing temperatures (Renz and Hirche 2006, PUBLICATION I and II, Peters et al. 2006, PUBLICATION III). A similar life cycle strategy of *P. acuspes* was also observed in Bedford Basin, Nova Scotia by McLaren et al. (1989a), who described this basically annual life cycle to be clearly designed for life at high latitudes. He related this life cycle in Bedford Basin to the ensuring of maturation of the bulk of the population during the spring bloom at high latitudes rather than to food shortage. However, there is evidence that life cycle of *P. acuspes* in the Baltic Sea might result more from physiological constraints put on the species living in the deeper part of the central Baltic Sea. As a result of low salinity in the upper part of the water column adult stages remain at the halocline where they experience more suitable salinity conditions. In return, they have to hazard the consequences of food shortage from May on, when the thermocline develops and they are restricted from direct utilisation of food from the euphotic zone (Renz and Hirche 2006, PUBLICATION I and II, Peters et al. 2006, PUBLICATION III). However, a potential interposition of minor summer generations can not be excluded. Furthermore, first maturing females in particular might produce nauplii, which benefit from high food concentration before the thermocline develops and largely prevents the sinking of material into intermediate waters. These individuals might undergo a more rapid development, determined by prevailing temperatures and produce a first generation. We performed first experiments on development in May and might have missed a minor spring generation which was not detectable in the stage structure because of high nauplii abundances.

The North Sea congener *P. elongatus* exhibits a completely different life cycle. As a result of warmer temperatures during summer, higher salinity and a suitable food environment between March and August at least 3-4 generations in the German Bight were distinguished by length differences of females over the course of the year, before accumulation of overwintering stages took place (Renz and Hirche 2006, manuscript). This is similar to the maximal 3 generations in the Southern Bight of the North Sea (Bossicart 1980), but with fewer generations, if food requirements are not met. Evans (1977) separated 4-6 generations of *P. elongatus* in Northumberland coastal waters (North Sea). As in the Baltic Sea, the *Pseudocalanus* population in the North Sea showed high abundances of CIV and CV in autumn, indicating them as overwintering stages. However, the restricted investigation period from February to October in the North Sea and the lack of nauplii in September and October did not allow for direct comparison of stage structure during winter months (Renz and Hirche 2006, PUBLICATION I, manuscript).

### 4.3 Population dynamics

#### 4.3.1 Reproduction

*Pseudocalanus elongatus* and *P. acuspes* exhibit significant differences in their reproductive strategies. Both species showed highest reproduction in April/May, when the food concentration was at its upper level in the study areas. However, as a result of larger clutches and a higher proportion of spawning females, maximum EPR of *P. elongatus* was about three times higher than maximum EPR of *P. acuspes* in the Baltic Sea (Renz and Hirche 2006, PUBLICATION II, manuscript). Within the calanoid copepods there exist relationships between brood volume and body volume (Kiørboe and Sabatini 1995). Corkett and McLaren (1978) showed clutch size of *Pseudocalanus* to be a function of female prosome length. We did observe a positive relationship between prosome length of females and clutch size for *Pseudocalanus* spp. at both study sites. However, this relationship was more pronounced for *P. elongatus* in the North Sea than for *P. acuspes* in the Baltic Sea (Renz and Hirche 2006, PUBLICATION II, manuscript). Temperature has a strong influence on EPR by affecting clutch size via female length and embryonic duration (Lee et al. 2003). The generally lower temperatures inhabited in intermediate and deep waters of the Baltic Sea might therefore be one reason for lower EPR in *P. acuspes*, despite the fact that females of *P. elongatus* were generally smaller compared to *P. acuspes*. A relationship of larger clutches in larger females was more pronounced in *P. elongatus*, who carried up to 41 eggs, while a maximum of 25 eggs was found for *P. acuspes* (Renz and Hirche 2006, PUBLICATION II, manuscript).

Egg production of *Pseudocalanus* is thought to be independent of food concentration above approx.  $100 \mu\text{g C l}^{-1}$  (Corkett and McLaren 1978), or  $\sim 2 \text{ mg Chl m}^{-3}$  (Bunker and Hirst 2004). While in the Baltic Sea this high concentration of food for *P. acuspes* was only available during the phytoplankton bloom in April (Beusekom et al. submitted), before females descended below the halocline, females of *P. elongatus* could utilise relatively high food concentrations in the North Sea between March and August (Mengedoht et al. in preparation) at most stations.

*Pseudocalanus* exhibits a primarily herbivorous feeding behaviour (e.g. Schnack 1975, Corkett and McLaren 1978, Fraser et al. 1989, Cotonnec et al. 2001), though several studies also suggest a more omnivorous feeding mode (Båmstedt et al. 1990, Norrbin et al. 1990). Sinking algae, detritus or microzooplankton are probably the only available food sources for deep living *P. acuspes* females. Indeed a strong coherence between the 18:1(n-9) fatty acid in the seston lipids and the occurrence of ciliates emphasised the importance of ciliates in the diet of *P. acuspes* in the Baltic Sea (Peters et al. 2006, PUBLICATION III). As indicated by changes in the amounts of fatty acid markers, other food sources varied over the year, suggesting an opportunistic feeding behaviour for this species in the highly stratified environment of the Baltic Sea. Due to high vertical mixing and high concentrations of chlorophyll in the water column (Mengedocht et al. in preparation), the southern North Sea *P. elongatus* was not reliant on alternative food resources (Renz and Hirche, manuscript).

#### 4.3.2 Development and growth

Low temperatures, restricted food availability and the low salinity in the Baltic Sea probably put strong constraints on the growth of all stages of *P. acuspes*. Stage durations measured in late spring and early summer exceeded stage durations derived from temperature-growth relationships from the literature by a factor of 3-4 (McLaren et al. 1989b, Eiane and Ohman 2004, Renz and Hirche 2006, PUBLICATION II). In contrast, stage durations measured for *P. elongatus* in the southern North Sea were within the range of those reported from laboratory and field studies in the literature (e.g. Paffenhöfer and Harris 1976, McLaren et al. 1989b, Klein Breteler et al. 1995, Koski et al. 1998, Renz and Hirche, manuscript).

Weight-specific growth is a key parameter, as it is a descriptor of the rate at which copepods process material (Hirst and Bunker 2003). Only a small number of species have been studied in detail, as methods for measuring growth are time consuming. Hirst and Bunker (2003), compiling a global data set of copepod in situ weight specific growth, stated temperature, quality and quantity of food to be clearly the variables, accounting for growth variability in copepod natural populations. However, they found weight-specific growth of juvenile sac spawners to be less dependent on food than growth of adults. In contrast to Ohman (1985) who stated growth of *Pseudocalanus* generally to be food satiated, we found evidence that growth of *P. acuspes* in the highly stratified environment of the central Baltic Sea is food limited during most of the year (Renz and Hirche 2006, PUBLICATION II). Furthermore, low growth rates of juveniles due to reduced food availability in intermediate waters in the central Baltic Sea might be amplified by the low summer temperature in intermediate waters in this region, when compared to the southern North Sea. In the later summer temperatures were almost twice as high leading, together with a suitable food environment, to up to 6 times higher weight-specific growth rates for copepodids (Renz and Hirche 2006, PUBLICATION II, manuscript). Many authors have stated that rates of specific egg production closely approximate the specific growth rates of earlier developmental stages (e.g. Corkett and McLaren 1978, Sekiguchi et al. 1980, Berggreen et al. 1988). In the Baltic Sea in particular the SEPR of *P. acuspes* females showed a

pronounced seasonal trend with highest rates in April 2002 and April and May 2003 while highest growth rates of copepodite stages were reached over the summer months (Renz and Hirche 2006, PUBLICATION II). In the North Sea the growth rates of younger copepodids exceeded growth rates of females (Renz and Hirche, manuscript).

#### 4.3.3 Secondary production

The estimation of copepod secondary production is one of the most important aims in marine ecology, elucidating the amount of energy, which is transferred within communities and ecosystems and provided for higher trophic levels. In addition it gives urgently needed information for the realistic simulation of prey fields for commercially important fish species and thus the modelling and management of aquatic resources. The secondary production of *Pseudocalanus* spp. plays a key role in the trophic ecology of northern temperate and subarctic waters (Corkett and McLaren 1978). Estimated secondary production of this genus is often much greater than that for large copepods such as *Calanus* (e.g. Davis 1984a). In the Gulf of Alaska, average annual production of *Pseudocalanus mimus* and *P. newmani* was estimated to be  $>700 \mu\text{g C m}^{-2}$ , seven times greater than in *Calanus* spp. (Napp et al. 2005). In the Skagerrak (North Sea), *P. elongatus* accounted for 20 % of total copepod secondary production with values up to  $24 \text{ mg C m}^{-2}$ . Secondary production of *P. elongatus* in the North Sea was up to  $110 \text{ mg C m}^{-2}$  and therefore 11 times higher than secondary production of *P. acuspes* in the Baltic Sea ( $9.1 \text{ mg C m}^{-2}$ ) (Renz and Hirche 2006, PUBLICATION II, manuscript). Maximum biomass of *P. acuspes* was comparable to max. biomass of *P. elongatus* particularly in 2003 after the MBI. However, both study areas showed a high variability in biomass distribution. The higher secondary production of *P. elongatus* mainly resulted from faster development and higher growth rates of copepodids (Renz and Hirche 2006, PUBLICATION II, manuscript). Several authors stated secondary production of *Pseudocalanus* to be more controlled by temperature than by food (Corkett and McLaren 1978, Davis 1984b, Frost 1985, Klein Breteler et al. 1995, Hirst and Lampitt 1998, Hirst and Bunker 2003). The higher temperatures up to  $14^\circ\text{C}$  below the thermocline in August in the North Sea when compared to the  $9\text{-}10^\circ\text{C}$  in the central Baltic Sea partly explain the higher growth rates of *P. elongatus*. However, even when applying temperature-growth relationships from the literature, growth rates of *P. acuspes* were 2-3 times lower than growth rates of *P. elongatus*. A food limitation of copepodids additionally diminishes secondary production of *P. acuspes* in the stratified environment of the Baltic Sea (Renz and Hirche 2006, PUBLICATION II).

#### 4.3.4 Mortality

*Pseudocalanus* is subject to predation by a variety of other animals, including fish, chaetognaths, ctenophores and omnivorous copepods (e.g. Davis 1984b, Sullivan and Meise 1996, Sell et al. 2001). Omnivorous copepods may be predators on copepod eggs and nauplii, though data on feeding rates or selectivity are scarce. Sell et al. (2001) generated functional response curves for the omnivorous copepods *Metridia lucens*, *Centropages typicus* and

*Temora longicornis* feeding on eggs and nauplii of *Calanus finmarchicus* and *Pseudocalanus* spp. in shipboard predation trials. Though they found *Calanus* to be more vulnerable to predation by omnivorous copepods than *Pseudocalanus*, they suggested predation to theoretically have a significant effect on populations of *Pseudocalanus*, as egg carrying species generally have lower production rates than broadcast spawners (Kjørboe and Sabatini 1995). In the Baltic Sea, nauplii of *P. acuspes* perform a distinct upward migration after hatching and are mainly distributed in the upper 30 m of the water column, where they share their habitat with omnivorous species such as *Temora longicornis*. They might be subject to predation especially during times when the establishment of the thermocline borders the direct availability of food from the euphotic zone. In the North Sea, copepods of the genus *Centropages*, *Acartia* and *Temora* showed a cannibalistic feeding behaviour when eggs and nauplii of either genus were offered in laboratory experiments (Wesche et al. in preparation).

In the central Baltic Sea, only local impact of invertebrate predators is expected. Barz (2006) found swarms of mysids and chaetognaths in higher concentrations sporadic in the marginal areas of the Bornholm Basin, suggesting only low predatory impact on the zooplankton. The occasionally occurring scyphomedusae of *Aurelia aurita* inhabit mainly the upper 20 m above the thermocline during summer and do not overlap with the bulk of the *P. acuspes* population (Barz 2006). In the North Sea, predation on *P. elongatus* might play a more important role in the recruitment of *Pseudocalanus* due to the high number of invertebrate predators. The chaetognath *Sagitta setosa* removed 26-48% d<sup>-1</sup> of the *Pseudocalanus* sp. population in the Gullmar Fjord (Kattegat, Sweden) (Tønnesson and Tiselius 2005). A model developed for Georges Bank suggested the summer decline of the *Pseudocalanus* population to be due to the combined activity of carnivorous copepods and other invertebrate predators (Davis 1984a).

In both study areas the feeding of fish populations on different stages of *Pseudocalanus* spp. plays an important role in the *Pseudocalanus* population dynamics. Predation of adult sprat and herring on *P. acuspes* in the central Baltic Sea is suggested to largely affect its life cycle during the main reproductive period in April and May, when herring return from their spawning areas and both planktivorous predators, herring and sprat, are reported to prey on older stages of *P. acuspes* in the region of the halocline (Möllmann and Köster 1999, 2002, Renz and Hirche 2006, PUBLICATION I). In late winter and spring, egg production of *Pseudocalanus* spp. is important for establishing prey levels of recently spawned fish larvae, such as cod, in the central Baltic Sea (Hinrichsen et al. 2002) as well as in the North Sea, where the group of *Pseudocalanus/Paracalanus* can comprise up to 50% of the stomach content of sprat larvae (Dickmann 2005). The key role of *Pseudocalanus* spp. in the stock dynamics of commercially important fish is especially emphasised in the Baltic Sea (Möllmann et al. 2003, Hinrichsen et al. 2003), while the high copepod diversity of the North Sea might provide alternative food resources for predators feeding on copepods.

Parasitism is commonly observed in copepods of the genus *Pseudocalanus*. While the dinoflagellate *Blastodinium* sp. was observed to parasitise the gonads of *Pseudocalanus* leading to immature females (Sewell 1951), the dinoflagellate *Dissodinium pseudocalani* is an

ectoparasite, feeding on the eggs of *Pseudocalanus* (Drebes 1972). Further parasites like trematodes and nematodes were often observed to parasitize *Pseudocalanus*, though they do not necessarily have detrimental effects.

#### **4.4 Climate variability and *Pseudocalanus* spp.**

Synchronous ecological regime shifts occurred in the North Sea and the central Baltic Sea in the late 1980s (Alheit et al. 2005). These regime shifts are thought to be a response to the North Atlantic Oscillation (NAO), the dominant mode of climate variability in the North Atlantic region. It ranges from central North America to Europe and into Northern Asia. The NAO is a large scale seesaw in atmospheric mass between the subtropical high and the polar low. The corresponding index varies from year to year, but also exhibits a tendency to remain in one phase for intervals lasting several years (<http://www.ldeo.columbia.edu/NAO/>). High indices of the NAO are associated with strong westerly winds and result in mild winters and milder temperatures in Northern Europe (Hurrell 1995). The impact of the NAO on the marine ecosystems proceeds mainly through the heat flux exchange between the atmosphere and the ocean, which controls the temperature in the upper mixed layer. The variability in the winter NAO is mirrored by surface temperatures in the North Sea and the Intermediate Winter Water in the central Baltic Sea.

The ecological regime shift in the North Sea in the late 1980s affected all trophic levels from phytoplankton to fish (Reid and Edwards 2001). Enhanced inflows of warm oceanic water from the Atlantic into the northern North Sea (Edwards et al. 2001) were generated by increased westerly winds, which were highly correlated with the NAO (Reid et al. 2003). During the same time, the zooplankton community of the North Sea changed considerably, with high positive anomalies in the abundance of *Calanus helgolandicus* and negative anomalies of *Calanus finmarchicus*. A general increase of warm water species was accompanied by a decrease of cold water species (Beaugrand 2003, 2004). Greve et al. (1996) reported an initially increasing biomass of the *Paracalanus/Pseudocalanus* in the beginning of the 1980s followed by a decrease of this combined group between 1988 and 1994. Unfortunately, they did not distinguish between species and a direct effect on *Pseudocalanus elongatus* alone can not be verified. However, climate related changes were not only detected in stock size of copepod species but also in changing seasonal cycles. The reproduction period of *P. elongatus* continuously decreased by 6 weeks during an observation period from 1948 to 1970 (Glover et al. 1972). During our study, mean annual abundance of *P. elongatus* in bongo net hauls with a comparable mesh size was in the lower range of the observed mean annual abundances of the *Pseudocalanus/Paracalanus* group at Helgoland Roads between 1988 and 1995 (Greve et al. 1996) but well in the range reported by previous studies of different locations in the North Sea (Lücke 1912, Krause and Trahms 1983, Krause 1995).

Rothschild (1998) demonstrated the co-occurrence of abundant cod and herring year-classes in the North Sea with either high abundances of *Calanus* or *Paracalanus/Pseudocalanus* suggesting that either of them to be an important item in the nutrition of commercially used fish

in the North Sea. Since about 1987, cod recruitment has been negatively affected Sea by a severe reduction of both quantity and quality of their larval food. Though there is no evidence that *Pseudocalanus elongatus* has a key role in the fish stock dynamics of the North Sea, cod survival largely depends on the abundance of calanoid copepods, which shows very low levels since the late 1980s.

In the central Baltic Sea, the long-term decreasing salinities, resulting from a reduction of high saline inflowing North Sea waters, increasing rainfall since the 1980s (Vuorinen et al. 1998) and a simultaneous increase in river runoff (Bergström and Carlsson 1994) were found to be related to the NAO (Hurrell 1995). During the same time, long-term dynamics of copepod species in the Baltic Sea were shown to largely depend on the hydrographic conditions (Ojaveer et al. 1998, Viitasalo 1992, Vuorinen and Ranta 1987, Vuorinen et al. 1998, Möllmann et al. 2000), controlled by climatic factors (Dippner et al. 2000, 2001, Hänninen et al. 2000). Especially the strong inter-annual fluctuations in the *P. acuspes* standing stock were attributed to the decreasing salinity in the deep basins of the central Baltic Sea (Dippner et al. 2000, Möllmann et al. 2003).

A number of subsequent inflows of warm and cold water from the North Sea were recorded between August 2002 and January/February 2003 (Feistel et al. 2003, Mohrholz et al. 2006). An exceptionally warm water inflow in August 2002 led to the highest temperatures ever observed in the halocline of the Bornholm Basin (Mohrholz et al. 2006). At the same time we observed elevated numbers of nauplii as a result of slightly increased reproduction (Renz and Hirche 2006, PUBLICATION I). The suggested temperature preferences of *P. acuspes* are usually below 13°C (Renz and Hirche 2006, PUBLICATION I) and the increased number of nauplii might therefore result from improved food conditions for females and nauplii, when a small bloom of diatoms occurred below the thermocline (van Beusekom et al. submitted). No increase in numbers of younger stages was observed during the following weeks. This indicates that food was not sufficient to maintain the growth of juveniles.

Möllmann et al. (2003) suggested that high salinities are especially important for *P. acuspes* reproduction and maturation in spring. The elevated abundance at central stations in the Bornholm Basin in April and May 2003 as compared to 2002 could therefore be related to the increased salinity level below the halocline after the MBI in the beginning of 2003. Renz and Hirche (2006, PUBLICATION I) discussed several mechanisms responsible for an increased biomass such as advection of *P. acuspes* populations from the western Baltic Sea or the increase of the habitat in the deep basins with more favourable conditions for reproduction due to higher salinity or oxygen levels. However, despite increased salinity in 2003, reproduction did not exceed the 2002 level, probably as a result of lower temperatures and increased development times of eggs, as egg bearing copepods do not produce a new clutch until nauplii from the old clutch have hatched. Suitable oxygen concentration after the inflow might further increase survivorship of nauplii and explain, together with elevated numbers of adult stages at several stations, the increased nauplii abundance. However, an effect of improved living conditions for younger copepodite stages was expected only with some delay after our sampling

period. The generally decreasing biomass of *P. acuspes* in the central Baltic Sea is thought to largely affect the fish stock dynamics of commercially important planktivorous fish. Voss (2002) showed cod larvae significantly selecting all development stages of *Pseudocalanus* sp. during May and several authors have found *Pseudocalanus* to be an important item for larval cod (Kane 1984, McLaren and Avendaño 1995), determining their growth and survival.

High survival of Baltic cod larvae is therefore strongly dependent on the occurrence of *P. acuspes*

The decreasing recruitment success of Baltic cod, however, was not only linked to the decreasing biomass level of *P. acuspes* (Jarre-Teichmann et al. 2000, Köster et al. 2001) but also to the decreasing salinity in the Baltic Sea. The consequential decrease of predation pressure on sprat by cod, led to a shift from a cod dominated system to a sprat dominated system, which enlarged the predation pressure on *P. acuspes* by sprat. A number of studies indicated the outstanding importance of *Pseudocalanus* sp. for nutrition of sprat (Möllmann and Köster 1999, 2002) and Baltic herring (Möllmann et al. 2003). Reduced growth of herring in the Baltic Sea was explained by declining abundances of *Pseudocalanus* sp. (Möllmann et al. 2003), with the amount of *Pseudocalanus* sp. available to individual herring in spring to be a key factor leading to decreasing herring growth.

## 5 Conclusions

The significance of the present study is that knowledge of the population dynamics (including reproductive processes and growth characteristics) of ecologically important species is essential to understand the functioning of marine ecosystems. *Pseudocalanus* spp. is often a highly abundant member of the zooplankton fauna in the northern hemisphere and plays a critical role in the diet of larval and adult planktivorous commercially used fish. Unless the factors controlling population dynamics of key species are not fully understood, an understanding of the dynamics of productive and commercially important ecosystems remains incomplete. The results of this study show that the vertical distribution of *P. acuspes* in the Baltic Sea is closely determined by temperature and salinity. Therefore any changes in hydrographic conditions might largely influence the survival of the species in this area. The comparison of the population dynamics of *P. acuspes* from the central Baltic Sea and its congener *P. elongatus* from the North Sea revealed extensive differences in reproduction and development. The notably extremely slow development of *P. acuspes* due to restricted food availability, lower temperatures and probably low salinity shows that earlier studies on population dynamics of the Baltic Sea *P. acuspes* species might have failed when using temperature-growth relationships for calculating secondary production in order to describe prey fields for fish. This emphasises the importance of careful identification and studies of key species for an understanding of their role in the marine ecosystem.



## 6 Publications

### PUBLICATION I

**Renz J and Hirche H-J (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Mar Biol 148: 567-580, DOI 10.1007/s00227-005-0103-5**

The initial idea originates from the co-author and myself. Sampling, analysing and interpretation of the data were done by myself. I wrote the manuscript, which was improved by the co-author.

### PUBLICATION II

**Renz J, Peters J, Hirche H-J (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: II. Reproduction, growth and secondary production. Mar Biol submitted**

The initial idea originates from the co-author and myself. Sampling, analysing and interpretation of the data were done by myself. I wrote the manuscript, which was improved by the co-authors.

### PUBLICATION III

**Peters J, Renz J, van Beusekom J, Boersma M, Hagen W (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin) – evidence from lipid composition. Mar Biol DOI 10.1007/s00227-006-0290-8**

The initial idea originates from the first and the fifth author. I conducted experiments on egg production, provided length measurements and helped interpreting the data.

### MANUSCRIPT

**Renz J and Hirche H-J Life cycle and population dynamics of *Pseudocalanus elongatus* Boeck in the southern North Sea. Manuscript**

The initial idea originates from the co-author and myself. Sampling, analysing and interpretation of the data were done by myself. I wrote the manuscript, which was improved by the co-author.

### Further publications

**Renz J, Peters J, Hirche H-J, Hagen W (2006) Does the calanoid copepod *Pseudocalanus acuspes* retain an arctic life cycle in the Central Baltic Sea? GLOBEC International Newsletter 12 (1): 71-73**

The initial idea originates from the second author and myself. Sampling, analysing and interpretation of the data were done by the second author and myself, who also wrote the manuscript, which was improved by the co-authors.

**Renz J, Hirche H-J (2004) Life cycle of *Pseudocalanus acuspes* in the Central Baltic Sea. ICES CM L:20**

The initial idea originates from the co-author and myself. Sampling, analysing and interpretation of the data were done by myself. I wrote the manuscript, which was improved by the co-author.

**Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution**

Jasmin Renz and Hans-Jürgen Hirche

**Marine Biology, 2006**

With kind permission of Springer Science and Business Media



Jasmin Renz · Hans-Jürgen Hirche

## Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution

Received: 7 June 2005 / Accepted: 15 August 2005 / Published online: 8 October 2005  
© Springer-Verlag 2005

**Abstract** The seasonal and spatial distribution of *Pseudocalanus acuspes* in the Bornholm Basin (Central Baltic Sea) was studied on 16 cruises between March 2002 and May 2003 from stratified (10 m) multinet samples. The highest abundances were reached in May 2002 and April 2003 ( $618 \times 10^3$  and  $869 \times 10^3$  ind.  $m^{-2}$ , respectively). Ontogenetic vertical distribution was stage specific with differences of mean annual weighted mean depth  $> 30$  m between nauplii and males; it followed closely the hydrography which was characterized by a permanent halocline and a summer thermocline. The vertical distribution showed a positive correlation with salinity especially in the older developmental stages; the relationship to temperature was negative in the nauplii and copepodite stage I (CI). Most of the stages performed a seasonal migration. The consequences of the vertical distribution patterns in relation to the effects of climate and predation are discussed. A stage shift from nauplii in April/May to CIV and CV as overwintering stages indicated slow seasonal development. However, nauplii were observed all the year round, and the resulting stage structure did not allow to distinguish generations. Changes in the prosome length of females seemed to be related to the advection of water masses with different temperatures rather than to different generations. It could not be clarified whether the strong increase of nauplii and adults after an inflow event of cold, saline North Sea water in the beginning of 2003 was a result of advection or improvement in habitat conditions.

### Introduction

Copepods of the genus *Pseudocalanus* often dominate the marine zooplankton communities of the northern hemisphere (Corkett and McLaren 1978; Conover and Siferd 1993; Kane 1993; Richter 1995). They are important grazers and prey for many commercially used fish (Mauchline 1998). In the zooplankton community of the Central Baltic Sea, *Pseudocalanus acuspes* is a key species. In earlier publications often called *P. elongatus* (e.g., Möllmann and Köster 1999; Walve and Larsson 1999; Möllmann et al. 2000, 2003; Dippner et al. 2001; Kornilovs et al. 2001; Viitasalo et al. 2001; Hinrichsen et al. 2002, 2003; Möllmann and Köster 2002), *P. minutus* (e.g., Dahmen 1995) or *P. minutus elongatus* (e.g., Hernroth 1985), (Bucklin et al. 2003; Grabbert et al., in preparation) identified mainly *P. acuspes*. Below we refer to earlier Baltic Sea references as *Pseudocalanus* sp.; in our own data set we call the species *P. acuspes*. It serves as a major food organism not only for many larval fish (Hinrichsen et al. 2002; Möllmann et al. 2003), but also for adult pelagic planktivorous fish such as sprat and herring (Flinkman et al. 1992; Möllmann and Köster 1999, 2002). Particularly, cod larvae were found to actively select older developmental stages of *Pseudocalanus* sp. (Voss et al. 2003).

*Pseudocalanus acuspes* is an inhabitant of the North Atlantic (Frost 1989), Norwegian fjords (Norrbin 1996), and Arctic and sub-Arctic seas (Siferd and Conover 1992; Runge and Ingram 1991). As in the North Sea the congener *P. elongatus* (Frost 1989; Bucklin et al. 2003) is the dominant species, there seems to be a gap between the North Atlantic and the Baltic Sea populations, suggesting it is part of the Baltic Sea glacial relict fauna together with several other species (e.g., Ojaveer et al. 1998; Kontula and Väinölä 2003). As in the brackish water of the Baltic Sea this marine species should live under marginal conditions, a high affinity to more saline waters is not surprising. Thus Hernroth and Ackefors (1979) and Hernroth (1985) observed especially older

Communicated by O. Kinne, Oldendorf/Luhe

J. Renz (✉) · H.-J. Hirche  
Alfred Wegener Institute for Polar and Marine Research,  
PO Box 120161, 27515 Bremerhaven, Germany  
E-mail: jrenz@awi-bremerhaven.de  
Tel.: +49-471-48311042  
Fax: +49-471-48311918

copepodite stages in deeper layers with higher salinity. In the Central Baltic Sea a permanent halocline restricts the water exchange between the bottom water and the surface layer (Launiainen et al. 1987). Hydrographic conditions are strongly dependent on the renewal of the bottom water through inflowing high saline and oxygenated water masses from the North Sea. This phenomenon occurs relatively rarely and is connected to the mean atmospheric circulation pattern (Matthäus and Franck 1992; Matthäus and Schinke 1994). Time series data for the biomass of *Pseudocalanus* sp. from the Central Baltic Sea showed large interannual variability with a positive relationship to salinity. Thus Behrends (1996), Ojaveer et al. (1998) and Möllmann et al. (2000) observed low abundances in years with low salinities. Vuorinen et al. (2003) compared biomass data and hydrographic parameters between the 1960s and 1992 and found also a relationship between abundance of *Pseudocalanus* sp. and salinity. More recently also top-down processes like predation by various species of fish larvae and fish were considered to be important controls for the *Pseudocalanus* sp. population (Möllmann and Köster 2002). As a result of the importance of this species in the pelagic food chain of the Central Baltic Sea and its sensitivity to climate, small hydrographic changes may strongly affect its predators (Möllmann and Köster 1999, 2002).

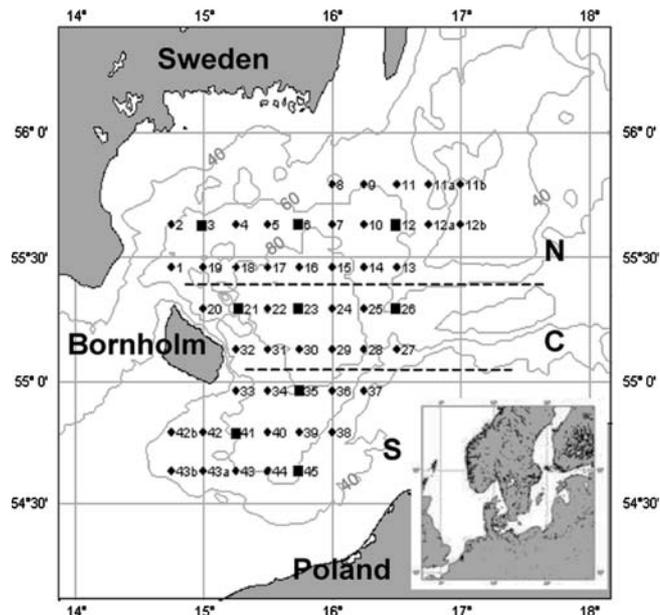
The understanding of the relationship between physical forcing and the population dynamics of *P. acuspes* requires a detailed knowledge of its vertical distribution, physiological requirements and life cycle strategy. However, its life cycle has never been described in detail in respect to the hydrographic conditions in the Central Baltic Sea. Hernroth and Ackefors (1979) provided an overview, but vertical resolution was low (25–50 m) and only one station was studied in the Bornholm Basin for 3–7 times per year.

Here we used data from a high-resolution annual time series collected in the Bornholm Basin of the Central Baltic Sea from March 2002 to May 2003 during German GLOBEC (Global Ocean Ecosystem Dynamics) to describe the seasonal and spatial abundance, development and vertical distribution of *P. acuspes* in relation to hydrographic conditions. As our study covered the transition period from a long stagnation beginning in 1993 to several intrusions of North Sea water during the summer and fall and the inflow of cold, saline North Sea water in January 2003 (Feistel et al. 2004) we were also able to study the effect of changing hydrography on the vertical distribution of *P. acuspes*.

## Materials and methods

### Sampling

The sampling of zooplankton was conducted on 16 cruises between March 2002 and May 2003 on a station grid in the Bornholm Basin, Central Baltic Sea (Fig. 1).



**Fig. 1** Study area in the Bornholm Basin, black dots sampling stations, black squares focus stations, northern (N), central (C) and southern (S) part of the basin

On every station double oblique bongo net hauls (mouth opening 0.2 m, mesh size 150  $\mu\text{m}$ , towing speed 3 kn) were taken vertically from above the bottom to the surface; on nine focus stations sampling was performed using a multinet (Hydrobios, 0.25  $\text{m}^2$  mouth opening, 50  $\mu\text{m}$  mesh size). The net was towed vertically with a 10 m resolution from the bottom to the surface. Furthermore at the focus stations samples were taken with a WP-2 net (UNESCO 1968, diameter mouth opening 0.57 m, mesh size 200  $\mu\text{m}$ , towing speed 0.2  $\text{m s}^{-1}$ ) which was towed vertically from above the bottom to the surface. All zooplankton samples were immediately preserved in a 4% borax-buffered formaldehyd–seawater solution. In the laboratory, subsamples of the multinet hauls were analyzed for developmental stages until at least 150 individuals of *Pseudocalanus* sp. were counted. Individuals were identified to nauplii, five copepodite stages and adult males (AM) and females (AF).

As an index of vertical distribution of different stages, weighted mean depths (WMD) (Bollens and Frost 1989) was calculated as:

$$WMD = \frac{\sum n_i d_i}{\sum n_i},$$

where  $n_i$  is the abundance (ind.  $\text{m}^{-3}$ ) in each depth stratum with the midpoint  $d_i$ .

While often a considerable diel vertical migration range is reported for the *Pseudocalanus* species (Corkett and McLaren 1978; Fortier et al. 2001; Hattori and Saito 1997; Runge and Ingram 1991) in the Baltic Sea during 24 h studies in different seasons the diel vertical migration of *Pseudocalanus* sp. was generally small (<10 m) (I.S. Hansen et al., personal communication). Furthermore 74% of our multinet samples were taken

between 5 a.m. and 9 p.m. Therefore our results on vertical distribution should not be affected too much by the time of sampling.

Concurrent to the zooplankton sampling, vertical profiles of temperature, salinity and oxygen (not available on every cruise and station) were recorded using a CTD-probe (SBE 911+, ME). As in March 2002 hydrographic measurements were not available for station 26, data from the nearby station 25 were used.

### Length measurement

For each month (except for December 2002 and June 2003), the prosome length of 30 females from either bongo-net or WP-2 net hauls from one northern, one central and one southern station, respectively (Fig. 1), was measured using a stereo microscope (Leica MZ 16) with a resolution of 80 $\times$ .

### Statistical analysis

To test for similarity between the vertical distribution of different stations, an overall distribution analysis of the WMD of all the focus stations was performed by non-metrical multi dimensional scaling (MDS) using the PRIMER package (Clarke 1993; Clarke and Warwick 1994). The method is based on the Bray-Curtis Similarity calculated between the WMD of each developmental stage, station and cruise. Stations where data for vertical resolution of at least one developmental stage were lacking were excluded, leading to an analysis of 110 from 130 stations. Based on the results of the MDS analysis vertical distribution was calculated for stations 23 (depth=96 m) and 26 (depth=62 m) (except in March 2002, when no sampling was conducted at station 26).

For the statistical analysis of vertical distribution in relation to hydrographic conditions, the population density of each developmental stage as a proportion of this stage per 10 m depth layer and station was used to calculate Spearman rank correlations between stage abundances and mean temperature and the salinity of each depth stratum.

Differences in prosome length between sampling dates were tested with one-way ANOVA using Tukey's honestly significant difference (HSD) as the post hoc test.

## Results

### Hydrography

During our study the hydrography of the Bornholm Basin was characterized by a permanent halocline at the deeper stations (Fig. 2b) and a summer thermocline (Fig. 2a, c). The halocline was located in 50–60 m in

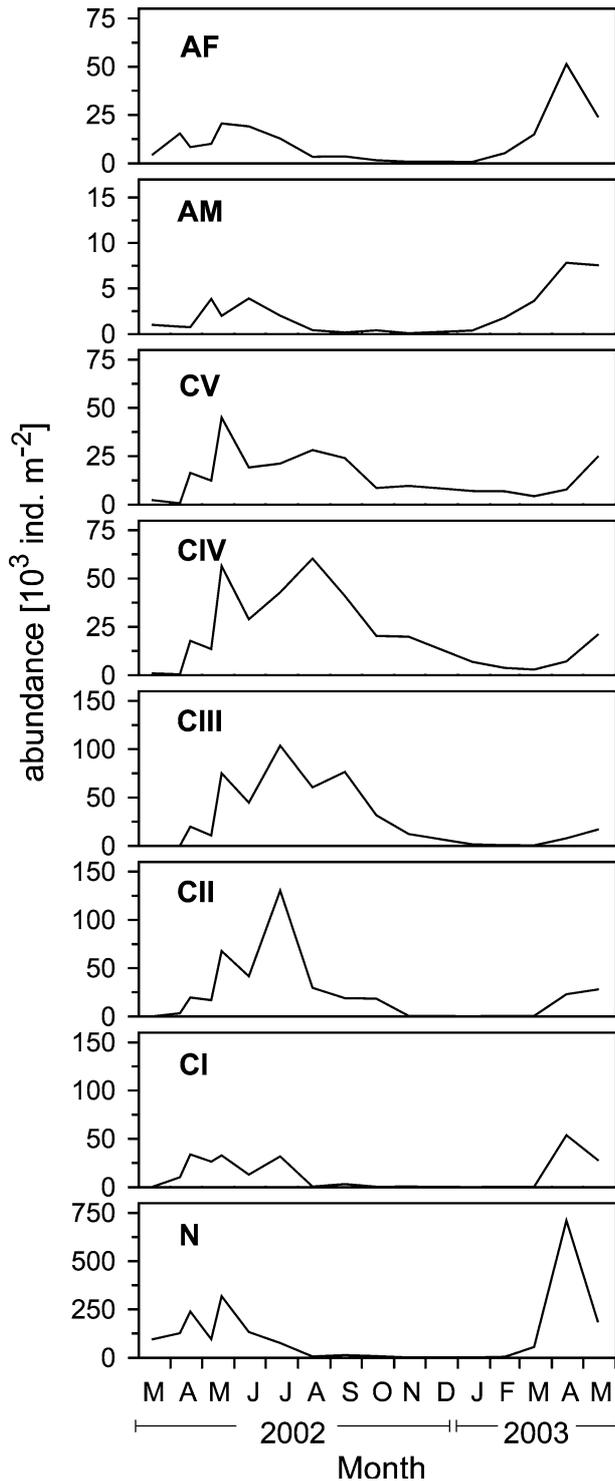
April 2002 and moved to 40–50 m in November 2002. During this period, salinity averaged 7 PSU above and 15 PSU below the halocline. At stations with 60 m or less water depth no halocline was observed (Fig. 2d). The temperature in the mixed layer was around 4°C and below the halocline 8°C in March 2002. In June 2002 a thermocline developed at a depth of 30 m; the temperature in the surface layer increased from 13°C in June to 17°C in July and 20°C in August, before cooling started. In November the thermocline was destroyed. In late summer a series of inflow events started, which terminated a long stagnation period in the Baltic Sea. For a detailed description we refer to Feistel et al. (2003a, b, 2004). Feistel et al. (2003b, 2004) distinguished two warm inflow periods. (1) The exceptionally warm summer inflow between August and October 2002, which showed up in the Bornholm Basin at 60 m (BB60); (2) a regular warm water inflow (BB90) between the end of October and the beginning of November 2002. The BB60 inflow caused the highest annual temperature (13.79°C) at the 60 m level on record in the Bornholm Basin (Feistel et al. 2004). Finally, in January 2003 the first major Baltic inflow (MBI) of cold, saline North Sea water after 7 years took place (Feistel et al. 2004), which caused a steep increase of salinity to 20 PSU from 30 m to the bottom. Thereafter the water cooled down to 2.5°C above the halocline and 4°C below the halocline and stayed low until May 2003. Consequently, the temperature was 1.5°C lower in the upper 40 m and 4°C lower in the rest of the water column than during the spring of the previous year (Fig. 2a). At the shallower station 26 the inflow caused only an increase of 2–3 PSU in the near-bottom layer.

The oxygen concentration above the halocline was always >7 ml l<sup>-1</sup> (Fig. 6a, b). In April and July 2002, water masses below 70 m at station 23 were characterized by an oxygen concentration <2 ml l<sup>-1</sup>. The MBI ventilated the deeper part of the Bornholm Basin; oxygen concentrations increased up to 6 ml l<sup>-1</sup> between the halocline and the bottom and remained high until April 2003. At station 26 oxygen concentration was always >5 ml l<sup>-1</sup> except in April and November 2002, when concentrations above the bottom decreased below 3 ml l<sup>-1</sup>.

### Abundance, stage-structure and horizontal distribution

The stock size of *P. acuspes* showed a large variability during the investigation period, with high abundance between April and September and much lower concentrations thereafter (Table 1). Maxima of 618 $\times$ 10<sup>3</sup> and 869 $\times$ 10<sup>3</sup> ind. m<sup>-2</sup> were recorded in May 2002 and April 2003, respectively, caused by large numbers of nauplii; the minimum stock size was 18 $\times$ 10<sup>3</sup> ind. m<sup>-2</sup> in January 2003. Abundance of nauplii in the study area ranged from 0.51 to 710 $\times$ 10<sup>3</sup> ind. m<sup>-2</sup> in January and April 2003, respectively, while abundance of copepodite stages varied between 4.6 and 361 $\times$ 10<sup>3</sup> ind. m<sup>-2</sup> in April and





**Fig. 3** Stage resolved abundance ( $10^3$  ind.  $m^{-2}$ ) of *Pseudocalanus acuspes* at station 23 in the Bornholm Basin, March 2002 to May 2003

#### Vertical distribution

In Fig. 6 (a, b) the vertical distribution of all the developmental stages of *P. acuspes* on stations 23 (96 m) and 26 (62 m) is presented for all cruises together with

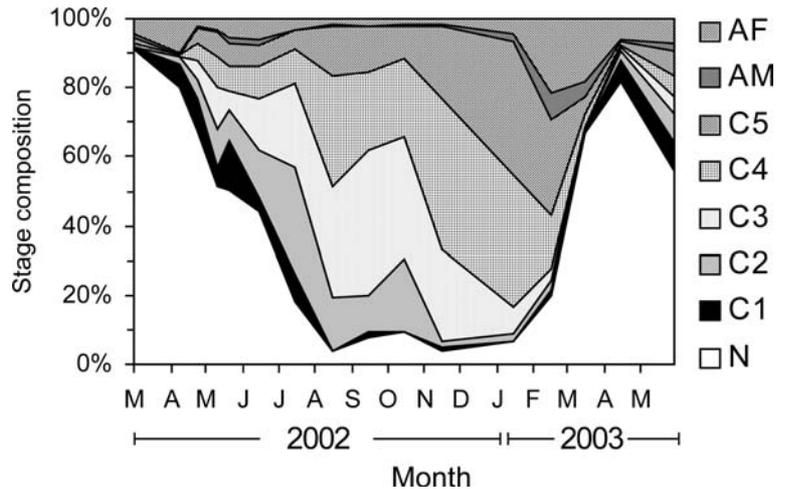
the profiles of environmental parameters. At station 23 in March 2002, most of the nauplii and CI were found in the upper 30 m. The highest proportion of CII was distributed a little deeper between 30 and 70 m, while CIII concentrated in 20–30 m with a small part of this stage distributed down to 80 m. During the same time, most of the CIV and CV were evenly distributed between 10 and 80 m, regardless of the halocline, while adult stages, inhabiting the depth range between 20 and 80 m, showed a slight concentration between 70 and 80 m. This pattern changed dramatically until the second half of April when CIII to CVI had all aggregated in waters below the halocline, where salinity was 15–16 PSU and oxygen concentration  $<0.15$  ml  $l^{-1}$ . During the following months a slight upward trend of these stages was observed and in June and July, CII–CIV inhabited the region in the upper part and above the halocline, while CV and adults were distributed exclusively in the upper part of the halocline. Between the end of May and August hardly any *P. acuspes* were found in the upper 20 m and  $>80\%$  of the nauplii and CI concentrated in the 20–40 m layer in June and July. From August to October nauplii, CI and most of the CII were distributed above the halocline. Most of the CIII–CV concentrated in 60–70 m in August while females, with a small part of the population even distributed in the upper 20 m, centered above and in the upper part of the halocline. In November the distribution of most stages had changed considerably. A high proportion of nauplii, CI and females were found in the upper 10 m, while males exclusively inhabited the layer between 50 and 60 m. CII–CV were evenly distributed over the mixed layer in contrast to the previous months, when they were centered around the halocline. By January and February, all nauplii to CV were distributed in the mixed layer and only half of the adult stages remained in the halocline. From March on, the situation was comparable to the previous year with older stages and adults showing a deeper distribution than nauplii and CI. In contrast to late April and May 2002, females inhabited a wider depth range in 2003.

At the shallower station 26 the vertical distribution of nauplii, CI and CII looked quite similar to station 23. As station 26 was only 60 m deep, the older stages CIII to CVI seemed to migrate as deep as possible until November and were concentrated below 40 m. In contrast, in the beginning of 2003, they inhabited the upper part of the water column, when the same stages at station 23 stayed mostly below 40 m.

#### Weighted mean depth

The representation of the seasonal vertical distribution patterns as WMD for each stage (Fig. 7) summarizes the ontogenetic vertical distribution patterns described before. The developmental stages preferred greater depths with increasing age, females lived close to CIV and/or CV, while males most of the time were found below all

**Fig. 4** Stage structure of *Pseudocalanus acuspes* at station 23 in the Bornholm Basin, March 2002 to May 2003



other stages at station 23. This trend was maintained during the whole investigation period and on all stations studied with only few exceptions. The differences in mean annual WMD were  $>30$  m between nauplii and males at station 23 and  $>23$  m at station 26. Seasonal changes in depth distribution were more pronounced in the older stages. The most remarkable feature was the vertical distribution of CIII to adults at station 23, which had reached their greatest depth in April 2002 and 2003. In contrast, some of the older stages were highest up between November and January.

#### Vertical distribution and environmental parameters

The results of the Spearman rank correlation analysis between the proportion of the eight developmental stages at the focus stations in all depth layers investigated, and hydrography, represented by temperature and salinity, are shown in Table 2. A significantly negative correlation ( $P < 0.05$ ) was found between all developmental stages and temperature, resulting from their distribution below the summer thermocline. The depth distribution of nauplii and CI showed a negative relation to salinity, reflecting their distribution above the halocline all the year round. However, the correlation was only significant for nauplii ( $P < 0.05$ ). Due to their deeper distribution, CII to CV and adult stages had a positive correlation to salinity ( $P < 0.05$ ). These results are underlined by the temperature and salinity range of each stage at its mean WMD compiled from all cruises (Table 3).

#### Vertical distribution and station depth

The application of the Bray-Curtis similarity index on the WMD of all focus stations for differences between stations revealed a high variability in WMD at stations shallower than 80 m (Fig. 8), while stations between 80 and 100 m showed a more consistent distribution. However, deeper and shallower stations could not be

clearly separated in the ordination plot. This result confirms the trend of the vertical distribution and the WMD of developmental stages presented for stations 23 and 26. Especially nauplii and younger copepodites were mainly distributed in the upper part of the water column above the halocline at both stations. In contrast, at station 23, older copepodites at stations  $>70$  m were found at the greatest depth possible. As the halocline was located at around 50 m, the older copepodites at the basin margins had to tolerate salinities below their preferences. The difference in WMD between stations with similar depth and salinity points to the existence of other triggers of depth distribution of older copepodites in addition to salinity.

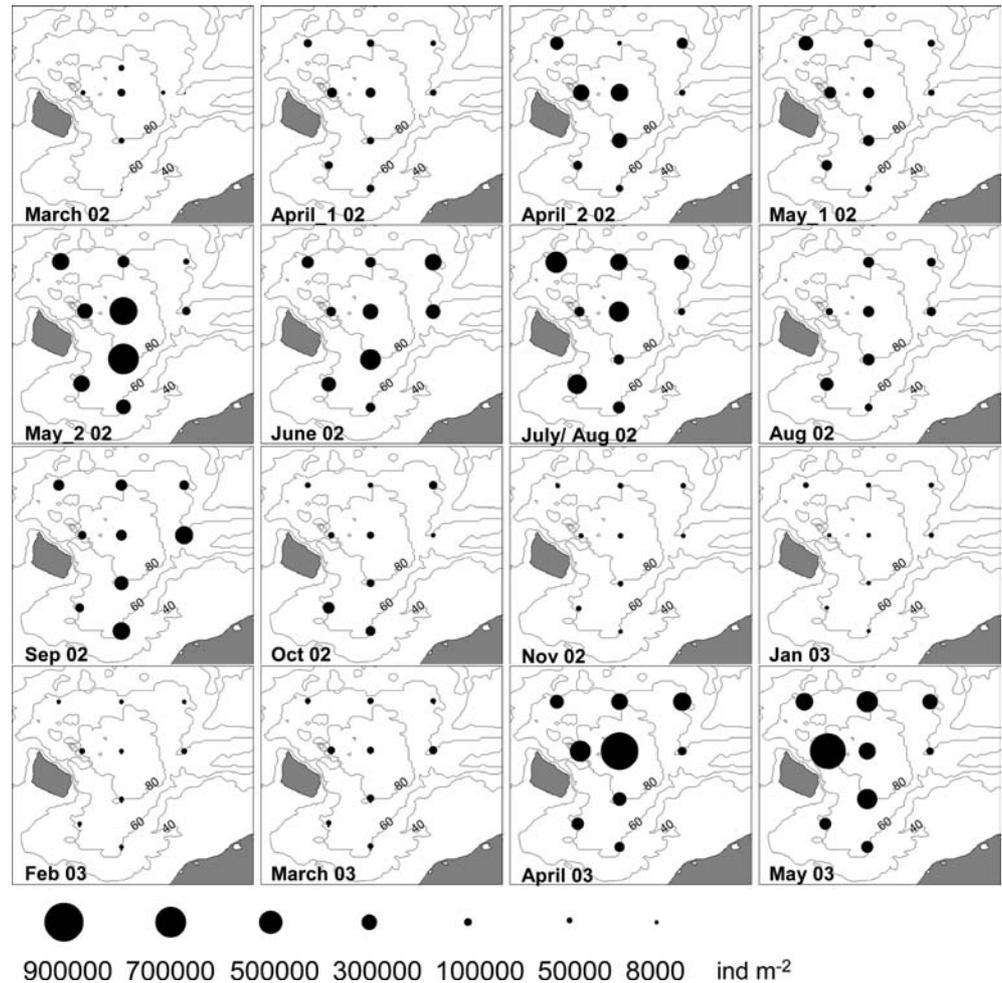
#### Prosome length

The mean prosome length of females varied between 0.870 mm in November 2002 and 0.976 mm in April 2003 (Fig. 9). Individual extremes ranged from a minimum of 0.702 mm in January and May 2003 to a maximum of 1.144 mm in May 2003. Three groups are distinguished during the study period connected by intermediate sizes, (1) from March to September 2002, (2) from October 2002 to January 2003 and (3) from February to July 2003. The statistical analysis of mean prosome length using one-way ANOVA showed significant differences ( $P < 0.05$ ) of mean length between sampling months. The post hoc test, comparing pairs of means, showed that the length of females from May 2002 and April to July 2003 was significantly larger ( $P < 0.05$ ) than over the rest of both years.

#### Discussion

Next to *Temora longicornis* and *Acartia* spp., *P. acuspes* is the most important copepod species of the Central Baltic Sea. During our study it contributed 22% to the total copepod abundance (Schulz et al., in preparation). Comparison of abundance data with previous studies is

**Fig. 5** Stage cumulative horizontal distribution (ind. m<sup>-2</sup>) in the study area, March 2002 to May 2003



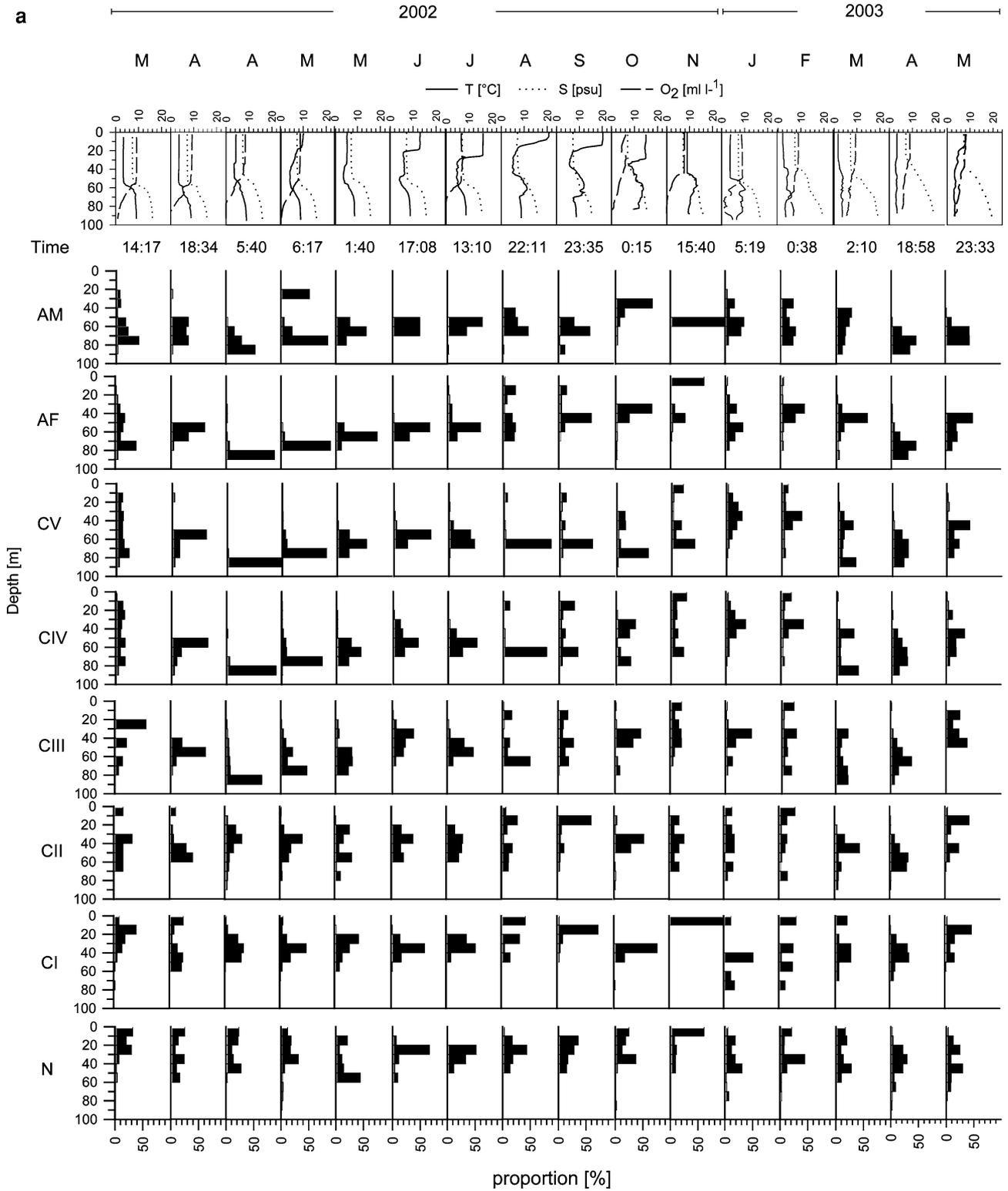
difficult due to the use of different mesh sizes, sampling depths and sampling locations. In addition, most data are presented as biomass pooled over stations, months or years. Thus direct comparison is only possible with studies by Hernroth and Ackefors (1979), who found maximum densities of up to  $800 \times 10^6$  nauplii m<sup>-2</sup> between 1968 and 1972, using a 160  $\mu$ m net at one station in the Bornholm Basin. Similar abundances ( $710 \times 10^6$  m<sup>-2</sup>) during our study were only reached in April 2003 at station 23, one of the deepest locations in the Bornholm Basin. At the shallower station 26 maximum nauplii abundance was only  $147 \times 10^6$  m<sup>-2</sup>. Maximum abundances of copepodites of  $200\text{--}600 \times 10^6$  ind. m<sup>-2</sup> in the same area from the Baltic Monitoring Programme (HELCOM) reported by Dahmen (1995) are in the range of our data in 2002 at station 23. Increased abundances of nauplii and adults in spring 2003 may be related to the January MBI, which increased salinity and oxygen concentrations in the deeper layers.

#### Vertical distribution and trophodynamics

The vertical distribution of the zooplankton species is the result of food availability (Hattori and Saito 1997),

predator avoidance (Bollens and Frost 1989) and physiological requirements (Saito and Hattori 1997). Little is known of the vertical distribution of *P. acuspes* in other regions. In the high arctic it is frequently observed under fast ice in spring (Conover and Gustavson 1999). In the Central Baltic Sea, the vertical distribution of *P. acuspes* showed a clear ontogenetic trend with the youngest stages highest up in the water column and the oldest stages in the deepest layers as reported before by Hernroth and Ackefors (1979) and Dahmen (1995). Especially during their deep aggregation in spring 2002, adult stages were exposed to extremely low oxygen levels. Stalder and Marcus (1997) showed a decline in survival rates with decreasing O<sub>2</sub> concentration for *Acartia tonsa*, *Centropages hamatus* and *Labidocera aestiva*. At hypoxia conditions Marcus (2004) predicted longer development rates for *Acartia tonsa* using age specific survival and egg-production data from experiments, and Sedlacek (2003) observed significantly larger egg production rates in normoxic waters than in hypoxic waters.

Our high vertical sampling resolution revealed differences in the center of distribution for almost every stage. From the analysis of long-term fluctuations, Möllmann et al. (2000, 2003) suggested this vertical distribution patterns resulting from different tempera-

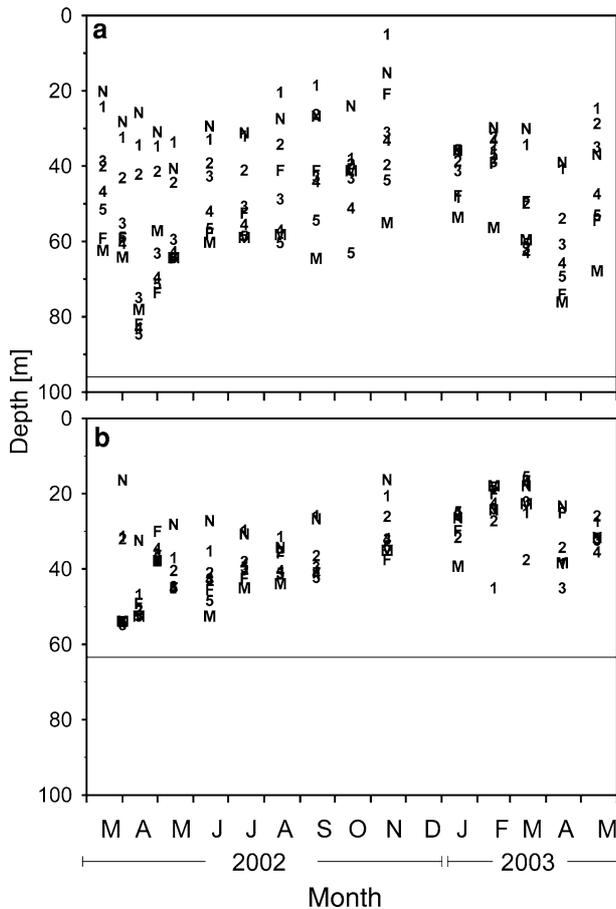


**Fig. 6** Vertical profiles of temperature (°C), salinity (PSU) and oxygen concentration (ml l<sup>-1</sup>) and vertical distribution (%) of nauplii, CI to CV and adults (AM and AF) at stations 23 (a) and 26 (b)

ture and salinity preferences. Our correlation analysis indeed revealed specific differences between older and younger stages, with the nauplii tolerating lower salinities and higher temperatures and older stages preferring

higher salinity. As a result, at shallower stations where the halocline was absent, older stages are dispersed upward or are completely missing as at station 26, where males were absent for several months with salinities





**Fig. 7** Weighted mean depth (*WMD*) of nauplii, copepodites and adult stages of *Pseudocalanus acuspes* in the Bornholm Basin; **a** station 23, **b** station 26 (N N, 1 CI, 2 CII, 3 CIII, 4 CIV, 5 CV, M AM, F AF); black line bottom

years was not directly related to hydrographic changes and has not been reported before.

Stage-specific differences in physiological tolerance and hence the ability to osmoregulate (Kimmel and

Bradley 2001; Goolish and Burton 1989; Devreker et al. 2004) has been reported for *Acartia tonsa* (Cervetto et al. 1999), *Eurytemora affinis* (Roddie et al. 1984; Bradley et al. 1992), and *Tisbe holoturiae* (Lazzaretto-Colombera 1970). Viitasalo (1992) concluded that *Pseudocalanus* sp. in the Gulf of Finland as a halophilic species tolerated lower salinities at lower temperatures. The physiological preferences of *P. acuspes* have important consequences for its susceptibility and response to climate change and trophodynamic interrelationships.

In time series studies in the northern and central parts of the Baltic Sea the biomass of *Pseudocalanus* sp. was significantly higher in years with higher salinity (Dippner et al. 2000; Möllmann et al. 2000, 2003). Several explanations are possible. (1) Decreasing salinity may directly slow down and finally completely stop growth and reproduction. For *Pseudocalanus* sp. in the Central Baltic Sea, Möllmann et al. (2000) and Möllmann and Köster (2002) suggested that older stages and especially females need high salinities and low temperatures for reproduction, which are encountered in the study region only in and below the permanent halocline of the deep Baltic Sea basins. Möllmann et al. (2002) reported a surprisingly deep and narrow distribution of reproducing *Pseudocalanus* females at 16 PSU and oxygen concentrations down to 1 ml l<sup>-1</sup> in April and May 2002, using a Video Plankton Recorder. (2) Advection of higher saline waters from the western Baltic may supply *Pseudocalanus* populations of higher biomass. Eventually the increased concentrations of especially adults in spring 2003 may be due to advection, as no significant growth is expected during winter. (3) Finally the advection of high saline water may increase the volume of the favorable habitat. Consequently older stages of *Pseudocalanus*, preferring higher salinity, could inhabit a wider depth range and hence increase the total biomass in the water column without increasing concentration. Unfortunately most of the time series data are based on non-stratified samples of the whole water column and

**Table 2** Spearman rank correlation of *Pseudocalanus acuspes* vertical distribution (ind. m<sup>-3</sup>) in 10 m layers and 10 m average of temperature (T) and salinity (S); N=number of analysed samples

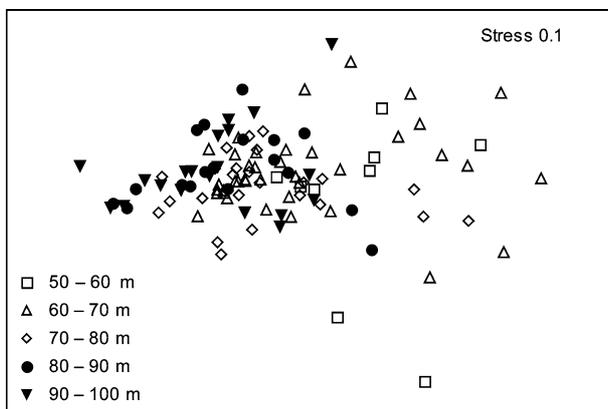
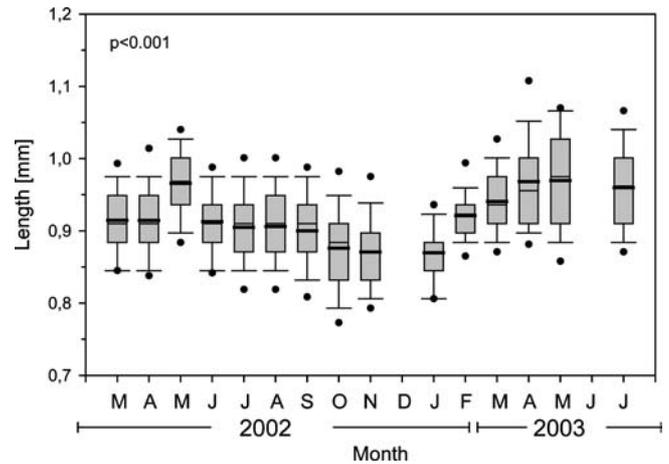
Stage	Parameter	N	Spearman R	t(N-2)	P
N	T	831	-0.2941	-8.8593	<0.0001
N	S	831	-0.2420	-7.1824	<0.0001
CI	T	814	-0.1719	-4.9712	<0.0001
CI	S	814	-0.0745	-2.1275	0.0337
CII	T	827	-0.1199	-3.4691	0.0005
CII	S	827	0.2127	6.2523	<0.0001
CIII	T	831	-0.1051	-3.0426	0.0024
CIII	S	831	0.4058	12.7849	<0.0001
CIV	T	815	-0.1506	-4.3446	<0.0001
CIV	S	815	0.4065	12.6877	<0.0001
CV	T	814	-0.1812	-5.2492	<0.0001
CV	S	814	0.4333	13.7018	<0.0001
AM	T	762	-0.1532	-4.2729	<0.0001
AM	S	762	0.5697	19.1117	<0.0001
AF	T	823	-0.2089	-6.1213	<0.0001
AF	S	823	0.4402	14.0474	<0.0001

**Table 3** Temperature and salinity range of mean weighted mean depth (WMD)(all cruises) of each developmental stage

Stage	WMD (m)	Temperature (°C)	Salinity (PSU)
N	29	1.9–14.9	7.1–8.0
CI	31	1.5–12.3	6.9–9.3
CII	40	2.5–9.2	7.3–14.4
CIII	49	2.7–9.5	7.3–15.6
CIV	54	2.5–10.8	7.3–16.4
CV	58	2.7–13.2	7.4–16.9
AM	61	2.9–12.4	7.4–18.4
AF	54	2.9–9.5	7.6–18.0

thus are not showing concentrations in the habitat of *Pseudocalanus*. In April and May 2003 adult *P. acuspes* inhabited a much wider depth range at station 23 than in 2002 after an increase in salinity from 15 PSU up to 19.3 PSU (Fig. 6). Thus the increased total number of *P. acuspes* after the MBI 2003 was probably due to a combination of advection of a population of higher concentration and increase of the volume inhabited.

Many studies focused on the effect of phytoplankton on the growth of *Pseudocalanus* (e.g., Vidal 1980; Klein Breteler and Gonzalez 1988; Klein Breteler et al. 1995; Koski et al. 1998). While it is thus expected to feed in the euphotic zone, in the Central Baltic Sea only nauplii and younger copepodite stages were collected there. Huntley and Brooks (1982) found the onset in diel vertical migration behavior in the first feeding stage of nauplii for *Calanus pacificus* which was concentrated close to the food-rich surface. The migration of late copepodite stages of this species was influenced by food availability. When phytoplankton was abundant, copepodites performed a high amplitude migration, while with declining food availability they remained in the relative food rich surface layers. In this study we found no indication for a distinctive diel vertical migration of *P. acuspes* in the Baltic Sea. As chlorophyll concentrations with few exceptions were very low below 30 m during this study (Menedoht et al., in preparation), the older stages near the halocline are dependent on other resources such as

**Fig. 8** MDS plot of weighted mean depth (WMD), calculated between WMD of each developmental stage, focus station and cruise**Fig. 9** Box-Whisker plot of female prosome length between March 2002 and July 2003 with mean (bold line) and median (regular line), 25th and 75th percentiles (box margins), 10th and 90th percentiles (whisker caps), 5th and 95th percentiles (dots)

sinking phytoplankton cells and faeces of surface dwelling zooplankton species, but this has not been studied yet. With respect to interannual variability, changes in the productivity of the surface layer due to climate variability will only indirectly reach the deep living part of the population.

Predation on *P. acuspes* is strongly affected by its vertical distribution pattern. Adult planktivorous fish, mainly herring, are feeding in the region of the halocline on the overwintering stock of older stages in winter and spring (Köster and Schnack 1994; Möllmann and Köster 1999; 2002) and also cod larvae feed mainly on older copepodite stages of *Pseudocalanus* sp. in the vicinity of the halocline (Voss et al. 2003). In contrast, sprat larvae feed in the upper layers and had no *P. acuspes* in their guts during our study period (M. Dickmann personal communication). The selective feeding of adult clupeids (Möllmann and Köster 1999, 2002) and cod larvae might partly explain the low abundances of older developmental stages and especially adults during spring and summertime, when herring return from their spawning migrations to shallower waters and cod recruits in the Bornholm Basin (Aro 1989). The increase in the sprat stock since the late 1980s might have contributed to a decline of *P. acuspes* (Möllmann and Köster 2002).

Little impact is expected from other predators in the study area. The most abundant invertebrate predator *Aurelia aurita* was present from June to September and inhabited usually the upper 10 m, where *P. acuspes* is absent; *Cyanea capillata* lived close to the halocline, but was very rare (Barz and Hirche 2005). Chaetognaths and mysids were only occasionally observed (K. Barz, personal communication).

It seems that their specific vertical distribution does not save *P. acuspes* from its most important predators, the adult clupeids and cod larvae. Thus vertical distribution in this species may be rather the result of physiological requirements than predator avoidance.

## Life cycle

Studies of the life cycle of *P. acuspes* are rare. McLaren et al. (1989) described a rather complex life cycle in Bedford Basin (Nova Scotia, Canada) with most of the population for much of the year in a resting phase, while a small number continued development and produced three generations per year. In the Canadian Arctic *P. acuspes* can complete a generation in 1 year, spawning begins in late spring and continues most of the summer (Conover and Siferd 1993). In the fjords of northern Norway females spend the winter in dormancy from August to late winter (Norrbin 1996). Stage development during our study showed a very slow shift from nauplii to older stages between April and February of the following year. A similar stage structure was observed by Möllmann and Köster (2002) who analyzed four samples per year in the Gotland Basin and the Gdansk Deep over 20 years, but used a mesh size of 160 µm, which may not quantitatively collect the youngest stages. During our study the main overwintering stages were CIII to CV, like in all other regions investigated. From the nauplii maximum the main reproductive period began in February, peaked in April and May and ended in August, but nauplii were found however in smaller numbers all the year round. The resulting stage structure does not allow to distinguish generations. Even high-resolution sampling during FLEX did not allow to clearly separate generations of *P. elongatus* (Eiane and Ohman 2004). The high water temperatures in the Baltic Sea when compared to the Bedford Basin and the Arctic Ocean should allow the production of several generations per year, but sub-optimum growth conditions may have slowed down development.

Seasonal changes in the body size of the multivoltine species due to temperature and feeding conditions during development were often used to separate between successive generations (Ohman 1985). In our study small changes in body size were observed between September and October 2002 and January to February 2003, when stage composition did not indicate a shift of generations. Alternatively, these changes might be related to the inflow of warm water in the beginning of August (Fig. 2a) and cold water in January 2003. The fact that females in 2003 were larger than in the beginning of 2002 may be related to the temperature difference of 4°C in the water column below 40 m after the MBI. However, the presence of the larger *P. elongatus* especially from the near North Sea locations cannot be excluded.

The prosome length of female *P. acuspes* varied from 0.85 mm in Lancaster Sound to 1.35 mm in the Chuckchi Sea (Frost 1989). Females collected during our study (monthly means range from 0.870 to 0.976 mm (Fig. 9); individual extremes from 0.702 to 1,144 mm) are at the lower end of the range. Hernroth (1985), covering areas between the Kattegat and the Gdansk Deep, found generally larger females ranging from 1.5 ± 0.12 mm in the Kattegat and 1.17 ± 0.13 mm in the Slupsk Trough, an area near our study site.

**Acknowledgements** We thank the crews of R.V. Alkor, R.V. Heincke and R.V. A.v.Humboldt and all cruise participants involved in collecting the samples. This work was funded by GLOBEC Germany, BMBF 03F0320D.

## References

- Aro E (1989) A review of fish migration patterns in the Baltic. *Rap P-V Reun Ciem* 190:72–96
- Barz K, Hirche HJ (2005) Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). *Mar Biol*. DOI 10.1007/s00227-005-1572-2
- Behrends G (1996) Long-term investigation of seasonal mesozooplankton dynamics in Kiel Bight, Germany. In: *Proceedings of 13th Baltic Mar Biol Symp*, Jurmala, Latvia, pp 93–98
- Bollens SM, Frost BW (1989) Predator-induced diel vertical migration in a planktonic copepod. *J Plankton Res* 11:1047–1065
- Bradley BP, Lane MA, Gonzalez CM (1992) A molecular mechanism of adaptation in an estuarine copepod. *Neth J Sea Res* 30:3–10
- Bucklin A, Frost BW, Bradford-Grieve J, Allen LD, Copley NJ (2003) Molecular systematic and phylogenetic assessment of 34 calanoid copepod species of the Calanidae and Clausocalanidae. *Mar Biol* 142:333–343
- Cervetto G, Gaudy R, Pagano M (1999) Influence of salinity on the distribution of *Acartia tonsa* (Copepoda, Calanoida). *J Exp Mar Biol Ecol* 239:33–45
- Clarke KR (1993) Non-parametric multivariate analyses of change in community structure. *Aust J Ecol* 18:117–143
- Clarke KR, Warwick RM (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth Marine Laboratory, Bourne Press Limited, Plymouth
- Conover RJ, Gustavson KR (1999) Sources of urea in arctic seas: zooplankton metabolism. *Mar Ecol Prog Ser* 179:41–54
- Conover RJ, Siferd TD (1993) Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. *Arctic* 46:303–311
- Corkett CJ, McLaren IA (1978) The biology of *Pseudocalanus*. *Adv Mar Biol* 15:1–231
- Dahmen K (1995) Vertikalverteilung und produktionsbiologische Bedeutung des Mesozooplanktons im Bornholm-Becken (Südliche Ostsee). *Berichte aus dem Institut für Meereskunde an der Universität Kiel Nr. 273*:175
- Devreker D, Souissi S, Seuront L (2004) Development and mortality of the first naupliar stages of *Eurytemora affinis* (Copepoda, Calanoida) under different conditions of salinity and temperature. *J Exp Mar Biol Ecol* 303:31–46
- Dippner JW, Kornilovs G, Sidrevics L (2000) Long-term variability of mesozooplankton in the Central Baltic Sea. *J Mar Syst* 25:23–32
- Dippner JW, Hänninen J, Kuosa H, Vuorinen I (2001) The influence of climate variability on zooplankton abundance in the Northern Baltic Archipelago Sea (SW Finland). *ICES J Mar Sci* 58:569–578
- Eiane K, Ohman MD (2004) Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. *Mar Ecol Prog Ser* 268:183–193
- Feistel R, Nausch G, Matthäus W, Hagen E (2003a) Temporal and spatial evolution of the Baltic deep water renewal in spring 2003. *Oceanologia* 45:623–642
- Feistel R, Nausch G, Mohrholz V, Lysiak-Pastuszek E, Seifert T, Matthäus W, Krüger S, Hansen IS (2003b) Warm waters of summer 2002 in the deep Baltic Proper. *Oceanologia* 45:571–592
- Feistel R, Nausch G, Matthäus W, Lysiak-Pastuszek E, Seifert T, Hansen IS, Mohrholz V, Krüger S, Buch E, Hagen E (2004) Background data to the exceptionally warm inflow into the Baltic Sea in late summer of 2002. *Mar Sci Rep* 58:1–59
- Flinkman J, Vuorinen I, Aro E (1992) Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. *Can J Fish Aquat Sci* 49:73–77

- Fortier M, Fortier L, Hattori H, Saito H, Legendre L (2001) Visual predators and the vertical migration of copepods under Arctic sea ice during the midnight sun. *J Plankton Res* 23:1263–1278
- Frost BW (1989) A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can J Zool* 67:525–551
- Goolish EM, Burton RS (1989) Energetics of osmoregulation in an intertidal copepod: Effects of anoxia and lipid reserves on the pattern of free amino acid accumulation. *Funct Ecol* 3:81–89
- Hattori H, Saito H (1997) Diel changes in vertical distribution and feeding activity of copepods in ice-covered Resolute Passage, Canadian Arctic, in spring 1992. *J Mar Syst* 11:205–219
- Hernroth L (1985) Recommendations on methods for marine biological studies in the Baltic Sea: Mesozooplankton Biomass Assessment. *Baltic Mar Biol* 10:1–32
- Hernroth L, Ackefors H (1979) The zooplankton of the Baltic proper: a long-term investigation of the fauna, its biology and ecology. Report Fish Bd Sweden, Inst Mar Res 2:1–160
- Hinrichsen HH, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Biophysical modelling of larval Baltic cod (*Gadus morhua*) growth and survival. *Can J Fish Aquat Sci* 12:1858–1873
- Hinrichsen H, Lehmann A, Möllmann C, Schmidt J (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. *Fish Oceanport* 12:425–433
- Huntley M, Brooks ER (1982) Effects of age and food availability on diel vertical migration of *Calanus pacificus*. *Mar Biol* 71:23–31
- Kane J (1993) Variability of zooplankton biomass and dominant species abundance on Georges Bank, 1977–1986. *Fish Bull* 91:464–474
- Kimmel DG, Bradley BP (2001) Specific protein responses in the calanoid copepod *Eurytemora affinis* (Poppe, 1880) to salinity and temperature variation. *J Exp Mar Biol Ecol* 266:135–149
- Klein Breteler WCM, Gonzalez SR (1988) Influence of temperature and food concentration on body size, weight and lipid content of two Calanoid copepod species. *Hydrobiologia* 167/168:201–210
- Klein Breteler WCM, Gonzalez SR, Schogt N (1995) Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. *Mar Ecol Prog Ser* 119:99–110
- Kontula T, Väinölä R (2003) Relationships of Palearctic and Nearctic 'glacial relict' *Myoxocephalus sculpinus* from mitochondrial DNA data. *Mol Ecol* 2003 12:3179–3184
- Kornilovs G, Sidrevics L, Dippner JW (2001) Fish and zooplankton interaction in the Central Baltic Sea. *ICES J Mar Sci* 58:579–588
- Koski M, Breteler WCM, Schogt N (1998) Effect of food quality on rate of growth and development of the pelagic copepod *Pseudocalanus elongatus*. *Mar Ecol Prog Ser* 170:169–187
- Köster FW, Schnack D (1994) The role of predation on early life stages of cod in the Baltic. *Dana* 10:179–201
- Launiainen J, Matthäus W, Fonselius S, Francke E (1987) Hydrography (Baltic Sea). First Periodic Assessment of the state of the marine environment of the Baltic Sea area, 1980–1985. *Balt Sea Environ Proc* 17B:7–34
- Lazzeretto-Colombera I (1970) Effects of dilution on some population parameters in different geographical populations of *Tisbe holothuriae* Humes (Harpacticoida). *Oceanogr Limnol* 16:263–274
- Marcus NH, Richmond C, Sedlacek C, Miller G, Oppert C (2004) Impact of hypoxia on the survival and fecundity of *Acartia tonsa* Dana. *J Exp Mar Biol Ecol* 301:111–128
- Matthäus W, Franck H (1992) Characteristics of major Baltic inflows—a statistical analysis. *Cont Shelf Res* 12:1375–1400
- Matthäus W, Schinke H (1994) Mean atmospheric circulation patterns associated with major Baltic inflows. *Dtsch Hydrogr Z* 46:321–339
- Mauchline J (1998) The biology of calanoid copepods. *Adv Mar Biol* 33:1–710
- McLaren IA, Laberge E, Corkett CJ, Sévigny JM (1989) Life cycles of four species of *Pseudocalanus* in Nova Scotia. *Can J Zool* 67:552–558
- Möllmann C, Köster FW (1999) Food consumption by clupeids in the Central Baltic: evidence for top-down control?. *ICES J Mar Sci* 56:100–113
- Möllmann C, Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. *J Plankton Res* 24:959–978
- Möllmann C, Kornilovs G, Sidrevics L (2000) Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. *J Plankton Res* 22:2015–2038
- Möllmann C, Schmidt JO, Temming A, Herrmann JP, Flöter J, Sell A (2002) Video Plankton Recorder reveals environmental problems of marine copepod. *Int GLOBEC Newslett* 8.2:20–21
- Möllmann C, Kornilovs G, Fetter M, Köster F, Hinrichsen H (2003) The marine copepod *Pseudocalanus elongatus* as a mediator between climate variability and fisheries in the Central Baltic Sea. *Fish Oceanogr* 12:360–368
- Norrbin MF (1996) Timing of diapause in relation to the onset of winter in the high-latitude copepods *Pseudocalanus acuspes* and *Acartia longiremis*. *Mar Ecol Prog Ser* 142 (1–3):99–109
- Ohman MD (1985) Resource satiated population growth of the copepod *Pseudocalanus* sp. *Adv Limnol* 21:15–32
- Ojaveer E, Lumberg A, Ojaveer H (1998) Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). *ICES J Mar Sci* 55:748–755
- Richter C (1995) Seasonal changes in the vertical distribution of mesozooplankton in the Greenland Sea Gyre (75 degree N): Distribution strategies of calanoid copepods. *ICES J Mar Sci* 52:533–539
- Roddie BD, Leakey RJG, Berry AJ (1984) Salinity-temperature tolerance and osmoregulation in *Eurytemora affinis* (Poppe)(Copepoda, Calanoida) in relation to its distribution in the zooplankton of the upper reaches of the fourth estuary. *J Exp Mar Biol Ecol* 303:31–46
- Runge JA, Ingram RG (1991) Under-ice feeding and diel migration by the planctonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. *Mar Biol* 108:217–225
- Saito H, Hattori H (1997) Diel vertical migration and feeding rhythm of copepods under sea ice at Saroma-ko Lagoon. *J Mar Syst* 11:191–204
- Sedlacek C (2003) The Effect hypoxia has on feeding and egg production rates of *Acartia tonsa* Dana 1849 (Copepoda: Calanoida). Thesis, Florida State University ETD's URN: etd-11172003-151712, p 38
- Siferd TD, Conover RJ (1992) Natural history of ctenophores in the Resolute Passage area of the Canadian High Arctic with special reference to *Mertensia ovum*. *Mar Ecol Prog Ser* 86:133–144
- Stalder LC, Marcus NH (1997) Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. *Mar Biol* 127:599–607
- Vanderploeg HA, Gardner WS, Parrish CC, Liebig JR, Cavaletto JF (1992) Lipids and life cycle strategy of a hypolimnic copepod in Lake Michigan. *Limnol Oceanogr* 37:413–424
- Vanderploeg HA, Cavaletto JF, Liebig JR, Gardner WS (1998) *Limnocalanus macrurus* retains a marine arctic lipid and life cycle strategy in Lake Michigan. *J Plankton Res* 20:1581–1597
- Vidal J (1980) Physioecology of zooplankton: II Effects of phytoplankton concentration, temperature and body size on the metabolic rates *Calanus pacificus* and *Pseudocalanus* sp. *Mar Biol* 56:135–146
- Viitasalo M (1992) Mesozooplankton of the Gulf of Finland and northern Baltic proper—a review of monitoring data. *Ophelia* 35:147–168
- Viitasalo M, Flinkman J, Viherluoto M (2001) Zooplanktivory in the Baltic Sea: A comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. *Mar Ecol Prog Ser* 216:191–200
- Voss R, Köster FW, Dickmann M (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. *Fish Res* 63:97–111

- Vuorinen I, Hänninen J, Kornilovs G (2003) Transfer-function modelling between environmental variation and mesozooplankton in the Baltic Sea. *Prog Oceanogr* 59:339–356
- Walve J, Larsson U (1999) Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: implications for nutrient recycling. *J Plankton Res* 21:2309–2321

**Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: II. Reproduction, growth and secondary production**

Jasmin Renz, Janna Peters and Hans-Jürgen Hirche

**Submitted to Marine Biology**



---

## Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: II. Reproduction, growth and secondary production

Jasmin Renz<sup>1\*</sup>, Janna Peters<sup>2</sup> and Hans-Jürgen Hirche<sup>1</sup>

<sup>1</sup>Alfred Wegener Institute for Polar and Marine Research, PO Box 120161, 27515 Bremerhaven, Germany

<sup>2</sup>Marine Zoology, University of Bremen, PO Box 330440, 28334 Bremen, Germany

\*Corresponding author:

E-mail: [jrenz@awi-bremerhaven.de](mailto:jrenz@awi-bremerhaven.de)

Phone: +49-471-48311042

Fax: +49-471-48311918

### Abstract

The population dynamics of *Pseudocalanus acuspes* in the Central Baltic Sea were studied from March 2002 to May 2003 on a monthly basis. All stages were present year round with a stage shift from nauplii to older copepodite stages over the course of the year. Biomass, estimated from prosome length, peaked between May and September with maximum recorded values of 594 and 855 mg C m<sup>-2</sup> in May 2002 and 2003, respectively. Differences in biomass between stations up to a factor of 20 were observed especially in April/ May and October. Mean egg production rate (EPR) showed a seasonal course and was highest in April 2002 and 2003 with 3.6 and 2.1 eggs f<sup>-1</sup> d<sup>-1</sup>, respectively, corresponding to a mean weight-specific egg production rate (SEPR) of 0.13 and 0.04. Egg production seems to be limited by food from May on. Stage durations determined from moulting experiments turned out to be extremely long. Maximum growth rates based on stage durations of 15-25 days at 4°C in May and July 2003 amounted to 0.03-0.05 d<sup>-1</sup> in CI-CIV. Comparing these rates with rates derived from temperature-development relationships for *P. acuspes* from the literature resulted in 5 times higher growth rates for the latter case. Secondary production reached values up to 9.1 mg C m<sup>-2</sup> d<sup>-1</sup> (method for continuously reproducing populations) and 10.5 mg C m<sup>-2</sup> d<sup>-1</sup> (increment summation).

## Introduction

Life history traits of copepods, including egg production and growth provide information essential to understand the energy transfer in marine pelagic food webs (Lee et al. 2003), as calanoid copepods are the most important grazers on phytoplankton and prey for higher trophic levels. Physical processes, food and predation are the principle mechanisms accounting for variability in abundance and growth of natural populations (Ohman 1985). While the effect of temperature and food on growth rates of copepods is well studied in the laboratory, annual coverage of population dynamics in the field is scarce for many important species.

In the Central Baltic Sea, *Pseudocalanus acuspes* is a key species, serving as a major food item for commercially important zooplanktivorous fish. Recent studies emphasise the key role of this copepod in the stock dynamics of herring and cod (Möllmann et al. 2003, Hinrichsen et al. 2003). Originating from the Arctic and the Norwegian Sea, *P. acuspes* is considered to be a relict species and lives at marginal physiological conditions in this brackish water system characterised by a permanent halocline and a summer thermocline. Its ontogenetic vertical distribution with youngest stages in the upper water column and older stages concentrated within the halocline is probably a result of stage specific physiological requirements (Renz and Hirche 2006). A study by Möllmann and Köster (2002) based on four collection dates per year found an annual shift in stage composition from younger to older copepodids. A similar stage composition resulted also from our previously published results (Renz and Hirche 2006), suggesting the production of only one generation per year. In the Canadian Arctic Conover and Siferd (1993) described one generation for this species, while in Bedford Basin it produced 3 generations with most of the population in a resting phase as CIII and CIV for several months. Only a small number of individuals completed the life cycle at rates determined by the prevailing temperature (McLaren et al. 1989a). A similar situation was reported for *Pseudocalanus* sp. from the White Sea (Pertsova 1981). In contrast, in Dabob Bay under a temperature regime comparable to the Baltic Sea the congener species *Pseudocalanus* sp. produced several generations per year (Ohman 1985).

This study aims to describe the population dynamics and production of *Pseudocalanus acuspes* in the Bornholm Basin in relation to its physical environment, using data from a high resolution sampling program during German GLOBEC, and to discuss it in light of life cycle strategies and feeding conditions. The measurement of egg production and moulting rates together with data on abundance and stage composition were used to estimate growth and production.

## Materials and methods

### Sampling

Sampling of zooplankton was conducted on 16 cruises between March 2002 and May 2003 on a station grid in the Bornholm Basin (BB), Central Baltic Sea (Fig. 1). On every station double oblique bongo net hauls (mouth opening 0.2 m<sup>2</sup>, mesh size 150 µm, towing speed 3 kn) were taken vertically from above the bottom to the surface; additionally on 9 focus stations sampling was performed using a multinet (Hydrobios, 0.25 m<sup>2</sup> mouth opening, 50 µm mesh size, towing

speed  $0.2 \text{ m s}^{-1}$ ) towed vertically with a 10 m resolution from the bottom to the surface. Furthermore at the focus stations samples were taken with a WP-2 net (UNESCO 1968, mouth opening 0.57 cm, mesh size 200  $\mu\text{m}$ , towing speed  $0.2 \text{ m s}^{-1}$ ) towed vertically from above the bottom to the surface. Bongo and multinet samples were immediately preserved in a 4% borax-buffered formaldehyde-seawater solution.

In the laboratory, subsamples of the multinet hauls were analysed for developmental stages until at least 150 individuals of *Pseudocalanus acuspes* were counted. Individuals were identified to nauplii, 5 copepodite stages and adult males (AM) and females (AF). While in earlier publications the species was often called *P. elongatus* (e.g. Möllmann and Köster 1999, 2002), *P. minutus* (e.g. Dahmen 1995) or *P. minutus elongatus* (e.g. Hernroth 1985) a recent genetic publications found this species to be mainly *P. acuspes* (Bucklin et al. 2003). Therefore we consider it to be *P. acuspes*.

Concurrent to the zooplankton sampling, vertical profiles of temperature and salinity were recorded using a CTD-probe (SBE 911+, ME).

### Length measurement

For each cruise, prosome length of 30 preserved adult females (AF) from either bongo net or WP-2 net hauls from one northern (N), one central (C) and one southern station (S)(Fig. 1), was measured using a stereo microscope (Leica MZ 16) with a resolution of 80x. The prosome length of 30-60 preserved copepodite stages I-V (CI-CV) and adult males (AM) was measured for 11 cruises (Fig. 1) from 50  $\mu\text{m}$  multinet hauls from station 23. During time of highest egg production rate (Fig. 5b) the total length of nauplii stages I-VI (NI-NVI) was measured in April and May 2002 and March, April and May 2003 with a resolution of 200x.

Total biomass for every cruise and focus station was calculated using the length-weight relationship for *Pseudocalanus elongatus* by Hay et al. (1988).

$$\text{NI-NVI: } \text{LogDM} = 0.989 \log PL - 2.712$$

$$\text{CI-CVI: } \text{LogDM} = 3.346 \log PL - 8.899$$

where DM is the dry mass ( $\mu\text{g}$ ), TL the total length and PL the prosome length ( $\mu\text{m}$ ) of an individual. This relationship revealed the best length-weight regression for *P. acuspes* females from the Bornholm Basin (Peters et al. 2006). As length measurements of nauplii and copepodids were missing in some months, a mean between the previous and following month was used to calculate biomass. No correction was made for shrinkage of individuals by fixation as changes in prosome length of preserved copepods are contradictorily discussed. While some authors assumed only small changes in length after preservation with formalin (Williams and Robins 1982, Böttger and Schnack 1986), Kaipris et al. (1997) reported significant reduction of length after preservation of 4.4-15.1%, depending on sex and temperature. Halliday (2001) considered a general reduction of 8%. Assuming a reduction of 8% for all stages would lead to up to 25% higher biomass values during our study.

Differences in prosome length of copepodids between sampling dates as well as differences in prosome length of AF between stations were tested with one-way ANOVA using Tukey's honestly significant difference as the post-hoc test.

### Egg production

For measurement of in-situ egg production at the focus stations 30 females from the WP-2 net hauls were randomly sorted out immediately after capture under ambient temperature conditions. Niehoff et al. (1999) and Harris et al. (2000) have demonstrated that incubation in small volumes does not affect egg production and egg cannibalism of an egg carrying species can nearly be excluded, females were incubated individually in 15 ml cell wells for 48h under in-situ temperature using 50 µm prefiltered water from the upper halocline. Clutch size and number of reproducing females were recorded and females were preserved in a 4% borax-buffered formaldehyd-seawater solution for later length measurement.

At low temperatures, egg production rates (EPR) might be underestimated when females are incubated for only 24h. We therefore extended our incubation period to 48h. No differences were observed between 24h and 48h incubation periods. As in some cases only 24h incubations are available, we displayed EPR of the first 24h.

### Moulting rate

Moulting rates of copepodids were measured at the same station as EPR in the BB at station (sta.) 23 in May and July 2003 in short-term incubations (Klein Breteler et al. 1998). As no young copepodids were found in the BB in July 2003, an experiment from sta. 103 in the Gotland Basin (GB) was chosen to get the information on moulting rates of these stages in the Baltic Sea. In May, experiments were incubated at ambient temperature conditions in 50 µm prefiltered water from above the halocline. In July different temperature and salinity conditions (Table 2) were chosen to simulate habitat conditions (Renz and Hirche 2005). For each experiment, 4 sub-samples containing 100-150 copepodids CI-CV each were taken from a WP2 haul. Old exuviae of *Pseudocalanus acuspes* were removed and sub-samples were incubated for 4 days in 1 l Kautex bottles. Every 24h one sub-sample was preserved in a 4% borax-buffered formaldehyd-seawater solution for later enumeration of moults by counting of exuviae. The moulting rate (*MR*) of each stage was calculated after Peterson et al. (1991) as

$$MR_i = \frac{Ex_i}{[N_i + Ex_i]} * \frac{24}{T}$$

where  $N_i$  is the number of individuals in stage  $i$  at the beginning of the experiment,  $Ex_i$  is the number of exuviae in stage  $i$  at the end of the experiment and  $T$  is the incubation time (in hours). The minimum, maximum and mean moulting rate of each stage per experiment was calculated from the 4 sub-samples (Table 2).

### Weight-specific growth rate

The growth rate ( $g_i$ ) of nauplii and copepodite stages CI-CV was calculated from the expression

$$g_i = \ln\left(\frac{W_{i+1}}{W_i}\right) * \frac{1}{D}$$

where  $W_{i+1}$  is the mass calculated from length measurements of the stage moulted to and  $W_i$  the mass of the stage moulted from, respectively. No correction for shrinkage of individuals by fixation was made.  $D$  is the stage duration of stage  $i$ . An isochronal development was assumed and  $D$ , calculated for copepodite stages, was adopted for nauplii.

The carbon-specific growth rate of AF ( $g_f$ ) was calculated by first converting the number of eggs to carbon of eggs using  $0.14 * 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$  (Kjørboe et al. 1985, Huntley and Lopez 1992). Egg size for Baltic Sea *P. acuspes* was determined from unpreserved eggs in March 2004 from 10 egg production experiments (mean diameter eggs 130  $\mu\text{m}$ ). Length of AF was determined from preserved samples and we allowed for shrinkage of 8% by fixation (Halliday 2001) when calculating female dry mass and converting to carbon assuming  $0.4 \mu\text{g C } \mu\text{g}^{-1}$  dry mass (Parsons et al. 1984). Female growth rate is then

$$g_f = \frac{W_{eggs}}{W_{AF}} * \frac{24}{T}$$

where  $T$  is the incubation time (hours),  $W_{eggs}$  is the carbon mass of eggs ( $\mu\text{g}$ ) produced per day and  $W_{AF}$  the carbon mass of a female.

### Production and productivity

Production and productivity (P/B) were calculated by 2 different methods: 1. a standard method for continuously reproducing populations, 2. the increment summation method.

Method 1: Instantaneous growth method for continuously reproducing populations (Rigler and Downing 1984)

Production of nauplii, CI-CV and AF was calculated as

$$P_i = (g_i * B_i)$$

where  $P_i$  is the production of stage  $i$  ( $\mu\text{g dry mass produced m}^{-2}$ ),  $g_i$  is the growth rate of single stage  $i$  and  $B_i$  the biomass of stage  $i$ . Production of the whole population was calculated by summing up the production of every single stage.

Method 2: Increment summation according to Rigler and Downing 1984 (modified in Hirche et al. 2001) for populations where cohorts can be followed

This method computes production from stage to stage by daily increment in biomass as

$$P_{i,i+1} = (M_{i+1} - M_i) * (X_i / D_i + X_{i+1} / D_{i+1}) / 2$$

where  $P_i$  is the daily production,  $X_i$  is the abundance,  $M_i$  is the mean mass and  $D_i$  is the stage duration of stage  $i$ .

## Results

### Hydrography

Hydrography in the Bornholm Basin was characterised by a permanent halocline (Fig. 2b), which was located at around 40-50 m depth at station 23 between March 2002 and July 2003. From March to December 2002, salinity averaged 7 above the halocline and increased towards the bottom up to 16. Temperature (Fig. 2a) in March 2002 averaged 4°C above and 8°C below the halocline. A summer thermocline was developing from May on, leading to temperatures up to 20°C in the upper 20 m and between 4°C and 10°C in the intermediate layer. After a Major Baltic Inflow event (MBI, Feistel et al. 2004) in January 2003, salinity below the halocline reached values up to 20.

### Stage structure

The mean relative stage composition in the study area showed a seasonal stage shift from nauplii in spring and early summer to older copepodids in August (Fig. 3). Nauplii made up >63% of the total population in March and April 2002. Their proportion declined over the following months and was lowest during November 2002 (3.5%). The highest proportion of CI was found in May, followed by CII in May to July and CIII from August to October 2002. CIV and CV dominated the late autumn and early winter population, they made up >55% of the population from November to January.

### Prosome length of developmental stages

The mean prosome length of the developmental stages of *P. acuspes* is shown in Fig. 4. The length of copepodite stages ranged from 0.384 mm (CI) to 0.976 mm (adult female, AF). Nauplii were only measured in spring; their total length ranged from 0.162 mm (NI) to 0.462 mm (NVI). Length of all copepodids and adults increased by 0.04-0.05 mm between March and May 2002, except for the naupliar stages, which became smaller during this period. Subsequently length decreased in all stages measured starting in May with CI-CIII, followed by CIV in July and CV in September. This period of smaller individuals was followed by an increase in length from February/March on especially in the older stages and adults. Statistical analysis of mean prosome length of AF using one-way ANOVA and the associated post-hoc test showed significant horizontal differences ( $p < 0.05$ ) in length only between the N and S stations in April and June 2002 and between the N and S as well as S and C stations in July 2003 (data not shown).

Statistical analysis of mean prosome length of copepodite stages and adults using one-way ANOVA showed significant differences ( $p < 0.05$ ) of mean length between sampling months (data not shown). The post hoc test, comparing pairs of means, showed that especially CI-III and AF during May in both years were significantly larger than those found from August to November ( $p < 0.05$ ), while size of CIV and CV in May differed significantly in size from those found from October 2002 to March 2003 ( $p < 0.05$ ). Length variation in males was small and differences were only significant ( $p < 0.05$ ) between May 2002 and August 2002 as well as January and March 2003.

### **Biomass**

The biomass of *Pseudocalanus acuspes* (Table 1) showed a pronounced seasonal trend with highest values between May and September 2002 and in May 2003, when nauplii and younger stages dominated the population. Maximum biomass was observed in May 2002 ( $594 \text{ mg C m}^{-2}$ ) and in May 2003 ( $855 \text{ mg C m}^{-2}$ ). Concentrations below  $20 \text{ mg C m}^{-2}$  were recorded in autumn and winter. After the inflow of cold, saline North Sea water the maximum biomass was 1.4 times higher compared to the previous year. Differences in biomass between stations up to a factor of 20 were observed in May and September 2002.

### **Reproduction**

Egg production rate (EPR)(Fig. 5b) showed high variability and ranged from 0 at several stations to a maximum of  $3.6 \text{ eggs f}^{-1} \text{ d}^{-1}$  at station 23 in April 2002 and  $2.1 \text{ eggs f}^{-1} \text{ d}^{-1}$  at station 35 in April 2003. Mean EPR per cruise ranged from  $0.1 \text{ eggs f}^{-1} \text{ d}^{-1}$  in winter to  $1.2 \text{ eggs f}^{-1} \text{ d}^{-1}$  in spring and showed a peak in April and May 2003. A second small peak could be identified in August 2002. In 2002 highest EPR were recorded in the marginal areas of the BB, while in 2003 station 35 showed also high values.

Clutch size (Fig. 5a) ranged between 2 and 25 eggs  $\text{f}^{-1}$  with minimum and maximum mean values of 3.5 eggs  $\text{f}^{-1}$  in October 2002 and 12 in July 2003. The correlation between the proportion of spawning females and the EPR (Fig. 5e) revealed a significant positive relationship ( $r^2 = 0.79$ ,  $p < 0.001$ ). In contrast to other studies there was no significant correlation between clutch size and female prosome length ( $r^2 = 0.14$ ) (Fig. 5d), though a trend of larger clutches could be observed for larger females.

Population egg production rate ( $\text{eggs m}^{-2} \text{ d}^{-1}$ ) was calculated for each station where egg production was measured (Fig. 5c). Mean population egg production is shown using mean female abundance on the grid and mean egg production for the cruise. April to June was clearly the phase of highest egg production of the population, followed by a period of intermediate production in summer and a period of hardly any egg production, which lasted until February 2003. The proportion of nauplii (Fig. 3) closely reflects the seasonal population egg production.

### **Moulting rates and stage duration**

Moulting rates varied between different stages, sampling dates and regions (Table 2). In the GB CI and CII showed lower moulting rates than CIII. CIV and CV did not moult at all in this area during the 4 days of incubation. In May moulting rates of all stages examined were higher in the BB than in the GB and decreased in July. In the BB CIV/CV moulted during the experiments both in May and in July.

The temperatures and salinities chosen for the experiments reflected the environmental conditions at which the animals were collected. The increase of moulting rates with increasing salinity in Table 2 suggests a strong relationship. However, experiments on the salinity influence on stage duration revealed no clear relation (Renz unpublished data).

### **Weight-specific growth rates**

Stage durations in our experiment lasted 2-3 times longer than those calculated from temperature-development relationships for *Pseudocalanus* sp. from the literature (in Eiane and Ohman 2004). Therefore we used fixed stage durations of 15 and 25 days for each stage for further calculation of growth rates and production; no temperature effect was considered. (Fig. 6b, c). Continuous growth throughout the year was assumed. The resulting growth rates at 15 d stage durations were highest in CI to CIV (0.03 to 0.05 d<sup>-1</sup>). CV developing to small AM and larger AF, showed smallest growth (0 to 0.02 d<sup>-1</sup>). A 25 d stage duration reduced growth rates for CI-CIII down to 0.02 to 0.03 d<sup>-1</sup> for young copepodite stages and to below 0.1 d<sup>-1</sup> for CV. For comparison we estimated stage durations at different temperatures from generation times reported for *P. acuspes* from Nova Scotia by McLaren et al. (1989b), assuming an isochronal development. Application of these durations produced a pronounced peak in October and November and growth rates up to 5-9 times higher than for stage durations of 15 and 25 d (Fig. 6d).

Except for the maximum in April 2002 (0.13 d<sup>-1</sup>), weight-specific growth rates of females varied between 0.01 and 0.04 d<sup>-1</sup> with a mean of 0.03 d<sup>-1</sup>, when the high value in April 2002 is excluded (Fig. 6a). During times of highest reproduction in September 2002 as well as April and May 2003 they were comparable to growth rates of young copepodids for a stage duration of 15 d. Over the rest of the year, growth rates of females were comparable to those of older copepodids at a stage duration of 25 days.

### **Secondary production**

Cumulative secondary production (method 1) of all stages using the stage durations described before is shown in Fig. 7b-d; for calculation of female production, female weight-specific egg production was used. The main productive period of *Pseudocalanus acuspes* copepodids in the BB lasted from May to September, female production started one month earlier. The seasonal course was basically unimodal and consisted of a long increase originating from production of CI-II while the peak in July and the slow decrease until September were mainly caused by production of CIII and CIV. Applying a stage duration of 15 d, highest production of 4.8 mg C m<sup>-2</sup>

$\text{d}^{-1}$  was recorded for CIII in July 2002, followed by values of  $3.8 \text{ mg C m}^{-2} \text{ d}^{-1}$  of females in April 2002. The cumulative mean production of all stages (eggs to CV) was highest in July ( $9.1 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). A stage duration of 25 d reduced production of copepodite stages by 25% for CI-CII and 35-40% for CIII-CV. This led to a decrease in overall production of all stages of 35%.

Using the temperature dependent stage durations from generation times for *P. acuspes* reported by McLaren et al. (1989b), the seasonal course in production confirmed our data well (Fig. 7b). However, production exceeded our values up to 3.3 times and led to a cumulative mean secondary production up to  $30 \text{ mg C m}^{-2}$  adding up production of single stages.

A comparison of two methods for the estimation of secondary production and productivity is presented in Table 3 with both methods using a stage duration of 15 d. The increment summation (method 2) estimated daily mean production of the population to be up to  $10.5 \text{ mg C m}^{-2} \text{ d}^{-1}$  in July 2002, 14% higher than estimated by the method for continuously reproducing populations (method 1). The corresponding productivities were 0.035 and 0.031, respectively. Lowest production ( $<0.6 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) was measured in March and early April 2002. In general, comparing method 1 and 2 resulted in similar production and productivity values.

## Discussion

### Biomass

In temperate ecosystems biomass of copepods undergoes seasonal changes with a typical unimodal distribution and a peak usually during late spring and summer (Colebrook 1979). During our study biomass of *Pseudocalanus acuspes* showed a seasonal cycle with a minimum in March and an increase during a phytoplankton bloom in April (van Beusekom et al. submitted) It peaked between May and July with maxima in May 2002 ( $594 \text{ mg C m}^{-2}$ ) and May 2003 ( $858 \text{ mg C m}^{-2}$ ). Möllmann and Köster (1999), reporting historical biomass data collected in the Gdansk Deep during July found concentrations similar to our 2002 values.

Time series analysis showed significantly higher biomass of *Pseudocalanus* in years with higher salinities (Dippner et al. 2000; Möllmann et al. 2000; 2003). It was substituted by *Acartia* spp. in the long period of lower salinity in the Central Baltic Sea before 1993 (Kononen et al. 1996). The increased biomass at one deeper station in May 2003 as compared to 2002 could therefore be related to the inflow of cold, saline North Sea water with the MBI in the beginning of 2003. Renz and Hirche (2006) discussed several mechanisms responsible for an increased biomass such as advection of *P. acuspes* populations from the western Baltic Sea or the increase of the habitat in the deep basins. However, an effect of improved living conditions was to be expected only with some delay after our sampling period.

Differences in biomass between stations up to a factor of 20 were observed especially in April/May and October. The spatial variability in biomass clearly emphasizes the spatial and temporal resolution required for representative time series studies.

## Reproduction

*Pseudocalanus acuspes* produced eggs throughout the study period, though there was a seasonal trend with highest rates in April 2002 and 2003 and lowest values in October 2002 and January 2003. As egg production of this species has not been measured before comparisons are only possible with congeners. Our maximum (3.6 eggs  $f^{-1} d^{-1}$ ) coincides with the 2.5 eggs  $f^{-1} d^{-1}$  in the North Sea (Kiørboe and Johansen 1986) and 3.3 eggs  $f^{-1} d^{-1}$  at 12-14°C in *Pseudocalanus* sp. from Dabob Bay (Ohman 1985). In laboratory experiments with *P. elongatus* from the North Sea Koski et al. (1998) reported 2-5 eggs  $f^{-1} d^{-1}$  at 15°C and good food quality while Corkett and Zillioux (1975) found 1.1 eggs  $f^{-1} d^{-1}$  at 4°C, 2.3 at 8°C and 3.4 eggs  $f^{-1} d^{-1}$  at 16°C; similarly Paffenhöfer and Harris (1976) observed between 3.1 and 4.7 nauplii  $f^{-1} d^{-1}$  at 12.5°C. Highest egg production was reported by Halsband and Hirche (2001) for the German Bight, where *P. elongatus* produced up to 8 eggs  $f^{-1} d^{-1}$  at 3°C; however, these females were more than 150  $\mu m$  larger.

The relatively low egg production in this genus seems to be related to the large size of their eggs (diameter 130  $\mu m$ ). Our maximum egg production in April 2002 corresponds to a specific egg production rate (SEPR) of 0.13. This is very high when compared to the SEPR of 0.04 in April/ May 2003 and might result from a combination of warmer temperature and more suitable food conditions. However, only one experiment for the measurement of EPR was determined in April 2002. Our annual mean SEPR (0.03) is similar to the 0.055 (mean 0.014) of Kiørboe and Johansen (1986) in September at 9-12°C in the northern North Sea. For the same species, a weight-specific fecundity of 0.078 (Corkett and Zillioux 1975), 0.09 (Paffenhöfer and Harris 1976) and 0.03-0.11 at good food quality (Koski et al. 1998) is reported at 15°C.

The seasonal cycle of egg production is usually controlled by female size, food and temperature (Corkett and McLaren 1978 and references therein; Jónasdóttir 1989, Halsband and Hirche 2001). In the BB female size showed relatively small variations (Renz and Hirche 2006), and the correlation between egg production and prosome length was not significant. Only little effect could be expected from temperature, which slightly increased at WMD of females from 3°C to 6.5°C, except a short peak in November (9°C). Primary production in the BB is basically restricted to the waters above the thermocline (van Beusekom et al. submitted) which forms the upper boundary of the habitat of *P. acuspes* (Renz and Hirche 2006). Only in late April 2002 a sedimenting phytoplankton bloom reached down to the bottom (van Beusekom et al. submitted) and probably was responsible for the peak in egg production. This is also documented in an increase in diatom and dinoflagellate fatty acid markers (Peters et al. 2006). Surprisingly, during this period the females performed a descend and concentrated near the halocline (Renz and Hirche 2006). As indicated by signature fatty acids, the diet of *P. acuspes* mainly consists of microzooplankton and sinking detritus. Due to reduced food sedimentation in summer and winter, diet might limit egg production throughout most of the year. This is consistent with very low storage lipid amounts of females during summer and winter (Peters et al. 2006).

While in some *Pseudocalanus* species females are hardly present during winter in the Greenland Sea (Richter 1994), *P. elongatus* in the Kattegat (Kiørboe and Nielsen 1994) and in

the North Sea (Halsband and Hirche 2001) and *P. acuspes* in the Central Baltic Sea are breeding throughout the year, though the proportion of spawning females is low during this time. Based on lipid content of CV and females in winter (total lipid 1.8 and 1.2  $\mu\text{g}$  per individual, respectively; Peters et al. 2006) it is unlikely that females are able to fuel egg production from lipid reserves alone. Therefore food uptake was necessary to maintain the egg production observed during winter. McLaren et al. (1989a) further suggested that only copepodids with insufficient lipid content accomplish maturation during summer and autumn to potentially produce more successful offspring.

### **Moulting, development and growth**

Stage durations of the younger copepodids in May and July derived from moulting rates were low and not isochronous, but increased with age and depth inhabited (Renz and Hirche 2006). The older stages CIV/CV in the GB in July hardly moulted at all, indicating arrested development, while they moulted in the BB. According to temperature-growth relationships established for *Pseudocalanus* spp. by Eiane and Ohman (2004) from various sources, stage durations are around 8 d (CI-CIII), 6 d (CIV) and 11 d (CV) at 3-4°C. In the field, Ohman (1994) found generation times of approx. 40 days at 8°C and 26-27 days at 13.4 °C in Dabob Bay, which agree well with laboratory measurements by Klein Breteler et al. (1982) and Paffenhöfer and Harris (1976). At 5°C, Klein Breteler et al. (1995) reported stage durations of ~5 days for most developmental stages and a generation time of ~60 days. Our stage durations are extremely long when compared to field populations of the congener *P. elongatus* from the North Sea (Renz unpublished data) and at least twice those predicted from temperature-growth relationships. This results in considerably lower growth rates than reported for *Pseudocalanus* species from the literature (Paffenhöfer and Harris 1976, Klein Breteler et al. 1982, McLaren et al. 1989b, Peterson et al. 1991, Koski et al. 1998), but our growth rates for stage durations of 15 days are in good agreement with those reported by Ciszewski and Witek (1977) for *Pseudocalanus "elongatus"* from the Gdansk Bay at 5°C (0.026-0.058).

There are some uncertainties in our approach to calculate growth rate. The adoption of copepodid stage durations on nauplii might miscalculate growth rates as the first nauplii stages are known not to feed and have short developmental times. Furthermore, different copepodite stages experience different biotic and abiotic conditions due to their ontogenetic vertical distribution (Renz and Hirche 2006) and may therefore not grow at the same rate.

The large variability in the moulting experiments and the long incubation times necessary here without doubt suggest that our results have to be taken with caution, as previously discussed by Hirst et al. (2005) for such conditions. On the other hand, our observations show interesting similarities to observations by McLaren et al. (1989a) in Bedford Basin. They estimated generation times longer by approximately 30% than expected and proposed the population was in a resting phase as CIII and CIV for most of the year with only a small number of individuals maturing and producing further generations in summer and autumn. In the BB the portion of older copepodite stages was also high during more than six months of the year. The lipid

content of CV, which from May on contains a large portion of wax esters until January when compared to the very low values of females over summer (Peters et al. 2006) further supports the possibility of an arrested development in older copepodite stages. The low salinity in the BB may also contribute to the slow development. It puts strong constraints on the habitat of *P. acuspes* and forces older copepodids and adult stages to stick to the halocline where food is limited, as this habitat is for most of the time separated from the euphotic layer.

### **Life cycle**

The fact that *Pseudocalanus acuspes* was breeding continuously and most stages were present all the time (Fig. 3) together with obvious inhomogeneous horizontal distribution complicates understanding of the life cycle. Furthermore, the role of advection has to be taken into account, as several inflow events were observed during the study period. For these reasons our interpretation has to be tentative until better data are available. The appearance of a relatively large portion of males in the BB in February/March clearly indicates the beginning of the spawning period. According to Corkett and McLaren (1978) appearance of adult males is a good indicator of recruitment of a new generation in *Pseudocalanus* as they are short-lived. The highest proportion of females in 2002 was recorded during March and April. However, a female peak in February/March 2003 suggests that we may have missed the early peak in 2002. The main reproductive period started in March/April, as indicated by the high population egg production rate and the steep increase in nauplii abundance, and lasted until June. A mean stage duration of 15 days as found for CII-CIV in May 2003 in the Bornholm Basin would lead to a generation time of >150 days and the first adults of this generation would be expected at the end of August. Indeed this was the time when a second small peak in reproduction was recorded, though it was followed only by a minor peak in nauplii. Beginning in July CIII-CV were accumulating and formed the overwintering stock, which persisted until February. From stage composition, changes in prosome length and estimates of developmental times a further cohort may have developed during summer.

### **Secondary production and productivity (P/B)**

The measurement of copepod secondary production in the field requires detailed knowledge on the life cycle with abundance, mass determination and stage duration to be the regulating factors. Our mean estimates of secondary production in the BB using a stage duration of 15 days, is in the lower range of the 8-24 mg C m<sup>-2</sup> day<sup>-1</sup> found by Peterson et al. (1991) for *Pseudocalanus* sp. in August in the Skagerrak. Kiørboe and Nielsen (1994) found highest cumulative production for several copepod species in the Kattegat in March-April and August-September, associated with phytoplankton blooms. They related variation in copepod biomass primarily to mortality, rather than to temperature. Production of youngest stages, living in the upper part of the water column (Renz and Hirche 2006), started to increase with the phytoplankton peak in April. Highest production was recorded in July when the characteristic vertical distribution pattern already restricted *P. acuspes* from direct utilisation of food in the

euphotic zone. From May on food might therefore be a limiting factor. Additionally, this distribution exposed *P. acuspes* to his main predators, herring and cod (Möllmann et al. 2003, Hinrichsen et al. 2003). Mortality might therefore be an important factor regulating production of this species in the BB. A potential arrest of development of older stages further would limit secondary production of *P. acuspes* in the BB. Productivity in the study area was well in the range of values reported by Ciszewski and Witek (1977) for *Pseudocalanus "elongatus"* in the Gdansk Bay at 5°C with highest values observed between May and November.

Two different methods were applied to estimate production. While the increment summation describes production of populations, where cohorts can be followed, the method for continuously reproducing populations is applied for populations in a steady state (Rigler and Downing 1984). Both approaches do not exactly fit our observations and can only result in an approximation, as on the one hand no clear cohorts could be followed due to difficulties with interpreting the life cycle. On the other hand reproduction was not continuously high but decreased after April/ May. The resulting estimates of highest production in July however were very similar, 10.5 and 9.1 mg C m<sup>-2</sup>, corresponding to a productivity of 0.029 and 0.034, respectively. Stage duration is the factor influencing both methods and the exemplified year-round adoption of long stage durations, measured in May and July 2003, must result in comparably low production. Clearly, no concrete predictions can be made for stage durations beyond the investigation period. Especially an adequate food situation in spring might shorten developmental times. If this is the case, our estimates for winter and early spring would fairly underestimate secondary production of *P. acuspes*. This emphasizes the importance of measuring stage durations in field populations. The application of temperature-development relationships from the literature (McLaren et al. 1989b) might therefore firstly give best information. The comparably long stage durations in May and July however suggest that the generally used temperature dependent stage durations are insufficient to describe year round production of *P. acuspes* in the Central Baltic Sea.

### **Acknowledgements**

We like to thank the crews and scientific parties of the RV Alkor, Heincke and A.v.Humboldt for the provided support during the field phase, K. Barz for help with the egg production experiments and U. Holtz for help with length measurements. The critical revision and improvement of the manuscript by three anonymous reviewers is gratefully acknowledged. The study was funded by the German Federal Ministry for Education and Research within the GLOBEC GERMANY project (03F0320C).

## Literature

- Böttger R, Schnack D (1986) On the effects of formaldehyde fixation on the dry weight of copepods. *Meeresforschung* 31: 141-152
- Bucklin A, Frost BW, Bradford-Grieve J, Allen LD, Copley NJ (2003) Molecular systematic and phylogenetic assessment of 34 calanoid copepod species of the Calanidae and Clausocalanidae. *Mar Biol* 142: 333-343
- Ciszewski P, Witek Z (1977) Production of older stages of copepods *Acartia bifilosa* Giesb. and *Pseudocalanus elongatus* Boeck in Gdansk Bay. *Pol Arch Hydrobiol* 24: 449-459
- Colebrook JM (1979) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north Atlantic Ocean and the North Sea. *Mar Biol* 51: 23-32
- Conover RJ, Siferd TD (1993) Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. *Arctic* 46: 303-311
- Corkett CJ, McLaren IA (1978) The biology of *Pseudocalanus*. *Adv Mar Biol* 15: 1-231
- Corkett CJ, Zillioux EJ (1975) Studies on the effect of temperature on the egg laying of three species of calanoid copepods in the laboratory (*Acartia tonsa*, *Temora longicornis* and *Pseudocalanus elongatus*). *Bull Plankton Soc Jap* 21: 77-85
- Dahmen K (1995) Vertikalverteilung und produktionsbiologische Bedeutung des Mesozooplanktons im Bornholm-Becken (Südliche Ostsee). *Berichte aus dem Institut für Meereskunde an der Universität Kiel Nr. 273*: pp 175
- Dippner JW, Kornilovs G, Sidrevics L (2000) Long-term variability of mesozooplankton in the Central Baltic Sea. *J Mar Syst* 25: 23–32
- Eiane K, Ohman MD (2004) Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. *Mar Ecol Prog Ser* 268: 183-193
- Feistel R, Nausch G, Matthäus W, Lysiak-Pastuszek E, Seifert T, Hansen IS, Mohrholz V, Krüger S, Buch E, Hagen E (2004) Background data to the exceptionally warm inflow into the Baltic Sea in late summer of 2002. *Mar Sci Rep* 58: 1–59
- Halliday NC (2001) A comparison of morphometric and geometric methods for the estimation of individual zooplankton volumes. *Sarsia* 86: 101-105
- Halsband C, Hirche HJ (2001) Reproductive cycles of dominant calanoid copepods in the North Sea. *Mar Ecol Prog Ser* 209: 219-229
- Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds)(2000) *Zooplankton Methodology Manual*. Academic Press, pp 410-412
- Hay SJ, Evans GT, Gamble JC (1988) Birth, growth and death rates for enclosed populations of calanoid copepods. *J Plankton Res* 10: 431-454
- Hernroth L (1985) Recommendations on methods for marine biological studies in the Baltic Sea: Mesozooplankton Biomass Assessment. *The Baltic Marine Biologists* 10: 1-32
- Hinrichsen H, Lehmann A, Möllmann C, Schmidt J (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. *Fish Oceanogr* 12: 425-433

- Hirche HJ, Brey T, Niehoff B (2001) A high-frequency time series at Ocean Weather Ship Station M (Norwegian Sea): Population dynamics of *Calanus finmarchicus*. Mar Ecol Prog Ser 219: 205-219
- Hirst AG, Peterson WT, Rothery P (2005) Errors in juvenile copepod growth rate estimates are widespread: Problems with the Moulting Rate method. Mar Ecol Prog Ser 296: 263-279
- Huntley ME, Lopez MDG (1992) Temperature-dependent production of marine copepods: A global synthesis. Am Nat 140: 201-242
- Jónasdóttir SH (1989) Effects of food concentration on egg-production rates of two species of *Pseudocalanus*: Laboratory observations. J Exp Mar Biol Ecol 130: 33-43
- Kaipris K, Miliou H, Moraitou-Apostolopoulou M (1997) Effects of formaldehyde preservation on biometrical characters, biomass and biochemical composition of *Acartia clausi* (Copepoda, Calanoida). Helgoländer Meeresunters 51: 95-106
- Kjørboe T, Møhlenberg F, Hamburger K (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. Mar Ecol Prog Ser 26: 85-97
- Kjørboe T, Johansen K (1986) Studies of a larval herring (*Clupea harengus* L.) patch in the Buchan area. 4. Zooplankton distribution and productivity in relation to hydrographic features. Dana 6: 37-51
- Kjørboe T, Nielsen TG (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 1. Copepods. Limnol Oceanogr 39: 493-507
- Klein Breteler WCM, Franz HG, Gonzalez SR (1982) Growth and development of four calanoid copepod species under experimental and natural conditions. Neth J Sea Res 16: 195-207
- Klein Breteler WCM, Gonzalez SR, Schogt N (1995) Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. Mar Ecol Prog Ser 119: 99-110
- Klein Breteler WCM, Gonzalez SR, Schogt N, Franz HG (1998) Feasibility of incubation experiments to estimate moulting rates in marine copepods. J Plankton Res 20: 257-269
- Kononen K, Kuosa H, Leppänen J, Olsonen R, Kuparinen J, Postel L, Behrends G (1996) Overall assessment. Pelagic biology. HELCOM 1996: Baltic Sea Envir Proc 64 B: 215-222
- Koski M, Klein Breteler WCM, Schogt N (1998) Effect of food quality on rate of growth and development of the pelagic copepod *Pseudocalanus elongatus* (Copepoda, Calanoida). Mar Ecol Prog Ser 170: 169-187
- Lee HW, Ban S, Ikeda T, Matsuishi T (2003) Effect of temperature on development, growth and reproduction in the marine copepod *Pseudocalanus newmani* at satiating food condition. J Plankton Res 25: 261-271
- McLaren IA, Laberge E, Corkett CJ, Sevigny JM (1989a) Life cycles of four species of *Pseudocalanus* in Nova Scotia. Can J Zool 67: 552-558
- McLaren IA, Sevigny JM, Corkett CJ (1989b) Temperature-dependent development in *Pseudocalanus* species. Can J Zool 67: 559-564

- Möllmann C, Köster FW (1999) Food consumption by clupeids in the Central Baltic: evidence for top-down control?. ICES J Mar Sci 56: pp 100-113
- Möllmann C, Kornilovs G, Sidrevics L (2000) Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. J Plankton Res 22: 2015–2038
- Möllmann C, Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea, J Plankton Res 24: 959-978
- Möllmann C, Kornilovs G, Fetter M, Köster F, Hinrichsen H (2003) The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. Fish Oceanogr 12: 360-368
- Niehoff B, Klenke U, Hirche HJ, Irigoien X, Head R, Harris R (1999) A high frequency time-series at Weathership M, Norwegian Sea, during the 1997 spring bloom: the reproductive biology of *Calanus finmarchicus*. Mar Ecol Prog Ser 176: 81-92
- Ohman MD (1985) Resource-satiated population growth of the copepod *Pseudocalanus* sp. Arch Hydrobiol Beih Ergeb Limnol 21: 15-32
- Ohman MD, Runge JA (1994) Sustained fecundity when phytoplankton resources are in short supply: Omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. Limnol and Oceanogr 39: 21-36
- Paffenhöfer GA, Harris RP (1976) Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus* Boeck. J Mar Biol Assoc UK 56: 327-344
- Parsons TR, Takahashi M, Hargrave (1984) Chemical composition/ Zooplankton. In: Biological Oceanographic Processes. Pergamon Press, pp 323
- Peters J, Renz J, van Beusekom J, Boersma M, Hagen W (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin): evidence from lipid composition. Mar Biol DOI 10.1007/s00227-006-0290-8
- Peterson WT, Tiselius P, Kiørboe T (1991) Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. J Plankton Res 13: 131-154
- Pertsova NM (1981) Number of generations and their life span in *Pseudocalanus elongatus* (Copepoda, Calanoida) in the White Sea (in Russian). Zool Zh LX: 673-684
- Renz J, Hirche HJ (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I: Seasonal and spatial distribution. Mar Biol 148: 567-580
- Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Rep Pol Res 154: pp 87
- Rigler FH, Downing JA (1984) The calculation of secondary productivity. In: Downing JA, Rigler FH (eds) A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Science, Oxford, pp 19-58
- Williams R, Robins DB (1982) Effects of preservation on net weight, dry weight, nitrogen and carbon contents of *Calanus helgolandicus*. Mar Biol 71: 271-281

Table 1: Cruisedates, minimum, maximum and mean biomass [B] [ $\text{mg C m}^{-2}$ ] of *Pseudocalanus acuspes*

Date	B <sub>min</sub>	B <sub>max</sub>	B <sub>mean</sub>
12.03. - 22.03.2002	50.74	57.79	53.62
02.04. - 16.04.2002	47.03	178.64	102.64
16.04. - 30.04.2002	22.86	344.24	166.80
05.05. - 24.05.2002	32.55	271.76	103.20
15.05. - 30.05.2002	30.29	595.29	305.94
11.06. - 23.06.2002	121.80	494.26	296.46
22.07. - 07.08.2002	82.98	501.50	304.80
12.08. - 21.08.2002	85.78	309.45	201.96
03.09. - 13.09.2002	120.48	383.73	240.96
30.09. - 10.10.2002	19.36	196.50	96.47
11.11. - 29.11.2002	18.56	70.31	50.14
13.01. - 24.01.2003	17.36	92.71	46.80
10.02. - 21.02.2003	30.21	129.54	58.60
03.03. - 22.03.2003	30.11	202.41	74.30
17.04. - 28.04.2003	30.01	510.49	154.34
15.05. - 03.06.2003	81.39	855.03	339.49
01.07. - 19.07.2003	No data	No data	No data

Table 2: Moulting rates (MR) and stage duration (D) of *Pseudocalanus acuspes* at station (sta.) 103 in the Gotland Basin (GB) and sta. 23 in the Bornholm Basin (BB) at *in situ* temperature (T) and salinity

Area	Date	Stage	T [°C]	Salinity	MR [%]		D [days]	
					range	mean	range	mean
GB (sta. 103)	July 03	CI	3	7	1.62 - 5.15	3.81	19.4 - 61.7	26.2
		CII	3	7	2.17 - 7.14	3.74	14.0 - 46.1	26.7
		CIII	3	10.5	1.66 - 4.17	2.76	24.0 - 60.2	36.2
		CIV-V	3	10.5	0	-	-	-
BB (sta. 23)	May 03	CII	3.7	14.8	4.63 - 14.29	6.25	7.0 - 21.6	16.0
		CIII	3.7	14.8	3.33 - 13.33	7.01	7.5 - 30.0	14.3
		CIV-V	3.7	14.8	1.30 - 7.32	4.53	13.7 - 77.0	22.0
	July 03	CIII	4	16.2	2.35 - 4.44	3.39	22.5 - 42.6	29.5
		CIV-V	4	16.2	2.38 - 4.26	3.40	23.5 - 42.0	29.4

Table 3: Mean secondary production (P) and productivity (P/B) of *Pseudocalanus acuspes* in the Bornholm Basin; method [M] 1=method for continuously reproducing populations, 2=increment summation method

Month	P [mg C m <sup>-2</sup> d <sup>-1</sup> ]		P/B	
	M 1	M 2	M 1	M 2
<b>2002</b>				
March	0.27	0.53	0.005	0.011
April_1	0.23	0.45	0.005	0.008
April_2	1.54	1.89	0.013	0.015
May_1	2.35	2.60	0.024	0.026
May_2	6.90	8.24	0.027	0.030
June	6.54	7.62	0.024	0.027
Jul	9.14	10.45	0.031	0.035
Aug	5.71	6.70	0.029	0.034
Sep	7.09	8.14	0.029	0.034
Oct	2.75	3.14	0.029	0.033
Nov	1.39	1.58	0.028	0.032
<b>2003</b>				
Jan	0.95	1.24	0.019	0.011
Feb	0.66	1.09	0.011	0.008
March	0.41	0.81	0.004	0.015
April	1.75	1.96	0.013	0.026
May	6.36	7.58	0.023	0.030

### Figure captions

Fig. 1: Study area Gotland Basin and Bornholm Basin (Baltic Sea); *square* focus stations, *circle* stations for length measurements, *stations 23 and 103* measurement of moulting rates

Fig. 2: Hydrography in the Bornholm Basin at station 23 from March 2002 to May 2003; a. temperature [°C], b. salinity

Fig. 3: Mean stage structure of *Pseudocalanus acuspes* in the Bornholm Basin from March 2002 to May 2003

Fig. 4: Total length of *Pseudocalanus acuspes* nauplii stages and prosome length of copepodite stages and adults from March 2002 to July 2003 in the Bornholm Basin; *symbols* mean values, *error bars* standard deviation

Fig. 5: Reproduction of *Pseudocalanus acuspes* in the Bornholm Basin April 2002 to July 2003; a. clutch size, *black line* mean clutch size, b. egg production rate (EPR), *black line* mean EPR, *grey line* temperature [°C] at weighted mean depth (WMD) of females, c. population egg production d. correlation between number of eggs and length of females, e. correlation between proportion of spawning females and EPR

Fig. 6: a. Weight-specific growth rate (=specific egg production rate, SEPR) of AF and b.-d. Weight-specific growth rates of copepodite stages of *Pseudocalanus acuspes* from March 2002 to May 2003; *filled circle* CI, *open circle* CII, *filled triangle down* CIII, *open triangle down* CIV, *square* CV

Fig. 7: a. Mean productivity (P/B) of *Pseudocalanus acuspes* between March 2002 and May 2003 in the Bornholm Basin, b.-c. Cumulative mean secondary production of nauplii and copepodite stages for stage durations (D) of 15 days (b.), 25 days (c.) and a temperature dependent stage duration derived by a generation time from McLaren et al.(1989b)(*grey line*)(b.) together with production of adult females (AF)(b. and c.)

Fig. 1

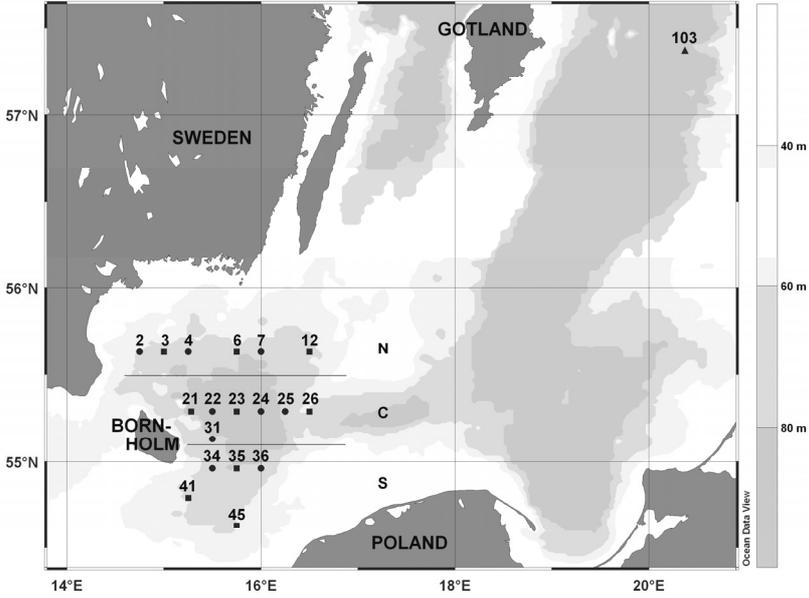


Fig. 2

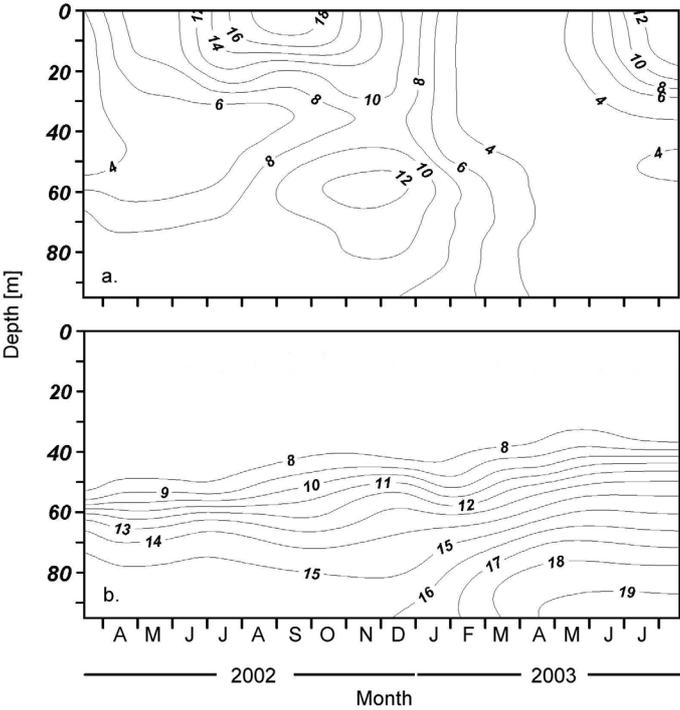


Fig. 3

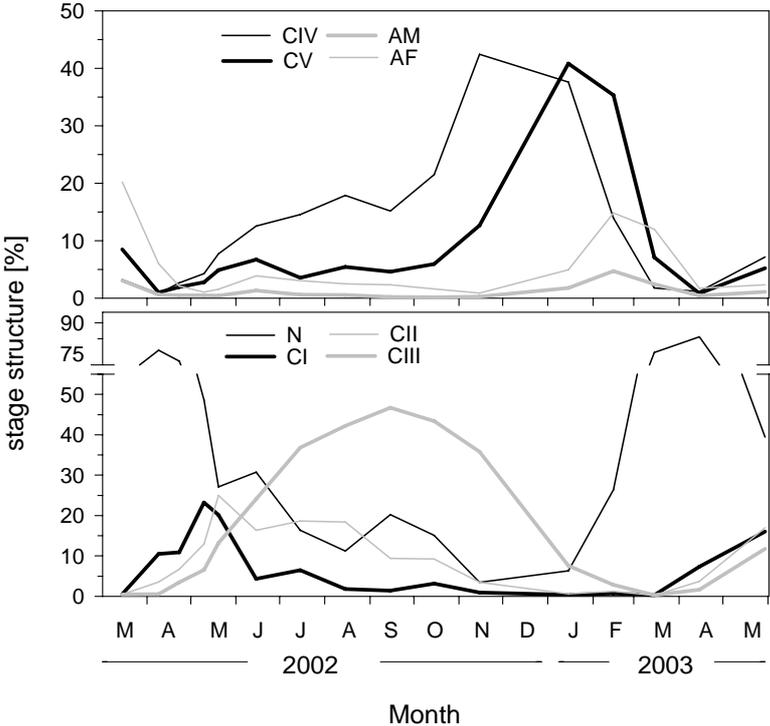


Fig. 4

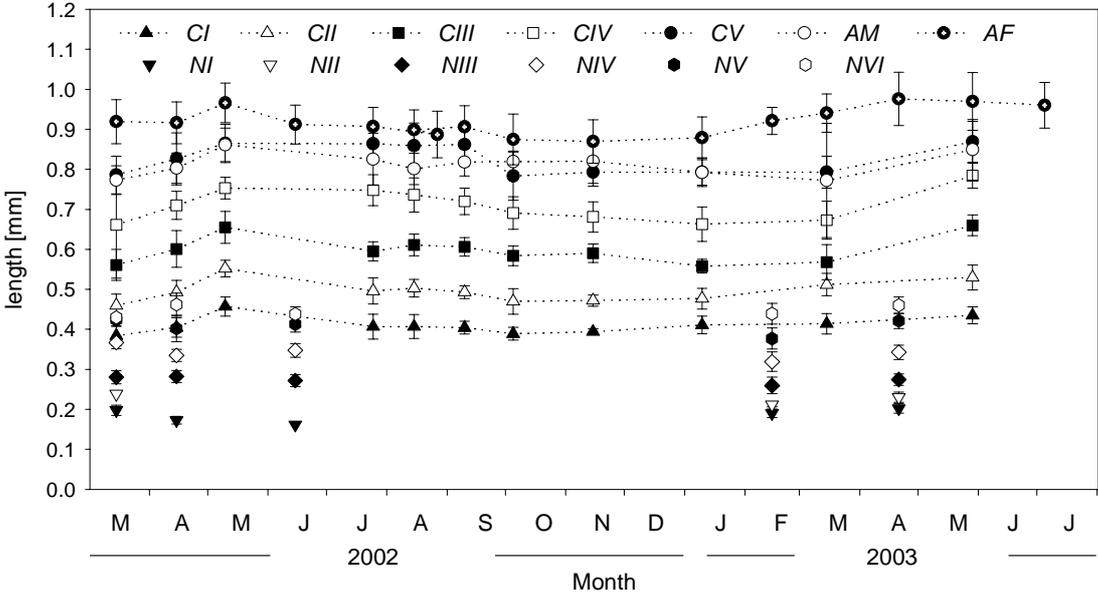


Fig. 5

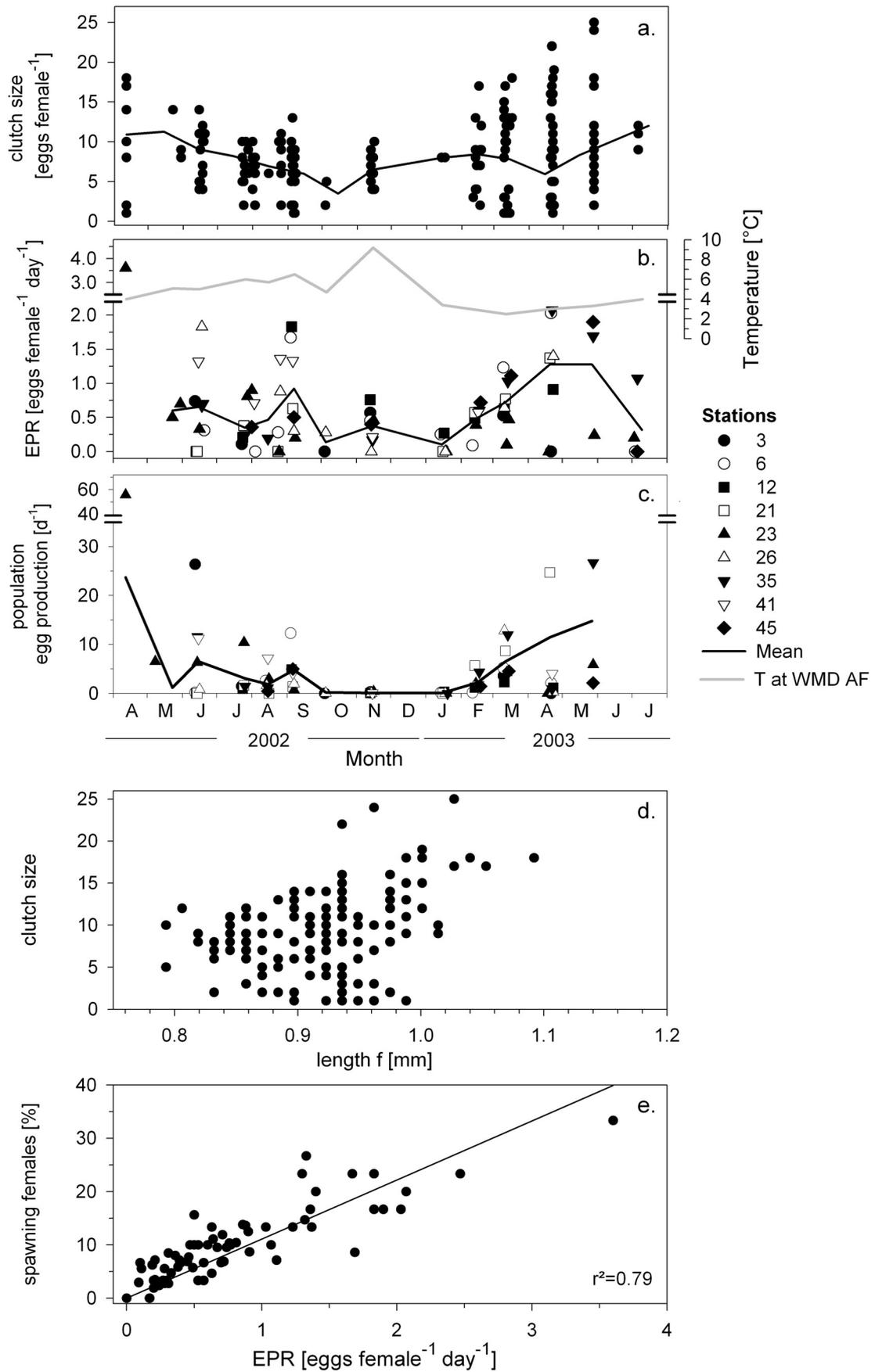


Fig. 6

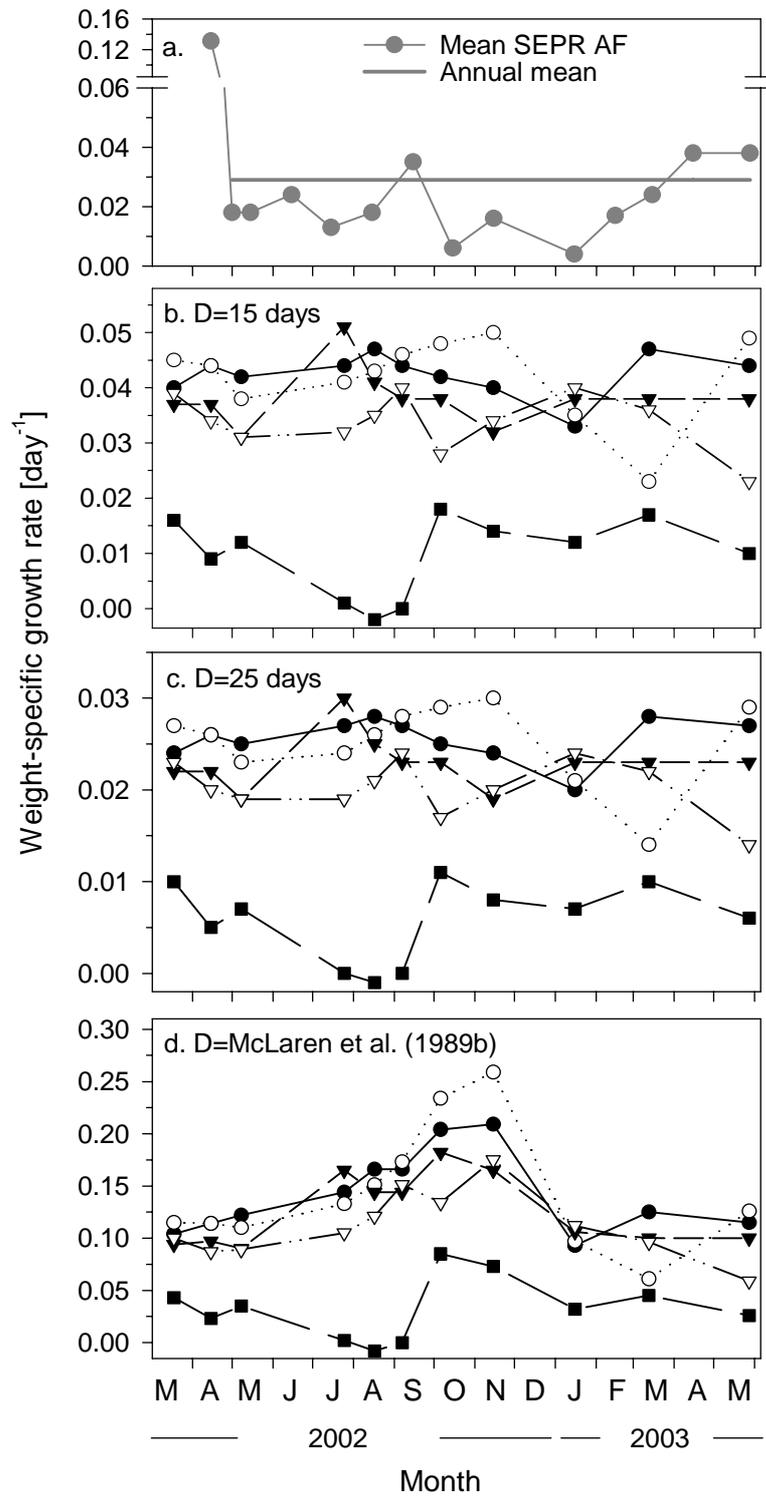
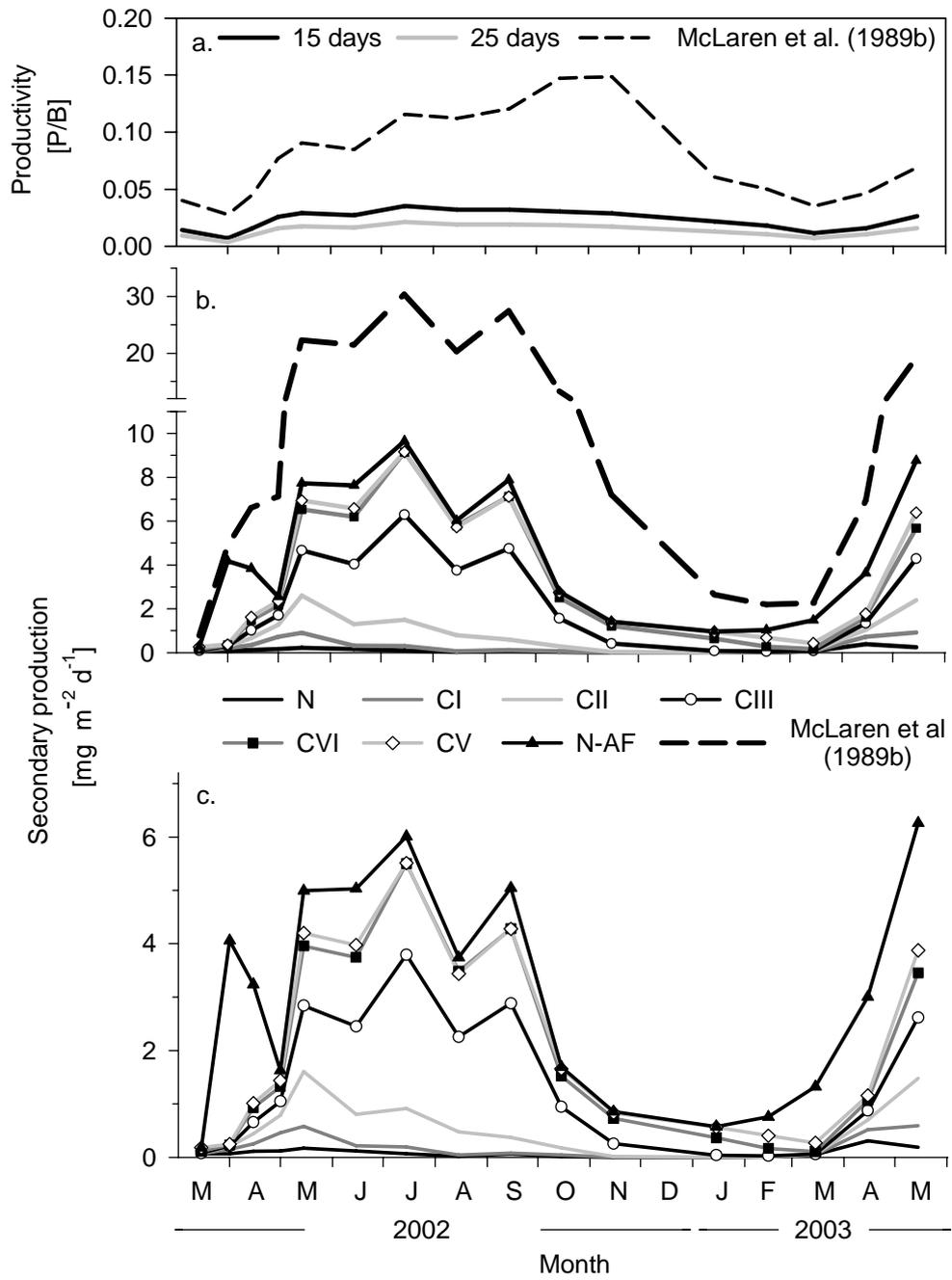


Fig. 7





**Trophodynamics and seasonal cycle of the copepod  
*Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm  
Basin): evidence from lipid composition**

Janna Peters, Jasmin Renz, Justus van Beusekom, Maarten Boersma, Wilhelm Hagen

**Marine Biology, 2006**

With kind permission of Springer Science and Business Media



Janna Peters · Jasmin Renz · Justus van Beusekom  
Maarten Boersma · Wilhelm Hagen

## Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin): evidence from lipid composition

Received: 15 November 2005 / Accepted: 20 February 2006  
© Springer-Verlag 2006

**Abstract** Seasonal lipid dynamics of the copepod *Pseudocalanus acuspes* were studied in the Bornholm Basin (Central Baltic Sea) on a monthly basis from March 2002 until March 2003 and were interpreted in light of life cycle strategies and diet selection. The individual total lipid content of females ranged from 0.9 to 1.8 µg, with relative wax ester content reaching a significant maximum in May (44% of total lipids) and minimum (17% of total lipids) in April and November. Significant changes in size, lipid content, lipid classes and fatty acid composition of structural as well as storage lipids suggested five characteristic seasonal phases that were induced by different feeding histories and environmental conditions. Storage lipids were characterized by 18:1(*n*-9) as major component, which ranged between 44% of total fatty acids in June and 23% in February. The strong coherence between 18:1(*n*-9) in the seston lipids and the occurrence of ciliates emphasized the importance of ciliates in the diet of *P. acuspes*. As indicated by changes in the amounts of fatty acid markers, other food sources varied over the year, suggesting an opportunistic feeding behavior. The spring period was characterized by an increase in typical diatom and dinoflagellate markers, whereas other sources, potentially cyanobacteria, became more important during summer. The life cycle strategy is discussed with respect to extant adaptations to high latitudinal habitats.

### Introduction

*Pseudocalanus acuspes* is a key species in the Central Baltic Sea, as it serves as a major food organism for larval as well as for adult planktivorous fish (Hinrichsen et al. 2002, 2003; Möllmann and Köster 1999, 2002; Möllmann et al. 2003). Knowledge about the processes regulating population dynamics of *P. acuspes* in the Baltic Sea is essential to understand the principal mechanisms accounting for the high variability of copepod production and reproductive success of fish, which is a main focus of the German GLOBEC project.

*Pseudocalanus acuspes* mainly inhabits high latitudes (Frost 1989; Runge and Ingram 1991; Siferd and Conover 1992; Norrbin 1996) and due to its absence in the adjacent North Sea (Bucklin et al. 2003) and wide distribution in the Arctic, it is most likely a member of the Baltic glacial relict fauna. Different life cycles were described for *Pseudocalanus* spp. in high Arctic regions: from biennial (Cairns 1967) and annual cycles (Davis 1976; Conover and Siferd 1993; Lischka and Hagen 2005) up to cycles with two or more generations per year (Pertsova 1981; McLaren et al. 1989; Norrbin 1992). In temperate regions several generations per year are commonly observed (Marshall 1949; Digby 1950).

As a characteristic of the Baltic Sea, adult females of *P. acuspes* are more abundant in water layers below the thermocline and often concentrate near the halocline, presumably induced by the strong vertical stratification of the water column (Hernroth and Ackefors 1979; Henroth 1985; Renz and Hirche 2006). Hence, sinking algae, detritus or microzooplankton are most likely the only available food sources. Feeding and growth conditions might therefore be suboptimal for this originally marine species (Renz and Hirche 2006) in the temperate brackish environment, with seasonal cycle and diet differing from those of other habitats. Valuable information on the life cycle and overwintering strategy of *P. acuspes* in the Baltic Sea can be derived from seasonal dynamics in storage lipid content and fatty acid

Communicated by O. Kinne, Oldendorf/Luhe

J. Peters (✉) · W. Hagen  
Marine Zoology, University of Bremen, P.O. Box 330440, 28334  
Bremen, Germany  
E-mail: [janna.peters@uni-bremen.de](mailto:janna.peters@uni-bremen.de)  
Tel.: +49-421-2189508  
Fax: +49-421-2182285

J. Renz · J. van Beusekom · M. Boersma  
Alfred Wegener Institute for Polar and Marine Research,  
P.O. Box 120161, 27515 Bremerhaven, Germany

composition of polar, i.e. structural lipids as well as from size variations, as these attributes reflect environmental conditions and food supply during growth of different cohorts.

Studies on in situ grazing rates and food selection of *Pseudocalanus* spp. are scarce. It has been described that *Pseudocalanus* spp. exhibits a primarily herbivorous feeding behavior (e.g. Schnack 1975; Corkett and McLaren 1978; Fraser et al. 1989; Cotonnec et al. 2001), whereas other studies suggested a more omnivorous feeding mode (Båmstedt et al. 1990; Norrbin et al. 1990; Peters et al. 2004). To elucidate seasonal dynamics in diet we applied signature fatty acids to identify trophic relationships. We specifically focused on the fatty acid composition of storage, i.e. neutral lipids, in order to obtain unambiguous signals.

The use of specific fatty acids to characterize feeding on different taxonomic groups is well established, e.g. the assignment of 16:1(*n*-7) and 20:5(*n*-3) to diatoms (Nichols et al. 1993; Dunstan et al. 1994; Skerrat et al. 1997) and 18:4(*n*-3) and 22:6(*n*-3) to dinoflagellates (Sargent et al. 1987; Graeve et al. 1994). However, it is essential to validate those results in the studied ecosystem by comparing fatty acid profiles of the seston with its taxonomic composition. Beside the fatty acid dynamics in the neutral lipids of the copepods, we therefore provide data on the seasonal variation of the seston composition to reveal seasonal changes in the diet of *P. acuspes*.

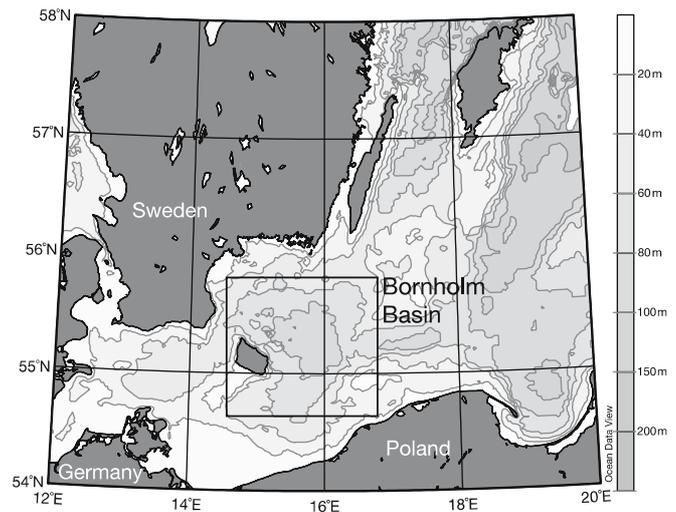
## Materials and methods

### Sampling and experiments

Zooplankton and seston samples were collected in approximately monthly intervals from March 2002 until March 2003 (except for October and December) on 11 cruises in the Bornholm Basin (Fig. 1). To provide representative data for the whole basin, both stations in central and in marginal areas were sampled on each cruise and combined in average values for each month, except for January and February 2003, where only samples from the central basin were available.

Zooplankton was sampled using a WP-2 net with a 10-l bucket end (vertically towed with 0.2 m/s, mesh size 200  $\mu$ m, 0.26 m<sup>2</sup> opening). Sampling depths were adjusted to hydrography covering the water column from the lower halocline up to the surface. Copepods were sorted on board under ambient temperature conditions into  $-80^{\circ}\text{C}$  precooled glass vials. Depending on availability each sample consisted of 20–150 adult females of *P. acuspes* or copepodite stages V (CV), respectively. On three stations of each cruise prosoma lengths of 30 females were measured using formalin preserved samples (4% in seawater).

Seston samples from five depths were taken with 10 l water sampler bottles. Vertical resolution was adapted to the hydrographic structure of the water column, with samples taken from the upper water layer (5 m), from



**Fig. 1** Map of investigation area, generated with ODV software (Schlitzer 2005)

above the thermocline (10 m), from the midwater layer, from above the halocline and in the halocline. Depending on seston concentrations 2–6 l of water were filtered with low pressure ( $-200$  mbar) on precombusted (12 h at  $400^{\circ}\text{C}$ ) GF/C filters. All zooplankton organisms were carefully removed under the stereomicroscope immediately after filtration and prior to freezing, so that they did not bias the seston data. Zooplankton samples and filters were permanently stored at  $-80^{\circ}\text{C}$  until further analysis.

For analyses of taxonomic seston composition aliquots of 100 ml were taken from water sampler bottles, preserved with 2% acid Lugol's solution and stored cool and dark until further investigation. Samples were analyzed using Uthermöhl microscopy and phytoplankton as well as protozooplankton cell size was converted to biomass according to Edler (1979) and Putt and Stoecker (1989), respectively.

### Analytics

After lyophilization dry mass of copepods was determined using a Sartorius micro-balance ( $\pm 2$   $\mu$ g). During weighing procedure, samples were temporarily stored in a vacuum desiccator to prevent unequal condensation on the tissue. Lipid extraction was performed with minor modifications as described in Folch et al. (1957) using ultrasonic disruption in dichloromethane:methanol (2:1/v:v) and a washing procedure with aqueous KCl solution (0.88%). For quantification of fatty acids, tricosanoic acid was added as an internal standard prior to extraction.

Lipid classes were separated by solid phase extraction, using 1 ml SiOH glass columns (CHROMABOND®, Macherey-Nagel) on a vacuum manifold. To remove residues the columns were washed with a solvent sequence of acetone, diethylether, and hexane:diethylether-mixtures, prior to sample load. After column conditioning with

4 ml of hexane, 4 µl of lipid extract (lipid concentration approx. 5 µg/µl) were added. The neutral lipid fraction was washed out with 2.5 ml hexane:diethylether (95:5/v:v) and 2.5 ml hexane:diethylether (1:1/v:v). Polar lipids were eluted with 2.5 ml methanol and subsequently 5 ml of dichloromethane were added. The polar fraction was then washed with 2 ml aqueous KCl solution (0.88%).

For fatty acid analyses a subsample of total lipids as well as the total neutral and polar lipid fraction were hydrolyzed and fatty acids were converted to their methyl ester derivatives (FAME) in methanol containing 3% concentrated sulfuric acid at 80°C for 4 h (Kattner and Fricke 1986). After cooling, 2 ml of Aqua bidest. were added, and FAMES were extracted three times with 1 ml hexane. Samples were analyzed using a gas chromatograph (HP 6890A) equipped with a DB-FFAP column (30 m length, 0.25 mm inner diameter, 0.25 µm film thickness) operated with a temperature program and helium as carrier gas. Samples were injected using a hot split/splitless inlet (250°C, split mode 1:20) or a programmable temperature vaporizer injector (solvent vent mode). The FAMES and fatty alcohols were detected by flame ionization and identified by comparing retention times with those derived from standards of known composition. The accurate identification of the substances was checked for selected peaks using GC-MS.

#### Calculations and statistical analyses

The proportions of wax esters (WE), triacylglycerols (TAG) and polar lipids (PL) were estimated based on comparisons of the relative fatty acid and alcohol composition of the neutral lipid fraction and the total lipid extract, whereas the composition of the polar lipid fraction was used to verify the results. Taking the non-fatty acid components into account, the usually dominating phosphatidylcholine was assumed to be the only polar lipid component and the corresponding mass ratio was used. However, this method does not account for sterol esters and cholesterol. Furthermore, the WE content was calculated based on the alcohol content in the total lipid extract.

All statistical analyses were performed using the software SPSS. For all statistical operations that require normal distribution, percentage data (e.g. relative fatty acid composition) were transformed using an arc sine square root transformation. Normal distribution and homogeneity of variances were checked using the Shapiro-Wilk- and the Levene-test, respectively, according to sample size. For identification of coherences between fatty acid markers and seston taxa, as well as within the fatty acids of seston and storage lipids of *P. acuspes* females, principal component analyses (PCAs) were performed on the correlation matrix, extracting non-rotated components with eigenvalues > 1. Relevant variables (i.e. length, biomass, total and storage lipid content) were analyzed using one-way ANOVA followed by a Tukey's HSD test for post hoc comparisons with time as independent variable.

To detect seasonal changes between fatty acid compositions in the neutral and the polar lipid fraction of females, the relative amount of each fatty acid was tested between two adjacent months using a Student's *t*-test. If the difference between 2 months was only due to one fatty acid on a significance level of  $P < 0.01$  or two fatty acids on a significance level of  $P < 0.05$ , the months were fused to one group. Afterwards, these groups were tested against each other. For months with less than three replicates, i.e. January and February, the months were assigned to the group with the highest similarity in a cluster analysis using the PRIMER software (based on Bray-Curtis similarity and complete linkage cluster mode, data not presented). Selectivity, here understood as ratio between availability of individual fatty acids in the seston and the incorporation into the storage lipids of *P. acuspes*, was calculated as ratio between their relative content in the seston and in the neutral lipids of the copepods using a logarithmic scale.

---

## Results

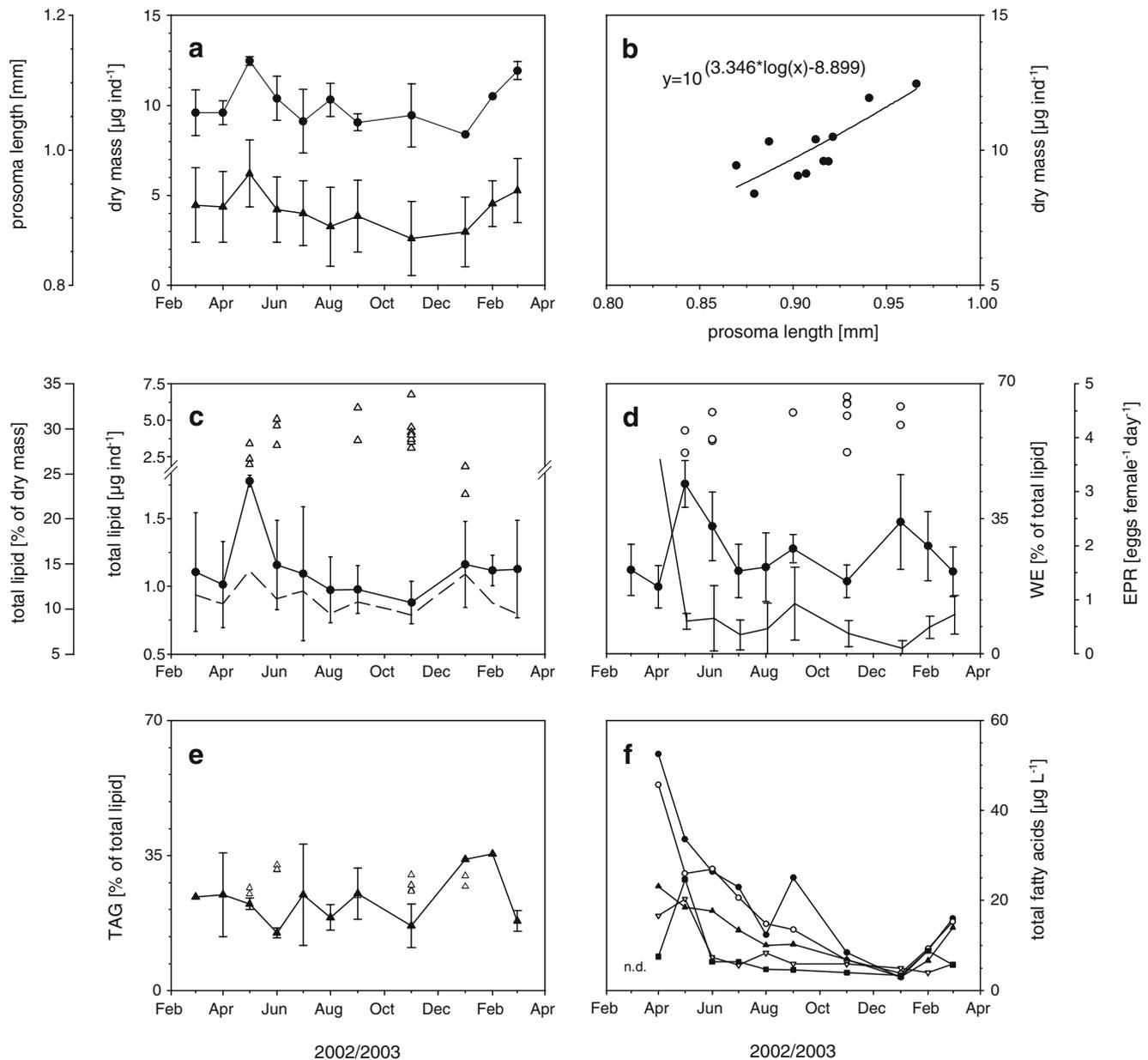
### *Pseudocalanus acuspes*

Females of *P. acuspes* differed substantially in size between succeeding months (Fig. 2a), with a highly significant increase of prosoma length as well as biomass in May up to an average of 966 µm (significant difference to April and June  $P < 0.001$ ) and 12.5 µg/individual, respectively. Over the summer their size decreased, reaching a minimum of 870–880 µm in length in November (significant difference to September  $P < 0.01$ ) and January (significant difference to February  $P < 0.001$ ). From February on, females increased in size again. Dry mass-length ratios, based on monthly averages of variables, basically followed the relationship established by Hay et al. (1988) (Fig. 2b).

The lipid content in terms of total fatty acids and alcohols of the females ranged from 0.9 to 1.8 µg/individual and from 9 to 14% of dry mass, respectively (Fig. 2c), with a maximum in May (significant difference to April  $P < 0.05$ ). There was no significant difference in May between the total individual lipid content of the females and the copepodite stage V (mean 2.6 µg/individual). In all other months examined, the lipid amount of CV was clearly higher than that of the females, with an average individual lipid content between 4.7 µg in September and 1.6 µg in January.

In both stages, females and CV, wax esters (WE) as well as triacylglycerols (TAG) served as storage lipids throughout the year. Neutral lipids of females (WE and TAG) comprised about two-thirds of total lipids in May and January, respectively, and one-third of total lipids in November (Fig. 2d, e).

The relative amount of TAG ranged between 15 and 35% of total lipids, but due to a high variability no seasonal trends could be identified, neither for



**Fig. 2** **a** Prosoma length and dry mass of adult females of *Pseudocalanus acuspes*: triangles monthly average of length, circles monthly average of dry mass, error bars standard deviation. **b** Length dry mass relationship of adult females of *P. acuspes*: circles monthly average of dry mass versus monthly average of prosoma length, line length dry mass relationship determined by Hay et al. (1988). **c** Total lipid content of *P. acuspes*: circles monthly average of total fatty acids and alcohols (TL) per female, error bars standard deviation, open triangles TL per copepodite stage V (data points stations, please note axis break), dashed line monthly average of TL in percent of dry mass in adult females. **d** Wax ester (WE) content and egg production rates (EPR) of *P. acuspes*: filled circles monthly average of WE [%

TL] in adult females, open circles WE [% TL] in copepodite stage V (data points stations), line without symbols monthly average of daily individual egg production, EPR modified from J. Renz et al. (submitted), error bars standard deviation. **e** Triacylglycerol (TAG) content of *P. acuspes*: filled triangles monthly average of TAG [% TL] in adult females, open triangles TAG [% TL] in copepodite stage V (data points stations), error bars standard deviation. **f** Monthly average of lipid concentration in the seston: filled circles upper water layer (5 m), open circles above thermocline (10 m), filled triangles midwater layer (20–30 m), open triangles above halocline (30–40 m), filled squares in halocline (40–60 m), n.d. no data

females nor CV. In contrast, the relative WE content of the females changed over the year, reaching a maximum of 44% of total lipids in May (significant difference to April  $P < 0.001$ ) and lowest values of 17% in April and November. From November the wax ester content increased until January, afterwards it

declined again until March. The WE content of CV was significantly higher during all months, except for May, when values were in the same range as for the females.

Egg production data were adopted from J. Renz et al. (submitted). Daily egg production rates (EPR) showed

an overall high variability in the Bornholm Basin (Fig. 2d), reaching a minimum of 0.1 eggs per female per day in January and increasing again in February. The highest EPR was measured in April, but was based only on data from one station, i.e. on the average EPR of 30 females. Whereas in summer mean EPR and WE content paralleled, EPR increased with decreasing WE content in spring 2003.

The total fatty acid composition of females was characterized by high amounts of the typical membrane components 16:0, 20:5( $n-3$ ), 22:6( $n-3$ ), as well as by elevated levels of 18:1( $n-9$ ). Alcohols were dominated by 14:0 and 16:0, while 18:0 and 18:1 were found in much lower quantities (Table 1).

Within the neutral lipid fraction ten important fatty acids (i.e. maximum values  $\geq 2\%$  of total fatty acids) were identified (Table 2). The fatty acid 18:1( $n-9$ ) dominated during all seasons, ranging between 44% of total fatty acids in June and 23% in February. Based on their relative fatty acid composition, females were merged into five seasonal groups, which exhibited highly significant differences (Table 2). The first group included females from March and April 2002 as well as from February and March 2003. This spring season was characterized by elevated amounts of the dinoflagellate marker 18:4( $n-3$ ), whereas the diatom marker 16:1( $n-7$ ) peaked in May. Both groups showed high percentages of

20:5( $n-3$ ) and 22:6( $n-3$ ), also indicating diatom- and dinoflagellate-based diets, respectively. In May, 18:1( $n-9$ ) strongly increased, reaching maximum values in June. From June to September fatty acids were characterized by rising levels of 18:2( $n-6$ ) and 18:3( $n-3$ ), reaching up to 12 and 8%, respectively. In winter higher amounts of the unspecific fatty acids 16:0, 16:1( $n-9$ ) and 18:0 prevailed.

The neutral lipids of CV showed a very similar fatty acid composition to those of the females (Fig. 3). Especially in May and June there was no significant difference between the fatty acids of both stages, whereas in autumn and winter the fatty acids 18:1( $n-9$ ), 18:2( $n-6$ ), 18:4( $n-3$ ) and 20:5( $n-3$ ) of CV showed higher percentages.

Principal component analysis on the storage lipid composition of females extracted three components with eigenvalues  $> 1$ . Only the major two, together explaining 68% of the variance, are presented (Fig. 4). The PCA revealed a strong coupling between the fatty acids 18:2( $n-6$ ) and 18:3( $n-3$ ), as well as between 22:6( $n-3$ ), 20:5( $n-3$ ) and 16:1( $n-7$ ). The fatty acids 16:1( $n-9$ ), 18:0 and 18:4( $n-3$ ) were important moieties to distinguish samples along component one, whereas 18:1( $n-9$ ), 22:6( $n-3$ ) and 16:1( $n-7$ ) mostly affected samples influenced by component two. Other fatty acids, like 18:3( $n-3$ ) and 18:2( $n-6$ ) had a high impact on both

**Table 1** Relative composition of fatty acids [percentage of total fatty acids] and fatty alcohols [percentage of total fatty alcohols] in total lipids of adult females and copepodite stage V (CV) of

*Pseudocalanus acuspes*, values are calculated on basis of monthly averages, values below 1% not shown

	Females				CV			
	Min	Max	Mean	SD	Min	Max	Mean	SD
<b>Fatty acids</b>								
14:0	<1	1.6	1.0	0.3	<1	<1	<1	–
15:0	<1	1.2	<1	–	<1	<1	<1	–
16:0	10.3	20.7	15.0	2.9	6.0	8.3	7.1	1.0
17:0	<1	1.0	<1	–	<1	<1	<1	–
18:0	<1	3.7	2.5	0.6	<1	1.3	<1	–
16:1( $n-7$ )	1.1	6.5	2.4	1.5	3.3	7.6	4.9	1.6
16:1( $n-9$ )	<1	2.6	<1	–	<1	<1	<1	–
18:1( $n-5$ )	1.6	4.1	2.8	0.9	<1	2.1	1.3	0.6
18:1( $n-7$ )	1.4	2.9	2.0	0.4	1.3	1.6	1.5	0.1
18:1( $n-9$ )	10.1	26.1	18.9	5.2	28.9	39.6	34.8	4.4
24:1	1.3	3.3	2.2	0.7	<1	<1	<1	–
16:2( $n-4$ )	<1	1.2	<1	–	<1	<1	<1	–
18:2( $n-6$ )	2.9	8.5	5.6	1.9	4.2	10.7	7.1	2.8
16:3( $n-4$ )	<1	1.0	<1	–	<1	<1	<1	–
18:3( $n-3$ )	1.7	4.8	3.3	1.1	2.2	6.9	5.1	1.9
18:3( $n-6$ )	<1	1.0	<1	–	<1	<1	<1	–
18:4( $n-3$ )	1.3	5.8	3.6	1.4	4.1	7.2	6.1	1.2
20:4( $n-3$ )	<1	1.6	1.1	0.4	1.0	2.9	2.1	0.7
20:5( $n-3$ )	12.4	19.5	15.2	2.4	9.8	14.3	12.0	2.1
22:6( $n-3$ )	16.6	26.2	22.0	3.1	10.6	20.5	15.2	4.0
<b>Fatty alcohols</b>								
14:0	21.4	33.2	26.7	3.7	22.9	30.0	27.2	2.7
16:0	55.2	70.2	62.7	5.1	59.5	69.6	65.6	3.9
18:0	<1	11.5	5.1	3.7	1.5	2.6	2.0	0.4
18:1	2.8	8.2	5.2	1.6	3.5	9.6	5.2	2.5
20:1	<1	1.6	<1	–	<1	<1	<1	–

Min Minimum, Max maximum, SD standard deviation, – SD not calculated

**Table 2** Relative fatty acid composition of neutral lipids of females of *Pseudocalanus acuspes*

	I		II		III		IV		V		Level of significance (Student's <i>t</i> -test)									
	Feb–Apr ( <i>n</i> =11)		May ( <i>n</i> =3)		June ( <i>n</i> =4)		July–Sept ( <i>n</i> =14)		Nov–Jan ( <i>n</i> =4)		Adjacent groups					Distant groups				
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	I:II	II:III	III:IV	IV:V	I:V	I:III	I:IV	II:IV	II:V	III:V
16:0	13.3	2.5	8.2	1.3	9.4	3.1	14.8	2.8	17.7	4.4	**		**		*	*		***	**	*
18:0	3.0	1.1	1.8	0.6	2.6	1.1	3.0	0.8	6.5	1.9				***	***			*	**	**
16:1( <i>n</i> =7)	5.0	1.3	9.2	1.0	5.0	0.4	2.5	0.5	3.8	1.1	***	***	***				***	***	**	**
16:1( <i>n</i> =9)	1.6	1.1	1.3	1.4	1.3	0.5	1.6	1.2	7.3	2.8				***	***				**	**
18:1( <i>n</i> =9)	26.7	5.0	39.1	1.4	43.8	0.5	35.9	4.5	35.7	5.0	***	**	**		**	***	***			*
18:2( <i>n</i> =6)	8.2	1.3	8.2	0.6	11.6	2.0	12.4	2.2	5.7	1.6		*		***	**	**	***	**		**
18:3( <i>n</i> =3)	5.7	0.9	3.0	0.3	5.2	1.5	7.9	2.2	2.7	1.0	***	*	*		***	***	**	***		*
18:4( <i>n</i> =3)	8.3	1.9	3.8	0.3	3.7	1.8	4.3	1.7	1.6	0.6	***			**	***	***	***		**	*
20:5( <i>n</i> =3)	9.4	2.2	8.5	0.5	6.6	0.4	5.6	0.8	4.7	1.4		**	*		**	**	***	***	*	
22:6( <i>n</i> =3)	6.3	3.3	8.6	0.9	5.5	0.6	3.6	1.3	3.7	0.9		**	*				**	***	**	*

I–V Seasonal groups, SD standard deviation

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

components and could not be assigned clearly. Samples from different months were separated, demonstrating seasonal changes in the fatty acid compositions of storage lipids.

Although polar lipids remained rather uniform throughout the year, with 16:0, 20:5(*n*=3) and 22:6(*n*=3) contributing between 50 and 73% of total fatty acids (Table 3), their fatty acid profiles divided into the same seasonal groups as the storage lipids. Small but significant differences were mainly due to changes of the 18:1 isomers, as well as of 18:3(*n*=3) and 18:4(*n*=3), with largest changes between early (March–April) and late spring (May).

### Seston

Maximum lipid concentrations in the seston were always found above the thermocline during spring and summer, whereas from autumn until spring, mixing caused more equally distributed lipid contents over the whole water column (Fig. 2f). In terms of total fatty acids and alcohols, maximal lipid contents with up to 52 µg/l were found in upper water layers in April. This lipid-rich seston reached lower water layers with a time delay of 1 month, resulting in a lipid peak near the halocline of 20–24 µg/l in May.

The PCA revealed a strong coherence within the relative seston composition in terms of biomass of different taxonomic groups and typical signature fatty acids (Fig. 5). There was a distinct correlation between 18:1(*n*=9) and ciliates and to a lesser degree flagellates, between 16:1(*n*=7), 20:5(*n*=3) and diatoms as well as a coherence between 22:6(*n*=3), 18:4(*n*=3) and dinoflagellates. The strong connection between 18:2(*n*=6) and 18:3(*n*=3) could not be assigned to a specific algal group, but they both had a very similar impact on component one as cyanobacteria and chlorophytes, whereas component two differentiated them. Due to their relative position on component three 18:2(*n*=6) grouped with chlorophytes, whilst 18:3(*n*=3) correlated with cyanobacteria.

Ciliates contributed significantly to seston biomass at all seasons (Table 4), maximum proportions of diatoms were found in spring, of ciliates and dinoflagellates in May. In contrast, other flagellates and cyanobacteria increased during the summer. No data were available for the winter season.

### Trophic interactions

When compared with seston lipids, some fatty acids of *P. acuspes* females developed with a time lag of 1–2 months at the beginning of 2002, whereas in autumn and winter seston and copepods showed relatively parallel progressions (Fig. 3). Specifically the increase of 18:3(*n*=3) and 18:2(*n*=6) in May and June was reflected with some delay in the storage lipids of females. In May, the increase of 18:1(*n*=9) in females co-occurred with a rise in the seston from lower water layers, whereas the peak in the upper water column in July was not found in the copepods.

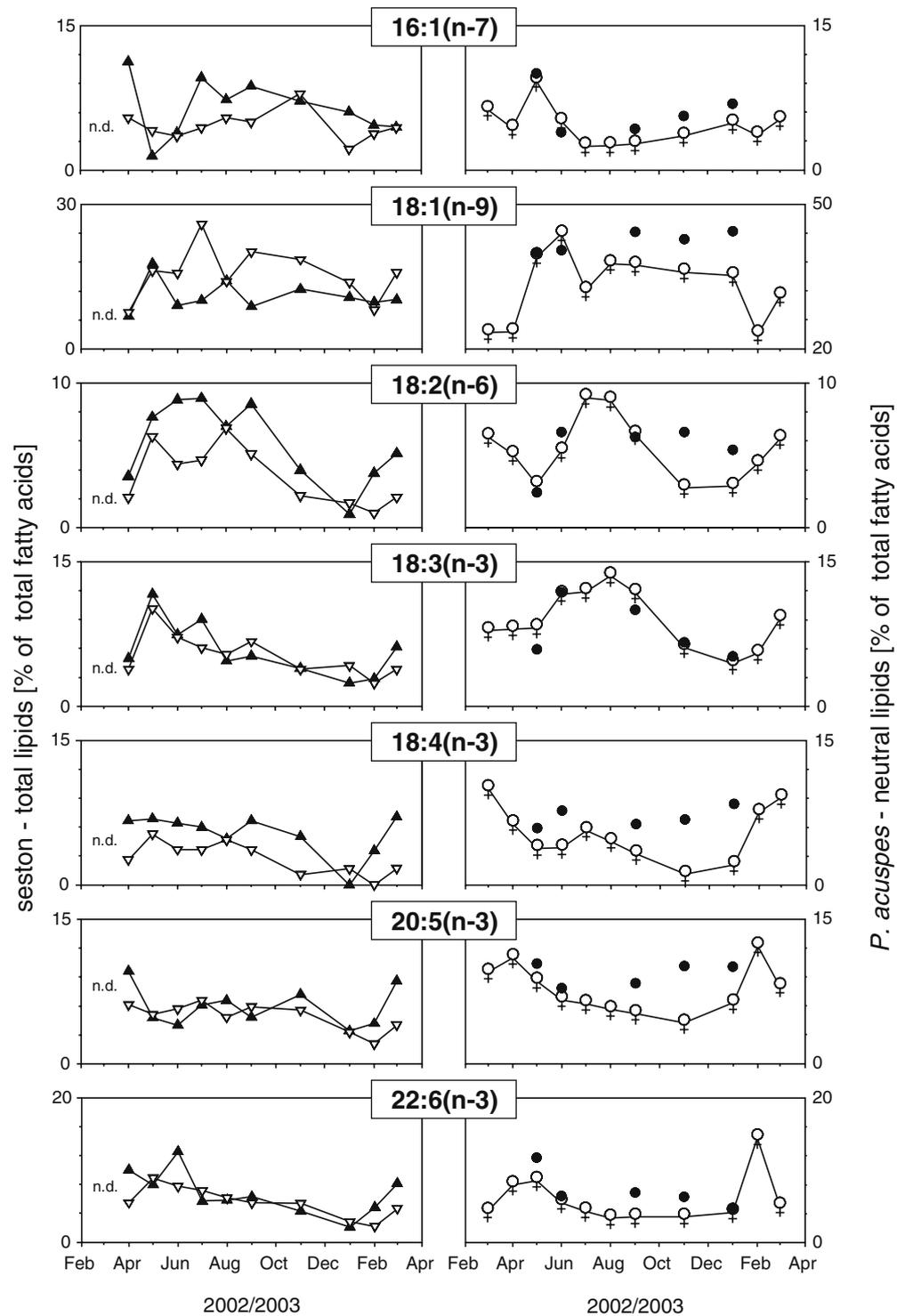
As indicated by a selection index (Fig. 6), 16:0 and 18:0 were usually negatively selected during all seasons, whereas 18:1(*n*=9), 18:2(*n*=6) and 20:5(*n*=3) were elevated in the neutral lipids most of the time. Selectivity for all other fatty acids changed with time or depth. In early spring 18:3(*n*=3), 18:4(*n*=3) and 22:6(*n*=3) were accumulated in storage lipids as compared to the seston, as well as 16:1(*n*=7) in May and June.

## Discussion

### Seasonal cycle

The seasonal cycle and condition of *P. acuspes* in the Bornholm Basin were described on the basis of lipid content and composition as well as prosoma length, to relate lipid dynamics and size variations to the life cycle of this originally Arctic copepod in the Baltic Sea. Pronounced changes in body size and fatty acid composition of

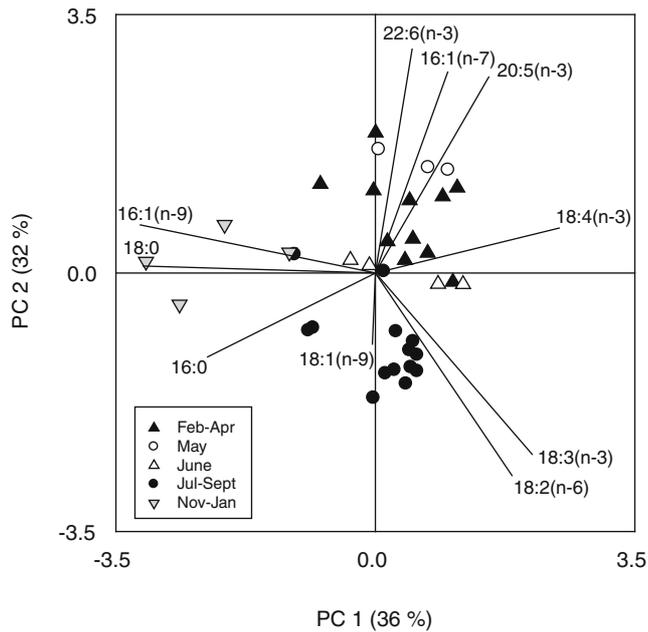
**Fig. 3** Seasonal development of mean fatty acid composition of seston (total lipids) and *P. acuspes* (neutral lipids): *n.d.* no data, *filled triangles* seston in upper water layer (5 m), *open triangles* seston in halocline (40–60 m), *filled circles* copepodite stage V, *open circles with cross* adult females



structural lipids of females revealed five “environmental cohorts”, which obviously experienced similar biotic and abiotic conditions during development, thus leading to constant attributes of females: early spring (February–April), late spring (May), early summer (June), late summer (July–September) and winter (November–January). Recent studies on stage composition and growth measurements (Renz and Hirche 2006; J. Renz et al., submitted) indicate that *P. acuspes* basically follows an annual

cycle in the Bornholm Basin, although the development of a second cohort in summer was also considered possible.

Aligning the “environmental cohorts” in this context, the early spring cohort consisted of females, which successively matured from older overwintering copepodite stages. Their growth was at least partly fueled by storage lipids, as indicated by the decrease in wax ester content. This cohort was followed by females in May, which were



**Fig. 4** Principal component analysis on the relative fatty acid composition of neutral lipids of adult females of *P. acuspes*, scales were adjusted to combine plots: scales of principal components (PC) refer to sample plot, scale of variables reaches from  $-1$  to  $+1$  for both PCs

probably larger due to better feeding conditions and lower temperatures (Vidal 1980; Klein Breteler and Gonzalez 1988). Strong changes in size co-occurred with variations in the composition of structural lipids and in storage lipid content, indicating different feeding histories during growth. The May cohort probably derived from younger overwintering copepodids of the previous year, which encountered a high food supply in the upper water column in April. In May lipid-rich seston reached lower water layers, thus providing better feeding conditions for older copepodite stages and females. It remains, however, a matter of conjecture, whether the drastic

changes in May were due to successively maturing cohorts or rather to the appearance of a new generation.

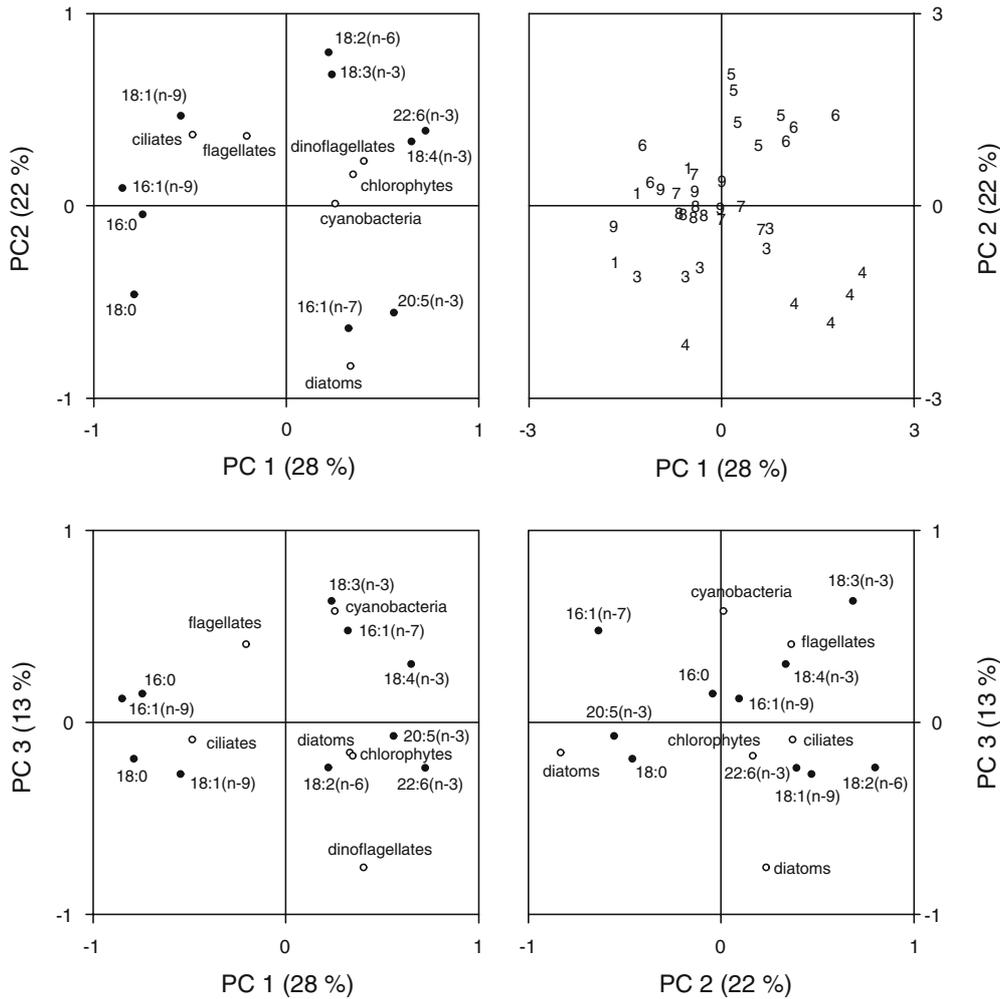
To better understand the further progression of the seasonal cycle, valuable information can be derived from comparisons of storage lipid content of CV and females. In May the amounts of storage lipids of females and CV hardly differed, whereas in summer the copepodids were always richer in wax esters. A similar decrease in storage lipids, measured as oil sac volume, was observed by McLaren et al. (1989) in summer females of *P. acuspes* in the Bedford Basin, Nova Scotia. Two, not mutually exclusive mechanisms, causing the pronounced differences between females and copepodids, can be assumed:

1. *Food supply*: The accumulated storage lipids were used up very quickly by the females for metabolic costs of last molt, gonad maturation and egg production. Due to reduced food availability, the depletion of reserves proceeded more quickly during summer than in May, explaining a high wax ester retention of females in late spring. Lipid retention is a direct expression for surplus of food. Apparently, the food supply alone was not sufficient to sustain egg production at ambient temperatures in summer. The pronounced utilization of storage lipids signifies that in summer food limitation might have been an important factor, whereas in May egg production was primarily determined by abiotic factors. Hence, sub-optimum growth conditions might reduce the number of generations per year.
2. *Onset of overwintering*: Only the lipid-poor copepodids accomplished maturation during summer and autumn to produce potentially more successful offspring, whereas the lipid-rich copepodids passed into an "active diapause", with ongoing feeding, suspended development and resting gonads (McLaren et al. 1989). According to this hypothesis, the females found in the Bornholm Basin from summer to winter would represent a still maturing but minor part of the population. This is consistent with the drastic decline

**Table 3** Relative fatty acid composition of polar lipids of females of *Pseudocalanus acuspes*

	I		II		III		IV		V				Level of significance (Student's <i>t</i> -test)				
	March-Apr ( <i>n</i> = 14)		May ( <i>n</i> = 3)		June ( <i>n</i> = 4)		July-Sept ( <i>n</i> = 14)		Nov ( <i>n</i> = 3)		Jan ( <i>n</i> = 1)	Feb ( <i>n</i> = 2)	Adjacent groups				
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	Mean	I:II	II:III	III:IV	IV:V	I:V
16:0	16.1	1.1	17.6	0.2	17.8	1.5	16.4	1.3	18.5	0.7	22.3	19.7	*			*	**
18:0	3.3	1.9	2.8	0.1	5.0	3.3	3.2	0.4	4.4	1.0	6.5	4.9				**	
18:1( <i>n</i> = 5)	5.1	0.8	3.3	0.1	3.2	0.5	3.5	0.3	3.7	0.1	3.5	4.0	**				**
18:1( <i>n</i> = 7)	1.9	0.2	1.1	0.0	1.3	0.3	1.6	0.3	1.6	0.1	2.2	2.1	***				*
18:1( <i>n</i> = 9)	3.7	0.9	5.4	1.1	7.5	1.0	5.4	1.6	4.9	0.6	7.4	7.8	*	*	*		*
18:2( <i>n</i> = 6)	3.9	1.6	2.5	0.1	6.3	3.4	5.0	1.5	0.5	1.4	1.7	6.4		*		***	***
18:3( <i>n</i> = 3)	1.4	0.3	0.9	0.0	1.8	0.2	2.6	0.8	0.7	0.1	0.6	1.6	**	***	*	***	***
18:4( <i>n</i> = 3)	3.3	0.9	1.6	0.1	2.1	0.6	2.9	1.1	1.0	0.2	1.0	3.4	**			**	***
20:5( <i>n</i> = 3)	21.0	3.1	20.0	1.1	16.8	3.0	20.2	2.0	17.7	0.7	12.9	12.6			**	*	
22:6( <i>n</i> = 3)	33.4	4.9	40.9	0.4	33.0	5.2	34.0	2.9	37.4	2.6	29.0	29.3	*	*			

I-V Seasonal groups, SD standard deviation  
 \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$



**Fig. 5** Principal component analysis on the relative taxonomic (in terms of biomass) and fatty acid composition of the seston: loading plots for the extracted principal components (PC) 1–3 (*open circles*

seston taxa, *filled circles* fatty acids) and sample plot for the extracted PCs 1 and 2 (*numbers* months of the year)

of female and nauplii abundance in the water column in July and August (Renz and Hirche 2006) and the slow developmental rates in late spring and summer (J. Renz et al., submitted). Such a continued development of only a minor part of the generation of *Pseudocalanus* sp. was also observed in the White Sea (Pertsova 1981). Norrbin (Norrbin et al. 1990; Norrbin 1996) suggested that it is less a continuous process, triggered by the physiological state as proposed by McLaren et al. (1989), but rather a specific switching date, at which *P. acuspes* copepodids stop maturation but proceed to accumulate lipids. Klein Breteler and Gonzalez (1988) suspected that changes to poor food conditions are necessary to induce hormonal cessation of development in favor of lipid production. Still, it remains unclear, how an external trigger, which would be effective early in the year, should function in the Bornholm Basin, with higher temperatures and longer periods of high food abundance as compared to high latitudinal habitats.

In conclusion, we found evidence that the life cycle of *P. acuspes* in the Baltic Sea resembles that of *Pseudocalanus* spp. in Arctic regions (e.g. Pertsova 1981; McLaren et al. 1989; Norrbin et al. 1990; Norrbin 1991; Conover and Siferd 1993), with highest reproductive activities in spring, a successive accumulation of resting copepodite stages starting in early summer and a potential interposition of minor summer generations. This is supported by the corresponding lipid-storing strategies of *P. acuspes*. Wax ester levels in the Baltic were similar to those found for CIV and CV of *P. acuspes* in Arctic regions (Båmstedt et al. 1990; Norrbin et al. 1990), with values reaching 72% of total lipids in autumn and around 55% in summer. To our knowledge, there are no data available on the wax ester content of *P. acuspes* females.

Based on these fundamental analogies, we hypothesize that life cycle and lipid-storing strategies of *P. acuspes* in the central Baltic Sea originate from extant adaptations to high latitudinal habitats.

**Table 4** Relative seston composition [percentage of total biomass]

	Depth (m)	Din	Dia	Chl	Cya	Div fl	Cil
Feb–Apr							
Upper water layer	5	24	18	0	3	9	45
Above thermocline	10	20	23	1	1	14	41
Midwater layer	20–30	7	38	1	2	11	42
Above halocline	30–40	15	45	1	1	5	33
In halocline	40–60	20	45	1	1	3	30
May							
Upper water layer	5	24	1	0	2	7	66
Above thermocline	10	20	0	0	1	8	71
Midwater layer	20–30	50	4	2	11	6	27
Above halocline	30–40	23	1	1	0	2	73
In halocline	40–60	29	0	8	0	7	55
June							
Upper water layer	5	43	1	1	19	17	19
Above thermocline	10	23	1	17	17	15	27
Midwater layer	20–30	25	3	1	11	29	30
Above halocline	30–40	17	2	0	1	10	70
In halocline	40–60	13	2	0	7	9	69
July–Sept							
Upper water layer	5	5	4	0	19	17	56
Above thermocline	10	3	11	2	9	17	57
Midwater layer	20–30	3	5	1	55	14	22
Above halocline	30–40	6	0	2	18	30	42
In halocline	40–60	14	11	1	0	15	59

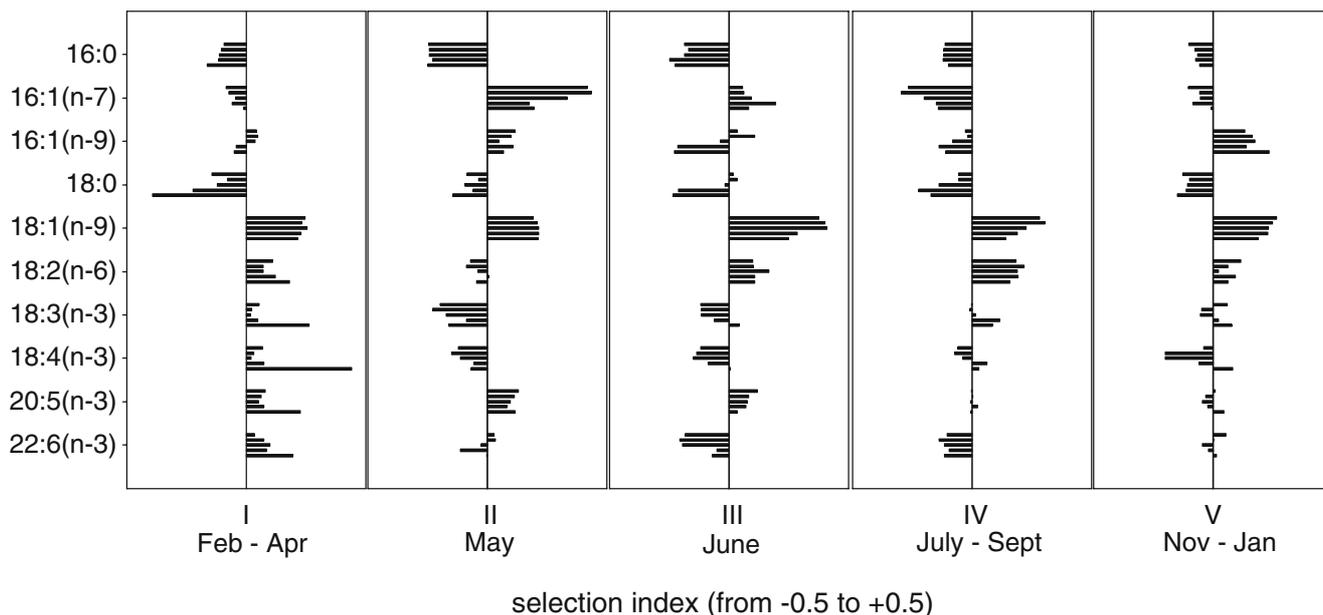
*Din* Dinoflagellates, *Dia* diatoms, *Chl* chlorophytes, *Cya* cyanobacteria, *Div fl* all flagellates except dinoflagellates, *Cil* ciliates

### Trophodynamics

The five different phases of the seasonal cycle were also reflected in the fatty acid dynamics of neutral lipids, although they are less conservative than structural lipid composition and body size. We applied signature fatty acids (Lee et al. 1971; Sargent and Whittle 1981; Sargent

et al. 1987; Graeve et al. 1994; Daalsgard et al. 2003) to identify feeding preferences and food selection of *P. acuspes*. Due to parallel analyses of the seston, we were able to assign the fatty acid markers to specific food sources.

Similar to all other studies dealing with the fatty acid composition of *Pseudocalanus* spp. (e.g. Kattner et al. 1981; Kattner and Krause 1989; Fraser et al. 1989; Norrbin et al. 1990; Cotonnec et al. 2001), we found 18:1(*n*–9) to be one of the most abundant fatty acids throughout the year. Apparently, this does not inevitably indicate similar feeding habits in different habitats, but rather a species-specific attribute, probably affected by metabolic processes. This fatty acid is not only known to be characteristic for carnivorous or detritivorous feeding (Sargent and Falk-Petersen 1981; Falk-Petersen et al. 1990), it is also synthesized de novo by copepods (Pascal and Ackman 1976; Sargent and Henderson 1986; Kattner et al. 1994; Kattner and Hagen 1998). Thus, a trophic assignment of 18:1(*n*–9) remains problematic. Nevertheless, as revealed by principal component analysis we found a strong coherence between 18:1(*n*–9) levels in the seston lipids and the occurrence of ciliates. Lipid profiles of ciliates have been reported to reflect, at least within species-specific ranges, the fatty acid composition of their diet (Ederington et al. 1995; Harvey et al. 1997; Broglio et al. 2003). Therefore, a comparison of field data with fatty acid profiles derived in laboratory studies is rather difficult. However, our data emphasize a high relevance of ciliates in the food spectrum of *P. acuspes*. The apparently intense use of heterotrophic organisms and/or detritus might be explained by the vertically stratified environment in the Baltic Sea. Due to the concentration of older copepodite stages of *P. acuspes* in deeper water



**Fig. 6** Selection index for fatty acids with vertical resolution [sorted top-down: upper water layer (5 m), above thermocline (10 m), midwater layer (20–30 m), above halocline (30–40 m), in halocline (40–60 m)]

layers (Hernroth and Ackefors 1979; Renz and Hirche 2006), their potential food mainly consisted of sinking material from the surface and organisms inhabiting the lower stratum of the water column. At least in May and June, those were mainly ciliates, representing approximately 75% of living biomass, co-occurring with very high 18:1( $n-9$ ) levels in the females. Feeding of *Pseudocalanus* spp. on ciliates (Klein Breteler et al. 2004) and heterogeneous particulate matter was documented in laboratory studies (Poulet 1974, 1976; Pavlovskaya and Pechen'Finenko 1975 as cited by Corkett and McLaren 1978). We did not quantify detritus, although an accumulation of degraded material on the halocline is to be expected.

A comparison between the fatty acid and taxonomic composition of seston revealed a relationship between 18:4( $n-3$ ), 22:6( $n-3$ ) and the biomass of dinoflagellates, as well as coherence between 18:4( $n-3$ ) and other flagellates. Those fatty acids are known to reach high levels in dinoflagellates and cryptophytes (Sargent et al. 1987; Graeve et al. 1994, 2001 and references therein; Daalsgard et al. 2003). In our study, the biomarker 18:4( $n-3$ ) was found in significantly higher amounts in early spring, and 22:6( $n-3$ ) was also more abundant from February until May. This indicates a preferential ingestion of flagellates or dinoflagellates in spring time, although dinoflagellates showed a rather constant portion of total biomass during all seasons examined, whereas other flagellates increased later in the year. *Pseudocalanus* spp. selectively feeds on flagellates such as cryptophytes and dinoflagellates (e.g. Geen and Hargrave 1966; Zagorodnyaya 1974). This high quality food (Brown et al. 1997) enhances growth, egg production and lipid accumulation and also decreases mortality (Klein Breteler et al. 1990; Koski et al. 1998; Koski and Klein Breteler 2003).

Diatom blooms, which have reappeared in the Bornholm Basin since 1999, were mainly restricted to early spring (February–April) (Wasmund et al. 2003, present study). However, the diatom marker 16:1( $n-7$ ) reached its maximum in *P. acuspes* not until May, when diatoms were of only marginal importance in the water column and their fatty acid markers in the seston had already decreased significantly. This suggests that lipids observed in the new females in May probably derived from lipid reserves built up during earlier copepodite stages. This time shift between fatty acid levels in seston and copepods related to the period of higher lipid accumulation or retention by females. Low lipid levels reflect changes much quicker, probably causing the more synchronous progression of fatty acid composition of seston and storage lipids later in the season. Alternatively, in spite of low standing stocks of diatoms, their production rates may have been high, as the production potential of diatoms was evident from a small diatom bloom during July.

Diatom marker levels were rather low in the Baltic. Especially in Polar Regions with more pronounced diatom and ice algal blooms 16:1( $n-7$ ) may reach values of up to 20% of total fatty acids in CIV and CV of

*P. acuspes* in the Arctic summer (Norrbin et al. 1990), thus exceeding twice the maximum value found for CV in the present study. Very similar results, indicating diatom-based feeding, were found for other *Pseudocalanus* species in Polar Regions with 16:1( $n-7$ ) levels reaching up to 40% of total fatty acids (Peters et al. 2004, S. Lischka and W. Hagen, submitted).

The rather limited ingestion of diatoms seems to be characteristic for temperate regions, as all studies show similarly low marker amounts (Kattner et al. 1981; Kattner and Krause 1989; Fraser et al. 1989; Cotonnec et al. 2001). Still, the levels of 16:1( $n-7$ ) found in our study belong to the lowest ever measured for *Pseudocalanus* spp., indicating a more intense use of other food sources. Especially cyanobacteria have to be considered as potential diet in the Baltic Sea, as they usually bloom intensively during summer, except for 2002, when only a minor bloom was registered (Wasmund et al. 2003). However, in our study cyanobacteria values reached up to 55% of seston biomass.

Cyanobacteria are very variable in their fatty acid compositions, with marked differences occurring even in the same genus (Gugger et al. 2002). Due to the coexistence of different cyanobacteria species in the Baltic Sea, it is not easy to identify a clear trophic signal. Many studies reported that a characteristic fatty acid pattern of cyanobacteria consists of 16:0, 16:1, 18:2( $n-6$ ) and 18:3( $n-3$ ) (e.g. Murata and Nishida 1987 and references therein, Vargas et al. 1998; Gugger et al. 2002). The simultaneous occurrence of 18:3( $n-3$ ) and 18:2( $n-6$ ) with cyanobacteria and chlorophytes in the seston, indicated that elevated amounts of these fatty acids in *P. acuspes* were due to an augmented use of cyanobacteria in summer, since chlorophytes were only of minor importance. Hoppe (1981) showed that cyanobacteria and microzooplankton often build up agglomerates especially in the late bloom phase, which might improve food quality and attractiveness for copepods, leading to a more intensive use in the later phases (Meyer-Harms et al. 1999). This might explain why cyanobacteria were reflected in the storage lipids with a delay of some months.

We conclude that *P. acuspes* displays a basically opportunistic feeding behavior in the Baltic Sea. Five different seasonal fatty acid profiles were determined in the neutral lipids with high levels of 18:1( $n-9$ ) at all times, indicating a species-specific storage pattern as well as a ciliate-dominated diet. Other food sources varied over the year. In early spring dinoflagellates were increasingly utilized, whereas in late spring diatom markers were most strongly reflected in the fatty acid composition. During summer, cyanobacteria, and probably to a lesser degree chlorophytes, seemed to contribute substantially to the diet of *P. acuspes*.

**Acknowledgements** The study was funded by the German Federal Ministry for Education and Research within the GLOBEC GER-MANY project (03F0320C). We wish to thank the crews and scientific parties of the RV *Alkor*, *Heincke* and *A.v.Humboldt* for the excellent support during the field phase. We also thank M. Graeve

for GC-MS measurements. The critical revision and improvement of the manuscript by H. Auel, D. Stübing and three anonymous reviewers are gratefully acknowledged.

## References

- Båmstedt U, Håkanson JL, Brenner-Larsen J, Björnson PK, Geertz-Hansen O, Tiselius P (1990) Copepod nutritional condition and pelagic production during autumn in Kosterfjorden, western Sweden. *Mar Biol* 104:197–208
- Broglio E, Jónasdóttir SH, Calbet A, Jakobsen HH, Saiz E (2003) Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. *Aquat Microb Ecol* 31:267–278
- Brown MR, Jeffrey SW, Volkman JK, Dunstan GA (1997) Nutritional properties of microalgae for mariculture. *Aquaculture* 151:315–331
- Bucklin A, Frost BW, Bradford-Grieve J, Allen LD, Copley NJ (2003) Molecular systematic and phylogenetic assessment of 34 calanoid copepod species of the Calanidae and Clausocalanidae. *Mar Biol* 142:333–343
- Cairns AA (1967) The zooplankton of Tanquary Fjord, Ellesmere Island, with special reference to the calanoid copepods. *J Fish Res Board Can* 24:555–568
- Conover RJ, Siferd TD (1993) Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. *Arctic* 46:303–311
- Corkett CJ, McLaren IA (1978) The biology of *Pseudocalanus*. *Adv Mar Biol* 15:1–231
- Cotonne G, Brunet C, Sautour N, Thoumelin G (2001) Nutritive value and selection of food particles by copepods during a spring bloom of *Phaeocystis* sp. in the English Channel, as determined by pigment and fatty acid analyses. *J Plankton Res* 23:693–703
- Daalsgard J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. *Adv Mar Biol* 46:225–340
- Davis CC (1976) Overwintering strategies of common planktic copepods in some north Norway fjords and sounds. *Astarete* 9:37–42
- Digby PSB (1950) The biology of the small planktonic copepods of Plymouth. *J Mar Biol Assoc UK* 29:393–438
- Dunstan GA, Volkman JK, Barrett SM, LeRoi J-M, Jeffrey SW (1994) Essential polyunsaturated fatty acids from 14 species of diatoms (Bacillariophyceae). *Phytochemistry* 35:155–161
- Ederington MC, McManus GB, Harvey HR (1995) Trophic transfer of fatty acids, sterols, and triterpenoid alcohol between bacteria, a ciliate, and the copepod *Acartia tonsa*. *Limnol Oceanogr* 40:860–867
- Edler L (1979) Recommendations on methods for marine biological studies in the Baltic Sea. *Phytoplankton and chlorophyll*. *Baltic Mar Biol Publ* 5:1–38
- Falk-Petersen S, Hopkins CCE, Sargent JR (1990) Trophic relationships in the pelagic, Arctic food web. In: Barnes M, Gibson RN (eds) *Trophic relationships in the marine environment*. Proceedings of the 24th European marine biological symposium. Aberdeen University Press, Aberdeen, pp 315–333
- Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for isolation and purification of total lipids from animal tissues. *J Biol Chem* 226:497–509
- Fraser AJ, Sargent JR, Gamble JC (1989) Lipid class and fatty acid composition of *Calanus finmarchicus* (Gunnerus), *Pseudocalanus* sp. and *Temora longicornis* Muller from nutrient-enriched seawater enclosure. *J Exp Mar Biol Ecol* 130:81–92
- Frost BW (1989) A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can J Zool* 67:525–551
- Geen GH, Hargrave BT (1966) Primary and secondary production in Bras d'Or Lake, Nova Scotia, Canada. *Verh Int Ver Theor* 16:333–340
- Graeve M, Kattner G, Hagen W (1994) Diet-induced changes in the fatty acid composition of Arctic herbivorous copepods: experimental evidence of trophic markers. *J Exp Mar Biol Ecol* 182:97–110
- Graeve M, Dauby P, Scailteur Y (2001) Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes in Antarctic amphipods. *Polar Biol* 24:853–862
- Gugger M, Lyra C, Suominen I, Tsitko I, Humbert J-F, Salkinoja-Salonen MS, Sivonen K (2002) Cellular fatty acids as chemotaxonomic markers of the genera *Anabaena*, *Aphanizomenon*, *Microcystis*, *Nostoc* and *Planktothrix* (cyanobacteria). *Int J Syst Evol Microbiol* 52:1007–1015
- Harvey HR, Ederington MC, McManus GB (1997) Lipid composition of the marine ciliates *Pleuronema* sp. and *Fabrea salina*: shifts in response to changes in diet. *J Euk Microbiol* 44:189–193
- Hay SJ, Evans GT, Gamble JC (1988) Birth, growth and death rates for enclosed populations of calanoid copepods. *J Plankton Res* 10:431–454
- Henroth L (1985) Recommendations on methods for marine biological studies in the Baltic Sea: Mesozooplankton biomass assessment. *Baltic Mar Biol Publ* 10:1–32
- Henroth L, Ackefors H (1979) The zooplankton of the Baltic proper: a long-term investigation of the fauna, its biology and ecology. *Rep Fish Bd Sweden Inst Mar Res* 2:1–160
- Hinrichsen H-H, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. *Can J Fish Aquat Sci* 12:1858–1873
- Hinrichsen H-H, Lehmann A, Möllmann C, Schmidt J (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic as a case study. *Fish Oceanogr* 12:425–433
- Hoppe HG (1981) Blue-green algae agglomeration in surface water: a microhabitat of high bacterial activity. *Kieler Meeresforschung Sonderhefte* 5:291–303
- Kattner G, Fricke HSG (1986) Simple gas-liquid chromatography method for simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. *J Chromatogr* 361:263–268
- Kattner G, Hagen W (1998) Lipid metabolism of the Antarctic euphausiid *Euphausia crystallorophias* and its ecological implications. *Mar Ecol Prog Ser* 170:203–212
- Kattner G, Krause M (1989) Seasonal variations of lipids (wax esters, fatty acids and alcohols) in calanoid copepods from the North Sea. *Mar Chem* 26:261–275
- Kattner G, Krause M, Trahms J (1981) Lipid composition of some typical North Sea copepods. *Mar Ecol Prog Ser* 4:69–74
- Kattner G, Graeve M, Hagen W (1994) Ontogenetic and seasonal changes in lipid and fatty acid/alcohol compositions of the dominant Antarctic copepod *Calanus propinquus*, *Calanoides acutus* and *Rhincalanus gigas*. *Mar Biol* 118:637–644
- Klein Breteler WCM, Gonzalez SR (1988) Influence of temperature and food concentration on body size, weight and lipid content of two Calanoid copepod species. In: Boxshall GA, Schminke HK (eds) *Biology of copepods*. Kluwer, Dordrecht, pp 201–210
- Klein Breteler WCM, Schogt N, Gonzalez SR (1990) On the role of food quality in grazing and development of life stages, and genetic change of body size during cultivation of pelagic copepods. *J Exp Mar Biol Ecol* 135:177–189
- Klein Breteler WCM, Koski M, Rampen S (2004) Role of essential lipids in copepod nutrition: no evidence for trophic upgrading of food quality by a marine ciliate. *Mar Ecol Prog Ser* 274:199–208
- Koski M, Klein Breteler WCM (2003) Influence of diet on copepod survival in the laboratory. *Mar Ecol Prog Ser* 264:73–82
- Koski M, Klein Breteler W, Schogt N (1998) Effect of food quality on the rate of growth development of the pelagic copepod *Pseudocalanus elongatus* (Copepoda: Calanoida). *Mar Ecol Prog Ser* 170:169–187
- Lee RF, Nevenzel JC, Paffenhöfer G-A (1971) Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. *Mar Biol* 9:99–108
- Lischka S, Hagen W (2005) Life histories of the copepods *Pseudocalanus minutus*, *P. acuspes* (Calanoida) and *Oithona similis*

- (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). *Polar Biol* 28:910–921
- Marshall SM (1949) On the biology of the small copepods in Loch Striven. *J Mar Biol Assoc UK* 28:45–122
- McLaren IA, Laberge E, Corkett CJ, Sévigny J-M (1989) Life cycles of four species of *Pseudocalanus* in Nova Scotia. *Can J Zool* 67:552–558
- Meyer-Harms B, Reckermann M, Voß M, Siegmund H, Bodungen Bv (1999) Food selection by calanoid copepods in the eutrophic layer of the Gotland Sea (Baltic Proper) during mass occurrence of N<sub>2</sub>-fixing cyanobacteria. *Mar Ecol Prog Ser* 191:243–250
- Möllmann C, Köster FW (1999) Food consumption by clupeids in the Central Baltic: evidence for top-down control? *ICES J Mar Sci* 56:100–113
- Möllmann C, Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. *J Plankton Res* 24:959–978
- Möllmann C, Kornilovs G, Fetter M, Köster FW, Hinrichsen H-H (2003) The marine copepod *Pseudocalanus elongatus* as a mediator between climate variability and fisheries in the Central Baltic Sea. *Fish Oceanogr* 12:360–368
- Murata N, Nishida I (1987) Lipids of blue-green algae (cyanobacteria). In: Stumpf PK (ed) *The biochemistry of plants*. Academic, New York, pp 315–347
- Nichols DS, Nichols PD, Sullivan CW (1993) Fatty acid, sterol and hydrocarbon composition of Antarctic sea ice diatom communities during the spring bloom in McMurdo Sound. *Antarct Sci* 5:271–278
- Norrbin MF (1991) Gonad maturation as an indication of seasonal cycles for several species of small copepods in the Barents Sea. In: Sakshaug E, Hopkins CCE, Øritsland NA (eds) *Proceedings of the pro mare symposium on polar marine ecology*, pp 421–432
- Norrbin F (1992) Overwintering strategies of small copepods in high latitude marine environments. Dissertation, Faculty of Natural Sciences, Göteborg
- Norrbin MF (1996) Timing of diapause in relation to the onset of winter in the high-latitude copepods *Pseudocalanus acuspes* and *Acartia longiremis*. *Mar Ecol Prog Ser* 142:99–109
- Norrbin MF, Olsen R-E, Tande KS (1990) Seasonal variation in lipid class and fatty acid composition of two small copepods in Balsfjorden, northern Norway. *Mar Biol* 105:205–211
- Pascal JC, Ackman RG (1976) Long chain monoethylenic alcohol and acid isomers in lipids of copepods and capelin. *Chem Phys Lipids* 16:219–223
- Pavlovskaya TV, Pechen'Finenko GA (1975) Comparison of the relative role of living and non-living organic matter in the nutrition of *Pseudocalanus elongatus* (Boeck) (in Russian). *Biol Morya Kiev* 34:65–70
- Pertsova NM (1981) Number of generations and their span in *Pseudocalanus elongatus* (Copepoda, Calanoida) in the White Sea (in Russian). *J Zool* 60:673–684
- Peters J, Tuschling K, Brandt A (2004) Zooplankton in the arctic Laptev Sea - feeding ecology as indicated by fatty acid composition. *J Plankton Res* 26:227–234
- Poulet SA (1974) Seasonal grazing of *Pseudocalanus minutus* on particles. *Mar Biol* 25:109–123
- Poulet SA (1976) Feeding of *Pseudocalanus minutus* on living and non-living particles. *Mar Biol* 34:117–125
- Putt D, Stoecker DK (1989) An experimentally determined carbon:volume ratio for marine “oligotrichous” ciliates from estuarine and coastal waters. *Limnol Oceanogr* 34:1097–1103
- Renz J, Hirche H-J (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. *Mar Biol* 148:567–580
- Runge JA, Ingram RG (1991) Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. *Mar Biol* 108:217–225
- Sargent JR, Falk-Petersen S (1981) Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschi* and *T. inermis* during mid-winter. *Mar Biol* 62:131–137
- Sargent JR, Henderson RJ (1986) Lipids. In: Corner EDS, O'Hara SCM (eds) *The biological chemistry of marine copepods*. Clarendon Press, Oxford, pp 59–108
- Sargent JR, Whittle KJ (1981) Lipids and hydrocarbons in the marine food web. In: Longhurst AR (ed) *Analysis of marine ecosystems*. Academic, San Diego, pp 491–533
- Sargent JR, Parkes RJ, Mueller-Harvey I, Henderson RJ (1987) Lipid biomarkers in marine ecology. In: Sleigh MA (ed) *Microbes in the sea*. Ellis Horwood, Chichester, pp 119–138
- Schlitzer R (2005) Ocean data view. <http://www.awi-bremerhaven.de/GEO/ODV>
- Schnack S (1975) Studies on the feeding biology of copepods (Crustacea) in the Kiel Bight (in German). Doctoral Thesis, Kiel University
- Siferd TD, Conover RJ (1992) Natural history of ctenophores in the Resolute Passage area of the Canadian High Arctic with special reference to *Mertensia ovum*. *Mar Ecol Prog Ser* 86:133–144
- Skerratt JH, Nichols PD, McMeekin TA, Burton HR (1997) Identification of dominant taxa in coastal Antarctic water and ice core samples using lipid signatures. In: Battaglia B, Valencia J, Walton DWH (eds) *Antarctic communities. Species, structure and survival*. Cambridge University Press, Cambridge, pp 79–85
- Vargas MA, Rodríguez H, Moreno J, Olivares H, Del Campo JA, Rivas J, Guerrero MG (1998) Biochemical composition and fatty acid content of filamentous nitrogen-fixing cyanobacteria. *J Phycol* 34:812–817
- Vidal J (1980) Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. *Mar Biol* 56:111–134
- Wasmund N, Pollehne F, Postel L, Siegel H, Zettler ML (2003) Assessment of the biological state of the Baltic Sea in 2002 (in German). *Meereswiss Ber* 56:1–78
- Zagorodnyaya YA (1974) Nutrition and migration of Black Sea *Pseudocalanus elongatus* (Boeck) in the winter period (in Russian). *Gidrobiol Zhurnal* 10:49–56



**Life cycle and population dynamics  
of *Pseudocalanus elongatus* Boeck (Copepoda, Calanoida)  
in the southern North Sea**

Jasmin Renz and Hans-Jürgen Hirche



---

## Life cycle and population dynamics of *Pseudocalanus elongatus* Boeck (Copepoda, Calanoida) in the southern North Sea

Jasmin Renz\* and Hans-Jürgen Hirche

Alfred Wegener Institute for Polar and Marine Research, PO Box 120161, 27515 Bremerhaven,  
Germany

\*Corresponding author:

E-mail: [jrenz@awi-bremerhaven.de](mailto:jrenz@awi-bremerhaven.de)

Phone: +49-471-48311042

Fax: +49-471-48311918

### Abstract

The seasonal distribution and population dynamics of *Pseudocalanus elongatus* were studied in the southern North Sea from February 2004 to May 2005 and interpreted in the light of food conditions. Highest population abundance up to  $564 \cdot 10^3 \text{ n m}^{-2}$  was recorded in June, with abundance of nauplii ranging from 1.2 to  $563 \cdot 10^3 \text{ n m}^{-2}$  and those of copepodids from 0.01 to  $94 \cdot 10^3 \text{ n m}^{-2}$ . Nauplii and youngest stages were most abundant in the southern-central part of the study area, while older stages and adults dominated in the central and westerly part. In general there were always more females than males, the sex ratio (females/males) ranged from 1.2 to 19.3 with highest ratios during summer. Mean prosome length of copepodids ranged from 0.359 mm (copepodite stage I, CI) to 1.075 mm (adult female, AF). At least 3 generations were identified between February and October 2004 by changes in prosome length of AF. Maximum egg production rate (EPR) was  $9.1 \text{ eggs f}^{-1} \text{ d}^{-1}$  in April 2004 and  $5.3 \text{ eggs f}^{-1} \text{ d}^{-1}$  in May 2005. Stage durations derived from moulting experiments ranged from 1 d for CII in February up to 9.2 d for CV in April, with highest stage durations generally observed at lowest temperatures. Weight specific growth rates were highest in youngest stages in April and August ( $0.31 \text{ d}^{-1}$ ), while growth rate of AF peaked in February/March and May ( $0.12\text{-}0.13 \text{ d}^{-1}$ ). Both, growth of copepodite stages and AF seemed not to be limited by food during the investigation. Maximum secondary production of *P. elongatus* was up to  $110 \text{ mg C m}^{-2}$  in May and June, corresponding to a productivity of 0.15.

## Introduction

The investigation of copepod population dynamics is one of the important aims in marine ecology, as production of copepods is an essential factor in providing energy for higher trophic levels. Studies of growth, fecundity and development have demonstrated that temperature and food supply are the chief variables controlling copepod vital rates. Huntley and Lopez (1992) proposed mostly non-limiting food conditions and found the same temperature response of growth rates in several copepod species. However, many authors observed food limitation in the field (e.g. Landry 1978, Durbin et al. 1983, Runge et al. 1985, Diel and Klein Breteler 1986, Kimmerer and McKinnon 1987, Kiørboe et al. 1988, Hirche et al. 2001).

Copepods of the genus *Pseudocalanus* are common in temperate and boreal pelagic ecosystems. Due to their high rate of production they are thought to play an important role in the trophic ecology of the systems (Corkett and McLaren 1978). *Pseudocalanus elongatus* is a neritic species (Hansen 1969) and is distributed in the temperate eastern North Atlantic Ocean and the western Mediterranean. Probably isolated populations occur in the Adriatic Sea and the Black Sea (Frost 1989). In the North Sea it is observed throughout the year in the south-western part (Künne 1952), the west coast of Sweden (Eriksson 1973) and the English Channel (Digby 1950). Particular high numbers of *P. elongatus* were found in the central part of the North Sea (Farran 1920, Wimpenny 1933) and the Fladen Ground (Krause and Trahms 1983, Franz et al. 1984). Its life cycle is described to show 3 generations in the Southern Bight (Bossicart 1980), with fewer numbers, if food requirements are not met, while Evans (1977) separated 4-6 generations of *P. elongatus* in Northumberland coastal waters (Great Britain).

The North Sea is a relatively shallow continental shelf sea. Atlantic water enters the southern North Sea through the Strait of Dover and continues towards the German Bight. Two water masses are found in the German Bight, Continental Coastal Water and Central (Southern) North Sea Water (Becker and Prahm-Rodewald 1983). The mean North Sea circulation shows a moderate transport of water from the southern German Bight into the northeast of the German Bight and continues in the Jutland Current, which flows into the Skagerrak. In the German Bight circulation is mainly cyclonic and strongly dependent on wind direction. Mesoscale variability is high both in space and time (Becker and Prahm-Rodewald 1983) and strong tides cause turbulent horizontal and vertical exchanges.

The aim of this study was to describe the life cycle and vital rates of *Pseudocalanus elongatus* in the southern North Sea in relation to food and hydrographical conditions. An almost monthly investigation of abundance and length of copepodite stages between February and October 2004 was conducted in the framework of German GLOBEC was used together with shipboard measurements of egg production and moulting rates from several cruises, to estimate growth and secondary production.

## Materials and methods

### Study site

The study area of the southern North Sea and the German Bight are characterised by depths of 20 to 40 m. Two water masses are found in the German Bight: the Continental Coastal Water, a mixture of Atlantic water, water from the English Channel and river waters from Rhine, Meuse, Ems and Elbe, and the Central (Southern) North Sea Water (Becker et al. 1983). The mean North Sea circulation shows a moderate transport of water from the Southern German Bight into the northeast of the German Bight. In the German Bight circulation is mainly cyclonic and strongly dependent on wind direction. Mesoscale variability in the German Bight is high in both, spatially and temporally with strong tides causing turbulent horizontal and vertical exchanges. (Becker and Prahm-Rodewald 1980). Temperature was rather uniform across the sampling grid during the cruises and ranged in ca. 10 m depth from 5°C in February to 14°C in October. Salinity varied according to freshwater input from several rivers between 30.5 in the eastern part and 34.5 in the western part of the study area.

### Sampling

Sampling of zooplankton was conducted on 8 cruises between February 2004 and May 2005 on a station grid in the German Bight, North Sea (Fig. 1). On every station double oblique bongo net hauls (mouth opening 0.2 m<sup>2</sup>, mesh size 150 µm, towing speed 3 kn) were taken vertically from above the bottom to the surface; on 9 focus stations sampling was performed using a multinet (Hydrobios, 0.25 m<sup>2</sup> mouth opening, 50 µm mesh size, towing speed 0.2 m s<sup>-1</sup>) towed vertically with a 10 m resolution from the bottom to the surface. Furthermore at the focus stations samples were taken with a WP-2 net (UNESCO 1968, mouth opening 0.26 cm<sup>2</sup>, mesh size 200 µm, towing speed 0.2 m s<sup>-1</sup>) towed vertically from above the bottom to the surface. Bongo and multinet samples were immediately preserved in a 4% borax-buffered formaldehyde-seawater solution.

In the laboratory, subsamples of the multinet hauls were analysed for developmental stages until at least 150 individuals of *Pseudocalanus elongatus* were counted. Individuals were identified to nauplii, 5 copepodite stages and adult males (AM) and females (AF).

Concurrent to the zooplankton sampling, vertical profiles of temperature were recorded using a CTD-probe (SBE 911+, ME).

### Length measurement

For each cruise, prosome length of 30 AF from WP-2 net hauls was measured using a stereo microscope (Leica MZ 16) with a resolution of 80x. The prosome length of 30-60 preserved copepodite stages I-V (CI-CV) and AM was measured for 7 cruises in 2004 (Table 1) from either WP-2 or bongo-net hauls at the focus stations.

Differences in prosome length of copepodids and adults between sampling dates were tested with one-way ANOVA using Tukey's honestly significant difference as the post-hoc test.

### Egg production

For measurement of in-situ egg production on all cruises at the focus stations 30 AF from the WP-2 net hauls were randomly sorted out immediately after capture under ambient temperature conditions. Furthermore, in April 2005 egg production was measured at one station at Helgoland Roads from 90 randomly sorted AF. All AF were incubated individually in 15 ml cell wells for 24h under in-situ temperature using 50 µm prefiltered water. Clutch size, length of eggs and females and number of reproducing females were recorded. To avoid egg cannibalism of females, egg sacs were carefully removed by slightly pressing the female body. The egg sacs were further incubated and the hatching success measured.

### Moulting rate

Moulting rates of copepodites were measured at several stations and cruises in short-term incubations (Klein Breteler et al. 1998) to calculate stage durations of copepodite stages. For each experiment, 1-4 sub-samples containing altogether 100-150 CI-CV each were taken from a WP-2 haul. Old exuviae of *Pseudocalanus elongatus* were removed and sub-samples were incubated at ambient temperature conditions in 50 µm prefiltered water for 1-4 days in 1 l Kautex bottles. Every 24h one sub-sample was preserved in a 4% borax-buffered formaldehyd-seawater solution for later enumeration of moults by counting of exuviae. The moulting rate ( $MR$ ) of each stage was calculated after Peterson et al. (1991) as

$$MR_i = \frac{Ex_i}{[N_i + Ex_i]} * \frac{24}{T}$$

where  $N_i$  is the number of individuals in stage  $i$  at the beginning of the experiment,  $Ex_i$  is the number of exuviae in stage  $i$  at the end of the experiment and  $T$  is the incubation time (in hours). The range and mean stage duration of each stage per experiment was calculated (Table 2).

### Weight-specific growth rate

The growth rate ( $g_i$ ) of nauplii and CI-CV was calculated from the expression

$$g_i = \ln\left(\frac{W_{i+1}}{W_i}\right) * \frac{1}{D}$$

where  $W_{i+1}$  and  $W_i$  are the masses calculated from length measurements of the stage moulted to and moulted from, respectively and  $D$  is the stage duration of stage  $i$ .

Dry masses of copepodite stages were calculated using the length-weight relationship by Klein Breteler et al. (1982):

$$\log DM = 2.730 \log PL - 6.912$$

The carbon-specific growth rate of AF ( $g_f$ ) (specific egg production rate, SEPR) was calculated by first converting the number of eggs to carbon-weight of eggs using  $0.14 \cdot 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$  (Kjørboe et al. 1985, Huntley and Lopez 1992). Egg size for *P. elongatus* was determined from unpreserved eggs from all egg production experiments performed between April and August 2004 (mean egg diameter  $130 \mu\text{m}$ ). Female dry mass was calculated according the length-weight relationship by Klein Breteler et al. (1982). Dry mass was converted to carbon assuming  $0.4 \mu\text{g C } \mu\text{g}^{-1}$  dry mass (Parsons et al. 1984). Female growth rate is then

$$g_f = \frac{W_{eggs}}{W_{AF}} * \frac{24}{T}$$

where  $T$  is the incubation time (hours),  $W_{eggs}$  is the carbon mass of eggs ( $\mu\text{g}$ ) produced per day and  $W_{AF}$  the carbon weight of a female.

### Production and productivity

Production of nauplii, CI-CV and AF was calculated as

$$P_i = (g_i * B_i)$$

where  $P_i$  is the production of stage  $i$  ( $\mu\text{g dry weight produced m}^{-2}$ ),  $g_i$  is the growth rate of single stage  $i$  and  $B_i$  the biomass of stage  $i$ . Production of the whole population was calculated by summing up the production of every single stage. As no experiments on growth rates of copepodite stages were performed in September and October, we applied growth rates measured in August to calculate secondary production. Productivity (P/B) was calculated for the whole population.

## Results

### Abundance

The stock size of *Pseudocalanus* is shown in Fig. 2. The seasonal course was characterised by a slight increase in adult and nauplii abundances between February and April. The peak in abundance of adults in late spring and early summer was accompanied by high concentrations of nauplii. Abundance of youngest copepodite stages was maximal between June and August, while high concentrations of CIV and CV were already recorded from April on at several stations. Highest population abundance was recorded in June and made up to  $564 \cdot 10^3 \text{ n m}^{-2}$ . Abundance of nauplii ranged from 1.2 to  $563 \cdot 10^3 \text{ n m}^{-2}$ , those of copepodids from 0.01 to  $94 \cdot 10^3 \text{ n m}^{-2}$ .

The horizontal distribution showed nauplii and youngest stages to be most abundant in the southern central part of the study area, while older stages and adults dominated in the central and westerly part. In general there were always more females than males, the sex ratio (females/males) ranged from 1.2 to 19.3 with highest ratios during summer.

### Prosome length of developmental stages

The mean prosome length of all copepodite stages is shown in Fig. 3. Mean length of copepodids ranged from 0.359 mm (CI) to 1.075 mm (AF). A size increase of up to 11% for all stages between March and April 2004 was followed by a decrease over the rest of the year. Statistical analysis of mean prosome length of copepodite stages and adults using one-way ANOVA showed significant differences ( $p < 0.05$ ) of mean length between sampling months (data not shown). The post hoc test, comparing pairs of means, showed all stages were significantly larger in April ( $p < 0.05$ ) and smaller between August and October ( $p < 0.05$ ) than over the rest of the year.

### Number of generations

The length-frequency distribution of females indicated the production of at least 3 generations between February and October (Fig. 4). The  $G_0$  generation, consisting of small females between 0.65 and 1.05 mm, showed up in February, followed by a generation of significantly larger females in April up to 1.27 mm length. This generation was followed by at least 2 generations of smaller size during summer.

### Reproduction

Egg production rate (EPR) (Fig. 5d) in the German Bight ranged between 0 eggs  $f^{-1} d^{-1}$  (station 47) and 9.1 eggs  $f^{-1} d^{-1}$  (station 22) in April 2004 and 1.7 eggs  $f^{-1} d^{-1}$  (station 02) and 5.3 eggs  $f^{-1} d^{-1}$  (station 40) in May 2005. Mean EPR per cruise ranged from 1.1 eggs  $f^{-1} d^{-1}$  in October to a maximum of 5.3 eggs  $f^{-1} d^{-1}$  in April 2004 and 3.5 eggs  $f^{-1} d^{-1}$  in May 2005. Except for low values in the south westerly part of the grid at station 47, no clear area related trend was detectable. Hatching success (Fig. 5c) was highest during times of highest reproduction ( $> 88\%$ ) and decreased slightly over the course of the year. With the exception of one station in August 2004 and May 2005 it stayed above 50%.

The proportion of spawning females (PSF) (Fig. 5b) showed high variability between stations and ranged from 3 to 59 % per station. PSF explained 44% of EPR ( $r^2=0.44$ ) and was highest in August 2004.

Clutch size ranged between 1 and 41 eggs  $f^{-1}$ , with largest clutches observed in April and May 2005 (Fig. 6a). Mean clutch size showed a seasonal trend and was highest in April 2004 (19 eggs  $f^{-1}$ ) and lowest in October (6 eggs  $f^{-1}$ ). There was no relationship between mean clutch size and EPR of females per station (Fig. 5f).

While size of eggs was constant over the course of the year, number of eggs per clutch seemed to increase with length of females ( $r^2=0.4$ ) (Fig 6b).

### Food

The seasonal cycle in egg production largely followed the seasonal cycle of Chl a concentration in the water column with a peak in April and a second small peak in August (Fig. 5a). However, neither egg production nor hatching success or proportion of spawning females were

significantly correlated to food conditions (Fig. 7a-c). Instead, the relation between proportion of spawning females and hatching success and Chl a resembled a hyperbolic shaped curve with saturated conditions already reached at Chl a concentrations around 3-4  $\mu\text{g l}^{-1}$ .

### **Moulting rates and stage duration**

Moulting experiments were conducted at several stations during 4 cruises between February and August 2004. Stage durations calculated from moulting experiments of copepodite stages showed small variations between different stages and stations (Table 2). Lowest moulting rates were observed at lowest temperatures in February and youngest stages mostly had highest moulting rates. Resulting stage durations at different stations ranged from 1 day at 5°C for CII in February up to 9.2 days for CV at 7°C in April.

Mean stage durations for all stages except for CII were lowest in April (1.9-6.0 days). Over the rest of the year stage durations ranged from 4.6 to 7.6 in February, 2.0 to 6.1 in June and 2.5 to 8.0 in August.

### **Weight specific growth rates**

Weight specific growth rates of copepodite stages (Table 1) were highest in stages CI in April and CII in August ( $0.31 \text{ d}^{-1}$ ), followed by CIII in April ( $0.17 \text{ day}^{-1}$ ), CIV in August ( $0.16 \text{ d}^{-1}$ ) and CV in April ( $0.12 \text{ d}^{-1}$ ). Weight specific growth rates of females derived from SEPR were highest in February/March and May ( $0.12\text{-}0.13 \text{ d}^{-1}$ ). During times of increasing reproduction in February/March they were comparable to those of youngest copepodite stages, while during highest reproduction in April and May weight specific growth rate of females was comparable to growth rates of older copepodite stages.

### **Secondary production**

The main productive period of *Pseudocalanus elongatus* in the study area lasted from May to August (Fig. 9) and was highest in the central part of the German Bight and lowest at the marginal stations. Minimum production values were recorded in February at station 9 ( $0.06 \text{ mg C m}^{-2}$ ) and in October at station 1 ( $0.001 \text{ mg C m}^{-2}$ ). Maximum values of  $110 \text{ mg C m}^{-2}$  were recorded at stations 37 and 40 in May and June, respectively. Due to differences in stage composition and abundance, the variability in secondary production between stations was high and differed up to 7300x between highest and lowest rates in May.

Productivity showed a seasonal cycle and mean values in the study area were lowest in February (0.068) and highest in April (0.150) (Table 1).

## **Discussion**

### **Abundance**

*Pseudocalanus elongatus* is one of the most prominent copepod species in the North Sea, which together with *Acartia clausi*, *Centropages* spp. and *Temora longicornis* dominates the zooplankton population of small calanoid copepods (Fransz 1975, Hickel 1975).

During our study the abundance of *P. elongatus* showed a strong seasonal cycle with highest cumulative abundance of  $564 \cdot 10^3 \text{ n m}^{-2}$ , resulting from high nauplii abundance, at a near coastal station in the inner German Bight after the phytoplankton bloom between June and August. Copepodite stages comprised up to  $94 \cdot 10^3 \text{ n m}^{-2}$  of the population. Concentrations in the same range were found by Krause et al. (1995), reporting copepodid abundances of '*P. minutus*' of up to  $46.5 \cdot 10^3 \text{ n m}^{-2}$  in the cold Continental Coastal Water off the Dutch and German coasts, while Lücke (1912) found concentrations of up to  $117 \cdot 10^3 \text{ n m}^{-2}$  in the German Bight in August. Nauplii abundances in the range of our values were observed by Krause and Trahms (1983) in the Fladen Ground area.

Abundance of individuals is strongly affected by physical factors such as temperature and salinity, food and predation. Abundance during our study was not directly related to phytoplankton concentration as highest concentrations were found one month after the phytoplankton bloom. Potential predators are abundant all year round, particularly fish larvae such as sprat (most abundant during spring and early summer, Dickmann 2005) and ctenophores (Barz 2006). The summer decline from August on may be related to decreasing food levels and quality and increased predation and cannibalism (Daan et al. 1988). The horizontal distribution seems to strongly depend on circulation of water masses. The North Sea and the German Bight hydrography are characterised by intensive advection (Otto et al. 1990) and the water circulation strongly dependent on wind direction.

## Reproduction

Food availability, temperature and female size are the principle mechanisms, accounting for seasonal variability in copepod fecundity (Corkett and McLaren 1978, Jónasdóttir 1989, Halsband and Hirche 2001), with food as a controlling factor most of the time (Frost 1985, Kiørboe and Johansen 1986, Kiørboe et al. 1988). The highest mean egg production of  $5.3 \text{ eggs f}^{-1} \text{ d}^{-1}$  at  $7^\circ\text{C}$  in April is twice as high as field data reported by Kiørboe and Johansen (1986) of  $2.5 \text{ eggs f}^{-1} \text{ d}^{-1}$  for *Pseudocalanus elongatus* in the North Sea. Our data of highest egg production up to  $9.1 \text{ eggs f}^{-1} \text{ d}^{-1}$  correspond well to those found by Halsband and Hirche (2001) for the German Bight, where *P. elongatus* produced up to  $8 \text{ eggs f}^{-1} \text{ d}^{-1}$  at  $3^\circ\text{C}$ . Timing of spawning coincided with the phytoplankton maxima in spring and autumn, as also found by e.g. Landry (1978), Nielsen (1991) and Kiørboe and Nielsen (1994), while highest temperatures in August and September did not correlate to high egg production. Comparison of observed egg production rates to laboratory experiments with *P. elongatus* suggests that food was sufficient to maintain egg production at maximum rates in the field over most of the investigation period. Koski et al. (1998) reported  $2\text{-}5 \text{ eggs f}^{-1} \text{ d}^{-1}$  at  $15^\circ\text{C}$  and good food quality and Corkett and Zillioux (1975) found  $2.3 \text{ eggs f}^{-1} \text{ d}^{-1}$  at  $8^\circ\text{C}$ . Paffenhöfer and Harris (1976) observed between  $3.1$  and  $4.7 \text{ nauplii f}^{-1} \text{ d}^{-1}$  at  $12.5^\circ\text{C}$ . Egg production in the southern North Sea was strongly related to the proportion of spawning females, which in turn showed a positive correlation to food concentration. During the same time, there was a weak, insignificant relation of clutch size to size of AF with larger clutches in bigger females and biggest females appearing at elevated food

levels and cold, but rising temperatures. Corkett and McLaren (1969) propose that clutch size in *P. elongatus* from the North Sea is predictable from female size alone and appears to be unaffected by food supply. In contrast, Halsband and Hirche (2001) showed a highly significant relationship between prosome length of *P. elongatus* and total phytoplankton carbon.

The coincidence between egg production and elevated concentrations of phytoplankton suggests that the food level is the prime determinant of egg production, though a direct correlation between these two factors showed only an insignificant positive relationship. Several authors propose that egg production in the field is less than maximal and food limited during most of the year (e.g. Durbin et al. 1983, Peterson 1985, Checkley 1980, Kiørboe et al. 1988). The strong annual variability in mid latitudes makes it difficult to discern between the various factors regulating copepod fecundity. Landry (1978) showed the expected increase in fecundity of *A. clausi* with increasing temperature to be overridden by a large decrease in female size, which might also be applicable for *P. elongatus* in the southern North Sea.

### **Stage duration and growth**

Stage duration of *P. elongatus* in the North Sea varied between 1.5 days (CI) and 7.6 days (CV) at 5-13°C in the study period between February and October. In general, stage duration was longer in older copepodids than in younger stages. This was also observed for *Centropages typicus* (Carlotti and Nival 1992), *Calanus marshallae* (Peterson 1986) and different species of *Pseudocalanus* (McLaren et al. 1989). No clear relationship could be detected between stage duration and temperature. Mean durations decreased with increasing temperature and food concentration between February and April, but varied from April onwards, suggesting decreasing food concentration to be an important factor influencing development in the southern North Sea. Several authors observed developmental rates to be strongly affected by temperature and to a lesser extent by food availability (e.g. Corkett and McLaren 1978, Vidal 1980, Ohman 1985, Campbell et al. 2001). At 10°C, Klein Breteler et al. (1995) reported stage durations of 2-3 days for most stages and a generation time of around 30 days at sufficient food which fits the present data for April. They showed decreasing food concentrations extending stage durations. Extended stage durations of CV in March and August, a stage which is known to have longer stage duration than other stages (Peterson 1986, Uye 1988), may additionally be traced back to still or already starting overwintering stages, undergoing slowed down development. Assuming nauplii development to fall in the range of those of youngest copepodite stages, our generation times would be similar to those found for *Pseudocalanus* sp. in Dabob Bay (Ohman and Runge 1994) of approx. 40 days at 8°C and 26-27 days at 13.4°C, and by Klein Breteler et al. (1982) and Paffenhöfer and Harris (1976) in laboratory measurements.

Growth rates during our study varied between 0.04 d<sup>-1</sup> in February/March (CV) and 0.31 d<sup>-1</sup> in April (CI) and were well in the range of growth rates of *Pseudocalanus* spp. in the Skagerrak (Peterson et al. 1991), and laboratory measurements by Klein Breteler et al. (1982), Paffenhöfer and Harris (1976) and Koski et al. (1998). There was a temporal pattern in growth rates of

copepodite stages in our study with high growth rates observed not at highest temperatures but at highest food concentration in April. Peterson et al. (1991) found growth rates declining with body size for individuals  $>5\mu\text{g}$  dry weight.

Our maximum weight specific growth rate of AF in May ( $0.13\text{ d}^{-1}$ ) at  $9^{\circ}\text{C}$  is in the upper range of the  $0.03\text{-}0.11\text{ d}^{-1}$  reported for laboratory reared *P. elongatus* from the North Sea at  $15^{\circ}\text{C}$  and good food quality (Koski et al. 1998). For the same species, a weight specific fecundity of  $0.078\text{ d}^{-1}$  (Corkett and Zillioux 1975) and  $0.09\text{ d}^{-1}$  (Paffenhöfer and Harris 1976) was observed. Kiørboe and Johansen (1986) found a SEPR of 0.055 (mean 0.014) in September at  $9\text{-}12^{\circ}\text{C}$  in the northern North Sea, which fits our data from October. No relationship was found between weight specific growth rate of copepodite stages and AF as reported by Berggreen et al. (1988), suggesting different regulating mechanisms for growth of youngest stages and adults and weight specific growth rate of AF to be an insufficient measurement of juvenile growth. This would have led to large underestimation of population growth. Several field studies have shown that growth in copepodids is less than maximal and food limited (Fransz and Diel 1985, Kimmerer and McKinnon 1987), while Ohman (1985) found the food limitation paradigm for *Pseudocalanus* sp. in Dabob Bay not to be applicable and predation to be a more likely mechanism of population regulation. We suggest that growth of young copepodids was not limited by food, as average rates were similar to maximum rates of laboratory studies.

### Life cycle

*Pseudocalanus elongatus* was abundant in the southern North Sea throughout the study period. The beginning of the spawning period was indicated by the increase in abundance of adult males and females in February, developing from overwintering CIV and CV. The main reproductive period lasted from February to May with continued reproduction until October. In the North Sea *P. elongatus* is known to produce eggs even throughout winter (Halsband and Hirche 2001). The sex ratio (AF:AM) varied between 1.2 and 19.3 and was high especially during summer. The low proportion of males, which are known not to feed, might be due to their short life span (Corkett and McLaren 1978) or higher rates of predation. At least 3 generations of *P. elongatus* were identified between February and October 2004 from changes in prosome length of females. Size is often used to distinguish between generations. However, in a highly advective area like the North Sea, sampling of a single population throughout the year is often impossible and makes it difficult to clearly differentiate between generations (Fransz et al. 1991). The 3 generations are in strong contrast to the life cycle of the congener *P. acuspes* from the adjacent Baltic Sea, which starts accumulating overwintering stages early the summer and probably produces only minor summer generations (Peters et al. 2006, Renz and Hirche submitted).

### Secondary production

Secondary production of *Pseudocalanus elongatus* showed a seasonal pattern with a pronounced peak in May/June following the main phytoplankton bloom. Maximum production in

the study area was up to  $86 \text{ mg C m}^{-2}$  in June (with two exceptional high recordings of 113-115  $\text{mg C m}^{-2}$  at one station in May and June) and was rather the result of high biomass than of high growth rates, which already peaked in April. Variability in the study area was therefore high as already shown for abundance. In general production at most stations was in the range of the  $34 \text{ mg C m}^{-2}$  reported by Fransz et al. (1984), but much higher than the max. secondary production of up to  $16 \text{ mg C m}^{-2} \text{ d}^{-1}$  of *P. acuspes* in the Baltic Sea (Renz and Hirche submitted). Our monthly mean P/B of 0.11 in May corresponded well to his measurements in the North Sea (0.07-0.15). Timohina (1968) found daily P/B of *P. elongatus* in the Norwegian Sea to be 0.003-0.013, Greze et al. (1968) reported a productivity of 0.16 in the Black Sea.

The problems in estimating production mainly result from the simultaneous determination of biomass and growth at natural temperature and food conditions. No account was made for nauplii production. Assuming a mean length of 0.32 mm, a mean concentration of  $16\text{-}201 \times 10^3$  nauplii  $\text{m}^{-2}$  and that nauplii would grow at rates of youngest stages we would have to add a mean production of  $1 \text{ mg C m}^{-2}$  in February/March up to  $18 \text{ mg C m}^{-2}$  in June. This production may be of major importance to studies of fish larvae which depend on nauplii as major food items (Dagg et al. 1984, Kiørboe and Johansen 1986).

When estimating growth rates, we did not account for spatial variability as different stations were only analysed in February and April. The large mesoscale variability in the southern North Sea hydrography with fronts caused by strong tides and river outflow might cause strong patchiness in the food environment (Holligan et al. 1984, Peterson 1986).

We found evidence, that reproduction and growth of *P. elongatus* in the southern North Sea shows no limitation by food during the summer months. Temperature might be the main factor regulating population growth. The resulting growth rates and 3 generations per year lead to a high secondary production. We conclude that *P. elongatus* can provide a high energy amount for commercially important fish in the North Sea.

## Literature

- Barz K (2006) Influence of pelagic invertebrate predators on the zooplankton in the Baltic Sea and the North Sea. PhD Thesis, University Bremen, Germany
- Becker GA, Prahm-Rodewald G (1980) Fronts in the Sea: Salinity Fronts in the German Bight. *Seewart* 41: 12-21
- Becker GA, Fiuza AFG, James ID (1983) Water mass analysis in the German Bight during MARSEN, Phase I. *J Geophys Res* 88: 9865-9870
- Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. *Mar Biol* 99: 341-352
- Bossicart M (1980) Population dynamics of copepods in the Southern Bight of the North Sea (1977-1979), use of a multicohort model to derive biological parameters. *ICES CM* 1980/L:24
- Campbell RG, Wagner MM, Teegarden GJ, Boudreau CA, Durbin EG (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Mar Ecol Prog Ser* 221: 161-183
- Carlotti F, Nival S (1992) Moulting and mortality rates of copepods related to age within stage: Experimental results. *Mar Ecol Prog Ser* 84: 235-243
- Checkley DM (1980) The egg production of a marine planktonic copepod in relation to its food supply: Laboratory studies. *Limnol Oceanogr* 25: 430-446
- Corkett CJ, McLaren IA (1969) Egg production and oil storage by the copepod *Pseudocalanus* in the laboratory. *J Exp Mar Biol Ecol* 3: 90-105
- Corkett CJ, Zillioux EJ (1975) Studies on the effect of temperature on the egg laying of three species of calanoid copepods in the laboratory (*Acartia tonsa*, *Temora longicornis* and *Pseudocalanus elongatus*). *Bull Plankton Soc Jap* 21: 77-85
- Corkett CJ, McLaren IA (1978) The biology of *Pseudocalanus*. *Adv Mar Biol* 15: 1-231
- Daan R, Gonzalez SR, Klein Breteler WCM (1988) Cannibalism in omnivorous calanoid copepods. *Mar Ecol Prog Ser* 47: 45-54
- Dagg MJ, Clarke ME, Nishiyama T, Smith SL (1984) Production and standing stock of copepod nauplii, food items for larvae of the walleye pollock *Theragra chalcogramma* in the southeastern Bering Sea. *Mar Ecol Prog Ser* 19: 7-16
- Dickmann M (2005) Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the Baltic Sea and the North Sea. PhD Thesis, University Rostock, Germany
- Diel S, Klein Breteler WCM (1986) Growth and development of *Calanus* spp. (Copepoda) during spring phytoplankton succession in the North Sea. *Mar Biol* 91: 85-92
- Digby PSB (1950) The biology of small planktonic copepods of Plymouth. *J Mar Biol Ass UK* 29: 393-438
- Durbin EG, Durbin AG, Smayda TJ, Verity PG (1983) Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. *Limnol Oceanogr* 28: 1199-1213

- Eriksson S (1973) Abundance and composition of zooplankton on the west coast of Sweden. *Zoon* 1: 113-123
- Evans F (1977) Seasonal density and production estimates of the commoner planktonic copepods of Northumberland coastal waters. *Est Coast Mar Sci* 5: 233-241
- Farran GP (1920) On the local and seasonal distribution of the pelagic copepoda of the south-west of Ireland. *Publs Circonst Cons Perm Int Expl Mer* 73
- Fransz HG (1975) The spring development of calanoid copepod populations in Dutch coastal waters as related to primary production. In: Persoone G, Jaspers E (eds) *Proc 10th Eur Mar Biol Symp Vol 2*. Universa Press, Wetteren, 247-269
- Fransz HG, Miquel JC, Gonzalez SR (1984) Mesozooplankton composition, biomass and vertical distribution, and copepod production in the stratified Central North Sea. *Neth J Sea Res* 18: 82-96
- Fransz HG, Diel S (1985) Secondary production of *Calanus finmarchicus* (Copepoda: Calanoidea) in a transitional system of the Fladen Ground area (northern North Sea) during the spring of 1983
- Fransz HG, Colebrook JM, Gamble JC, Krause M (1991) Zooplankton of the North Sea-Review. *Neth J Sea Res* 28: 1-52
- Frost BW (1985) Food limitation of the planktonic marine copepods *Calanus pacificus* and *Pseudocalanus* sp. in a temperate fjord. *Arch Hydrobiol Beih Ergeb Limnol* 21: 1-13
- Frost BW (1989) A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can J Zool* 67: 525-551
- Greze VN, Baldina EP, Bileva OK (1968) Production of plankton copepods in the neritic zone of the Black Sea. *Okeanologiya* 8: 1066-1070 (in Russian)
- Halsband C, Hirche HJ (2001) Reproductive cycles of dominant calanoid copepods in the North Sea. *Mar Ecol Prog Ser* 209: 219-229
- Hansen K vagn (1969) Investigations on the quantitative and qualitative distribution of zooplankton in the southern part of the Norwegian Sea. *Medd Danmarks Fiskeri- og Havunders. NS 2* (53): 1-53
- Hickel W (1975) The mesozooplankton in the Wadden Sea of Sylt (North Sea). *Helgoländer Wissenschaftl Meeresunters* 27: 254-262
- Hirche HJ, Brey T, Niehoff B (2001) A high-frequency time series at Ocean Weather Ship Station M (Norwegian Sea): Population dynamics of *Calanus finmarchicus*. *Mar Ecol Prog Ser* 219: 205-219
- Holligan PM, Harris RP, Newell RC, Harbour DS, Head RN, Linley EAS, Lucas MI, Tranter PRG, Weekley CM (1984) Vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel. *Mar Ecol Prog Ser* 14: 111-127
- Huntley ME, Lopez MDG (1992) Temperature-dependent production of marine copepods: A global synthesis. *Am Nat* 140: 201-242
- Jónasdóttir SH (1989) Effects of food concentration on egg-production rates of two species of *Pseudocalanus*: Laboratory observations. *J Exp Mar Biol Ecol* 130: 33-43

- Kimmerer WJ, McKinnon D (1987) Growth, mortality, and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. *Limnol Oceanogr* 32: 14-28
- Kjørboe T, Møhlenberg F, Hamburger K (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar Ecol Prog Ser* 26: 85-97
- Kjørboe T, Johansen K (1986) Studies of a larval herring (*Clupea harengus* L.) patch in the Buchan area. 4. Zooplankton distribution and productivity in relation to hydrographic features. *Dana* 6: 37-51
- Kjørboe T, Moehlenberg F, Tiselius P (1988) Propagation of planktonic copepods: Production and mortality of eggs. *Hydrobiologia* 167/168: 219-225
- Kjørboe T, Nielsen TG (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 1. Copepods. *Limnol Oceanogr* 39: 493-507
- Klein Breteler WCM, Franz HG, Gonzalez SR (1982) Growth and development of four calanoid copepod species under experimental and natural conditions. *Neth J Sea Res* 16: 195-207
- Klein Breteler WCM, Gonzalez SR, Schogt N (1995) Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. *Mar Ecol Prog Ser* 119: 99-110
- Klein Breteler WCM, Gonzalez SR, Schogt N, Franz HG (1998) Feasibility of incubation experiments to estimate moulting rates in marine copepods. *J Plankton Res* 20: 257-269
- Koski M, Klein Breteler WCM, Schogt N (1998) Effect of food quality on rate of growth and development of the pelagic copepod *Pseudocalanus elongatus* (Copepoda, Calanoida). *Mar Ecol Prog Ser* 170: 169-187
- Krause M, Trahms J (1983) Zooplankton dynamics during FLEX'76. In: Sündermann J and Lenz W. North Sea dynamics. Springer Verlag, Berlin: 632-661
- Krause M, Dippner J, Beil J (1995) A review of hydrographic controls on the distribution of zooplankton biomass and species in the North Sea with particular reference to a survey conducted in January-March 1987. *Prog Oceanogr* 35: 81-152
- Künne C (1952) Untersuchungen über das Grossplankton in der Deutschen Bucht und im Nordsylder Wattenmeer. *Helgoländer Wissenschaftl Meeresunters* 4: 1 – 54
- Landry MR (1978) Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. *Int Rev Gesamt Hydrobiol* 63: 77-119
- Lücke F (1912) Quantitative Untersuchung an dem Plankton bei dem Feuerschiff 'Borkumriff' im Jahre 1910. *Wiss Meeresunters Kiel* 14: 101-128
- McLaren IA, Sevigny JM, Corkett CJ (1989) Temperature-dependent development in *Pseudocalanus* species. *Can J Zool* 67: 559-564
- Nielsen TG (1991) Contribution of zooplankton grazing to the decline of a *Ceratium* bloom. *Limnol Oceanogr* 36: 1091-1106
- Ohman MD (1985) Resource-satiated population growth of the copepod *Pseudocalanus* sp. *Arch Hydrobiol Beih Ergebn Limnol* 21: 15-32

- Ohman MD, Runge JA (1994) Sustained fecundity when phytoplankton resources are in short supply: Omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. *Limnol Oceanogr* 39: 21-36
- Otto L, Zimmerman JTF, Furnes GK, Mork M, Saetre R, Becker G (1990) Review of the physical oceanography of the North Sea. *Neth J Sea Res* 26: 161-238
- Paffenhöfer GA, Harris RP (1976) Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus* Boeck. *J Mar Biol Assoc UK* 56: 327-344
- Parsons TR, Takahashi M, Hargrave B (1984) Chemical composition-Zooplankton. In: *Biological Oceanographic Processes*. Pergamon Press: 323
- Peterson WT (1985) Abundance, age structure and in situ egg production rates of the copepod *Temora longicornis* in Long Island Sound, New York. *Bull Mar Sci* 37: 726-738
- Peterson WT (1986) Development, growth, and survivorship of the copepod *Calanus marshallae* in the laboratory. *Mar Ecol Prog Ser* 29: 61-72
- Peterson WT, Tiselius P, Kiørboe T (1991) Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. *J Plankton Res* 13: 131-154
- Runge JA, McLaren IA, Corkett CJ, Bohrer RN, Koslow JA (1985) Molting rates and cohort development of *Calanus finmarchicus* and *C. glacialis* in the sea off Southwest Nova Scotia. *Mar Biol* 86: 241-246
- Timohina AF (1968) Production of mass species of zooplankton in Norwegian Seas. *Trudy Polyarnogo nauchno-issled. Inst morsk ryb khoz Okeanogr* 23: 173-192 (in Russian)
- Uye S (1988) Temperature-dependent development and growth of *Calanus sinicus* (Copepoda: Calanoida) in the laboratory. *Hydrobiologia* 167/168: 285-293
- Vidal J (1980) Physioecology of Zooplankton. II. Effects of Phytoplankton Concentration, Temperature, and Body Size on the Development and Molting Rates of *Calanus pacificus* and *Pseudocalanus* sp. *Mar Biol* 55: 135-146
- Wimpenny RS (1933) Variations in the North Sea plankton 1923-4. *Min Agric Fish, Fish Invest Ser II*, 8

Table 1: Cruisedates, growth rates and productivity (P/B) of *Pseudocalanus elongatus* in the southern North Sea from February to October 2004

Cruise	Growth rate [d <sup>-1</sup> ]						[P/B]
	CI	CII	CIII	CIV	CV	AF	
16.02. - 05.03.2004	0.12	0.11	0.07	0.08	0.04	0.12	0.057
06.04. - 27.04.2004	0.31	0.22	0.17	0.14	0.12	0.09	0.09
07.05. - 26.05.2004						0.13	0.105
17.06. - 06.07.2004	0.17	0.31	0.09	0.09	0.08	0.05	0.065
04.08. - 23.08.2004	0.19	0.17	0.08	0.16	0.05	0.10	0.085
06.09. - 12.09.2004							0.083
11.10. - 16.10.2004						0.05	0.086
17.05. - 28.05.2005							
30.06. - 08.07.2005							

Table 2: Stage durations, calculated by moulting rates, of *P. elongatus* in the southern North Sea at *in situ* temperature (T) and salinity (S)

Date	Station	T [°C]	S [PSU]	Stage duration [days]													
				range					Mean per month								
				CI	CII	CIII	CIV	CV	CI	CII	CIII	CIV	CV				
18.02.2004	47	5	32		1		5					4.6	5.6	5	7.6		
19.02.2004	42	5	32			7	3.5	7.3									
21.02.2004	32	5	32		9	5	8	7.5									
21.02.2004	32	5	32		3.8	4.8	3.5	8									
08.04.2004	7	7	32	1.5	3	2.3 - 3.5	1.4 - 3.3	3.0 - 3.6									
07.04.2004	7	7	32	2.3	1.7	3	3	4.5									
13.04.2004	22	7	32					4.8	1.9	2.4	2.9	3.5	6				
15.04.2004	20	7	32				5	8.3									
13.04.2004	49	7	32					9.2									
22.06.2004	31	12	32		2	3.7 - 6.5	3.4 - 3.8	5.9 - 6.3						2	5.1	3.6	6.1
08.08.2004	49	13	32		2.0 - 3.0	3.4 - 5.1	1.2 - 3.6	8						2.5	4.3	2.4	8

**Figure captions**

Fig. 1: Study area southern North Sea and German Bight with station grid; *squares* focus stations, *circles* additional stations for measurement of abundance

Fig. 2: Abundance of developmental stages of *Pseudocalanus elongatus* in the southern North Sea from February to October 2004

Fig. 3: Prosome length of copepodite stages, AM and AF of *Pseudocalanus elongatus* in the southern North Sea from February to October 2002; *symbols* mean values, *error bars* standard deviation

Fig. 4: Length-frequency distribution of *Pseudocalanus elongatus* AF and number of generations (*G*) in the southern North Sea between February 2004 and May 2005

Fig. 5: Reproduction of *Pseudocalanus elongatus* in the southern North Sea from February 2004 to May 2005; a. chlorophyll concentration; b. percentage of spawning females at different stations, *black line* mean; c. hatching success of nauplii, d. egg production rate (EPR) at different stations, *grey line* temperature in 10 m depth; e. correlation between EPR and percentage of spawning females; f. correlation between EPR and mean clutch size per station

Fig. 6: a. Clutch size of *Pseudocalanus elongatus* in the southern North Sea between February 2004 and May 2005; b. Correlation between clutch size and prosome length of females (AF)

Fig. 7: Relationship between chlorophyll concentration and egg production rate (EPR) (a.), hatching success (b.) and proportion of spawning females (c.) of *Pseudocalanus elongatus* in the southern North Sea

Fig. 8: Relationship between temperature and stage durations of developmental stages of *Pseudocalanus elongatus* in the southern North Sea

Fig. 9: Cumulative secondary production of *Pseudocalanus elongatus* copepodite stages and females in the southern North Sea from February to October 2002

Fig. 1

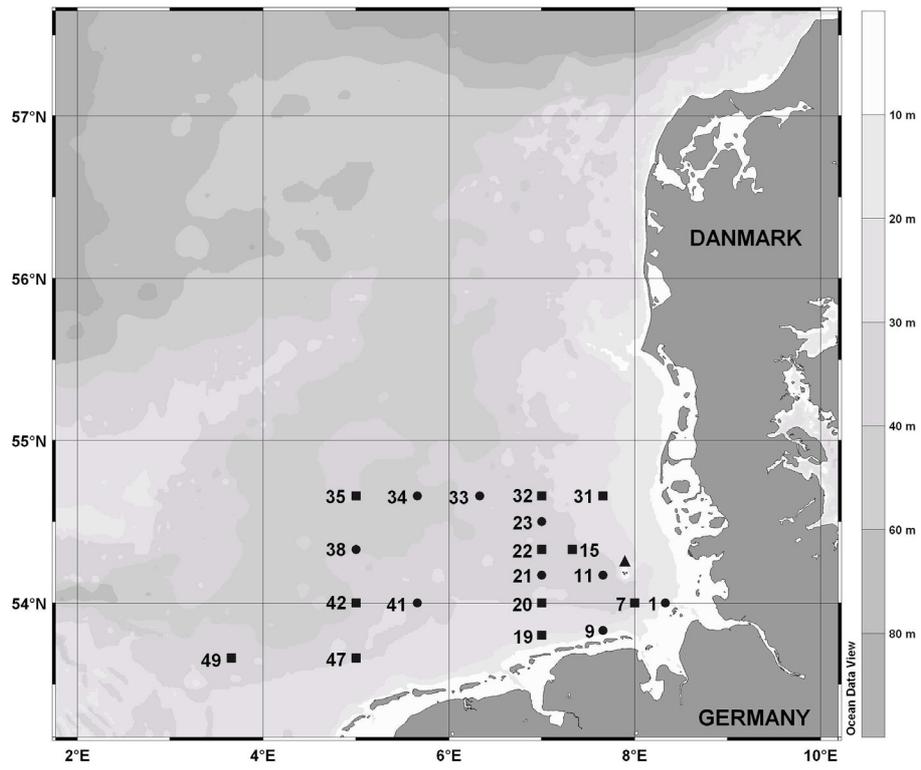


Fig. 2

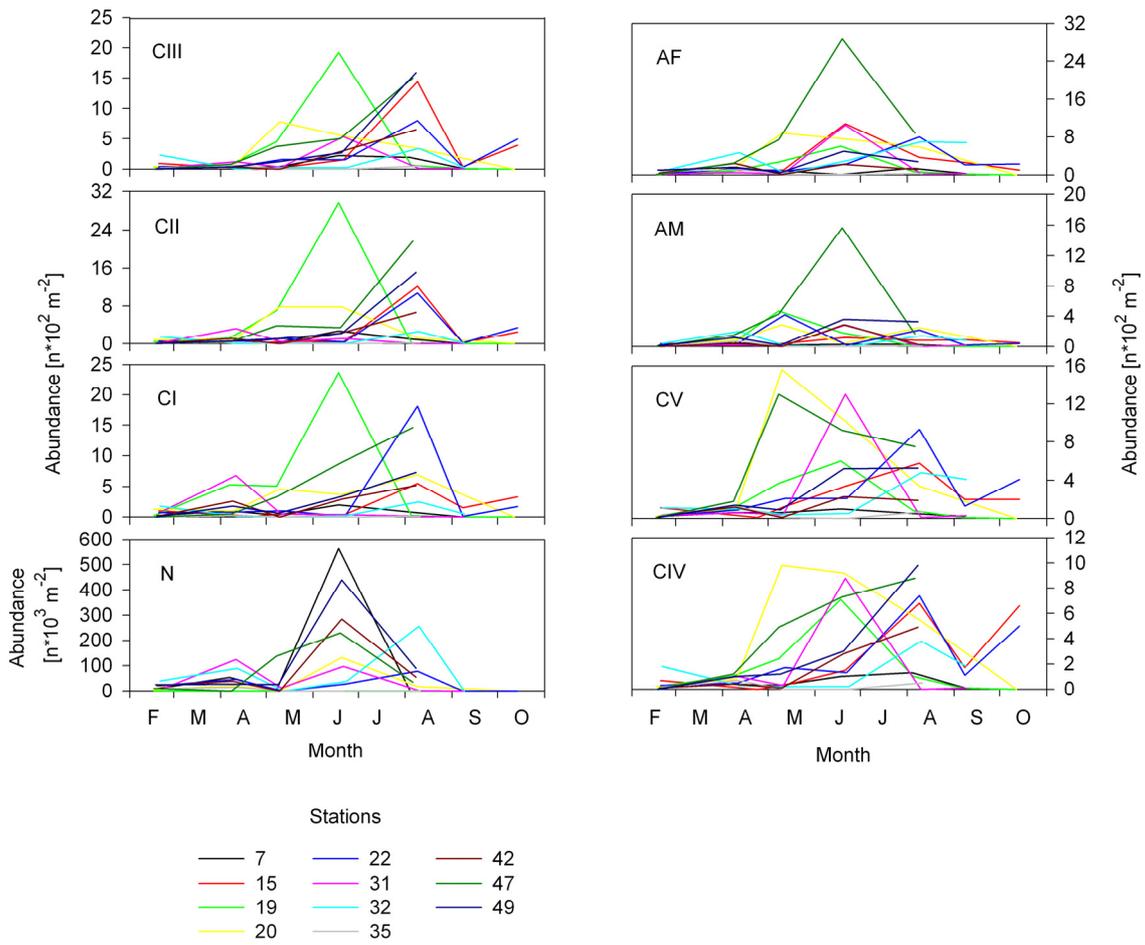


Fig. 3

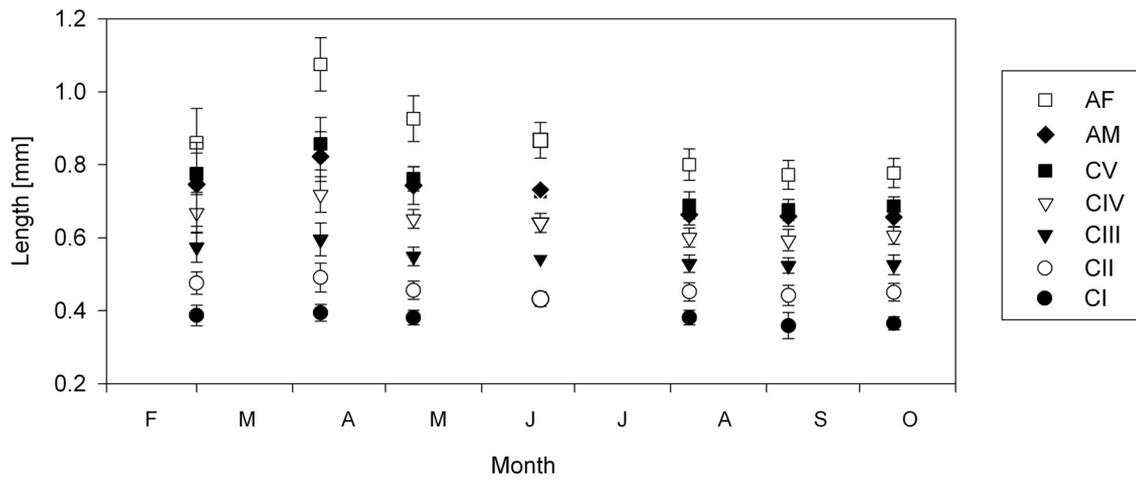


Fig. 4

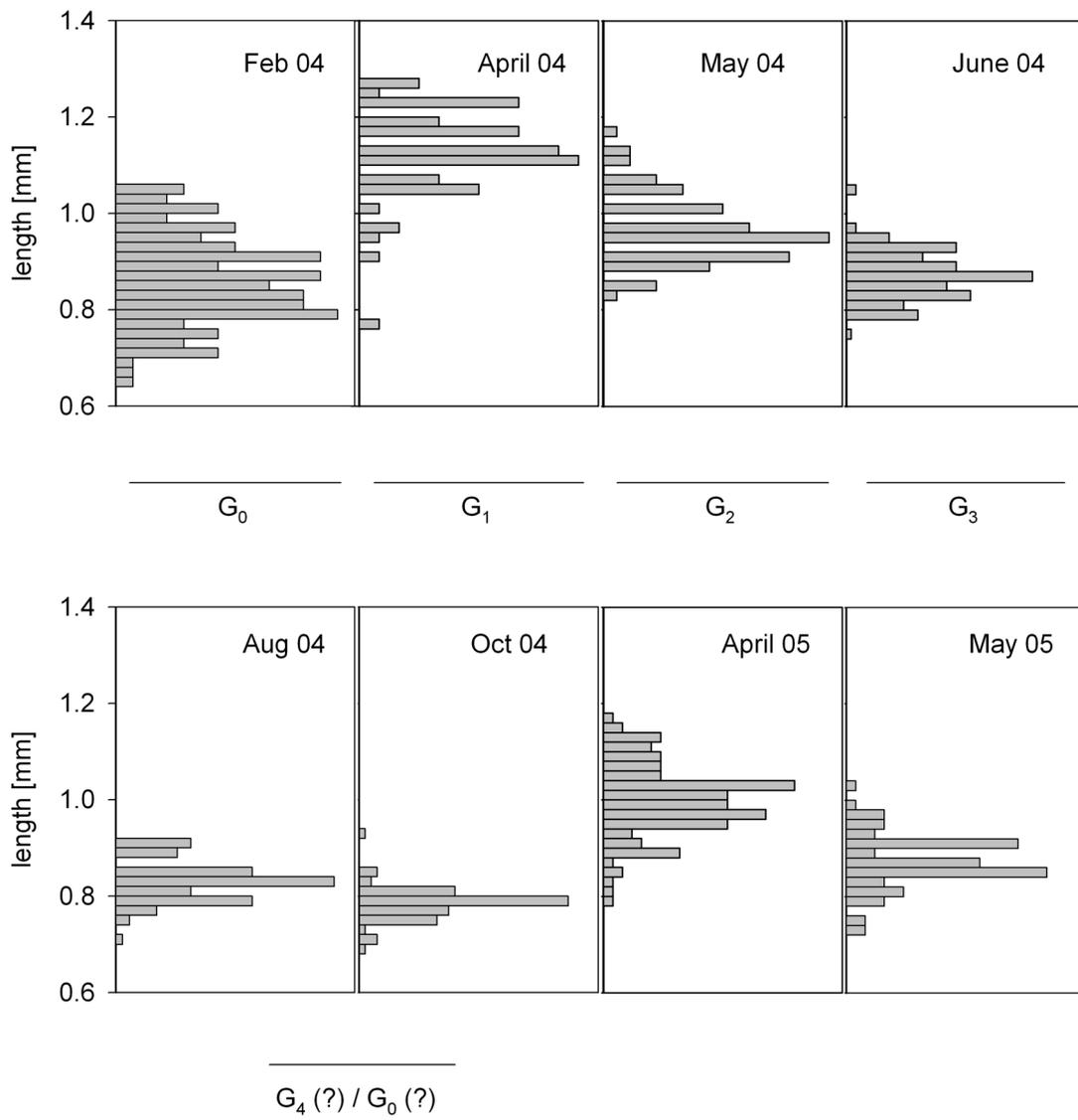


Fig. 5

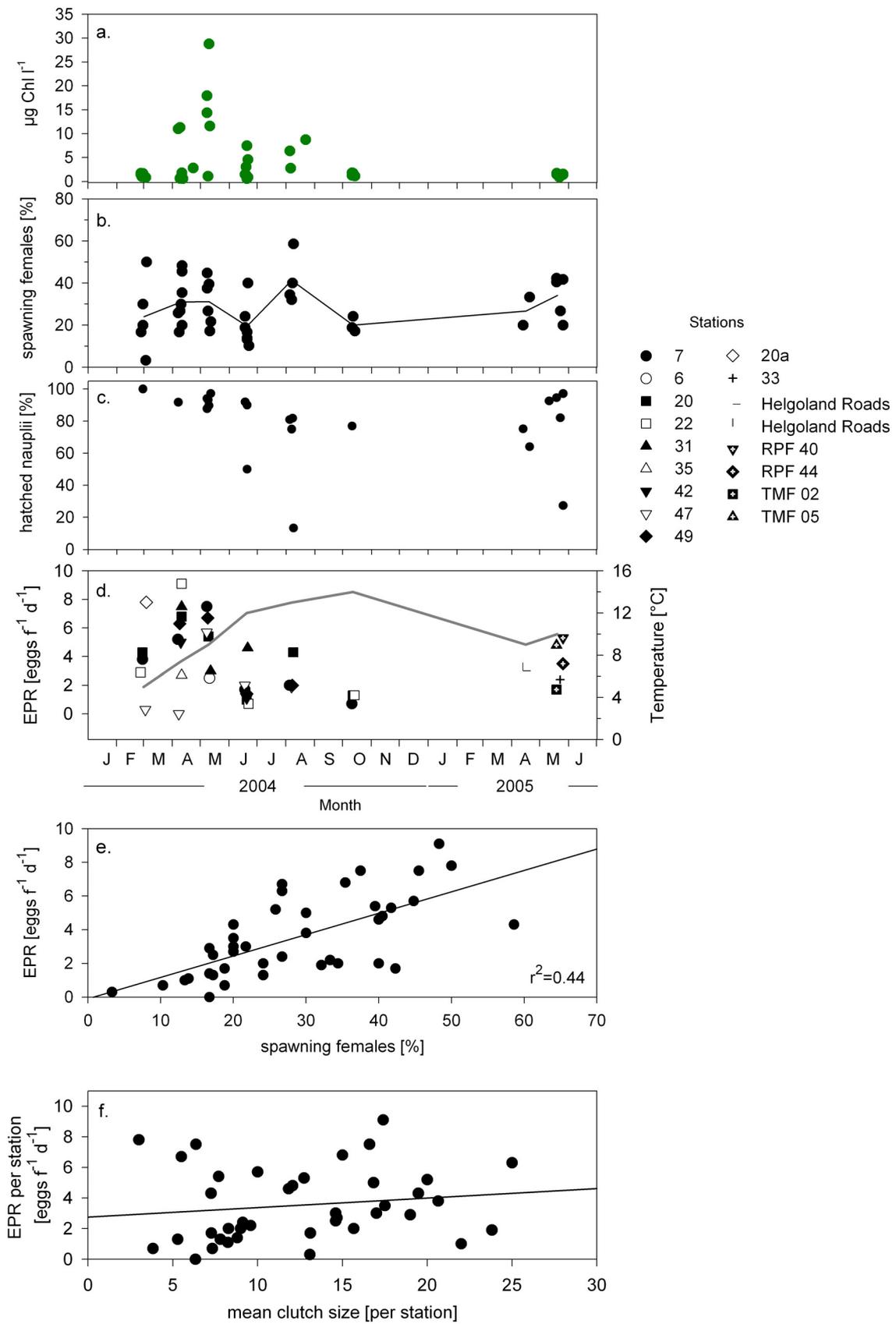


Fig. 6

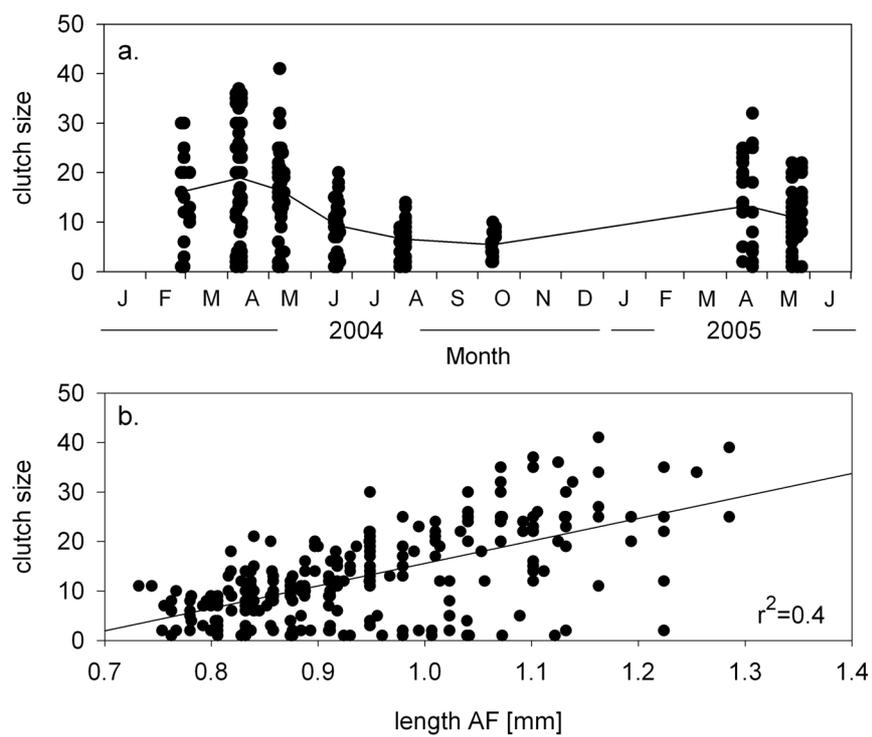


Fig. 7

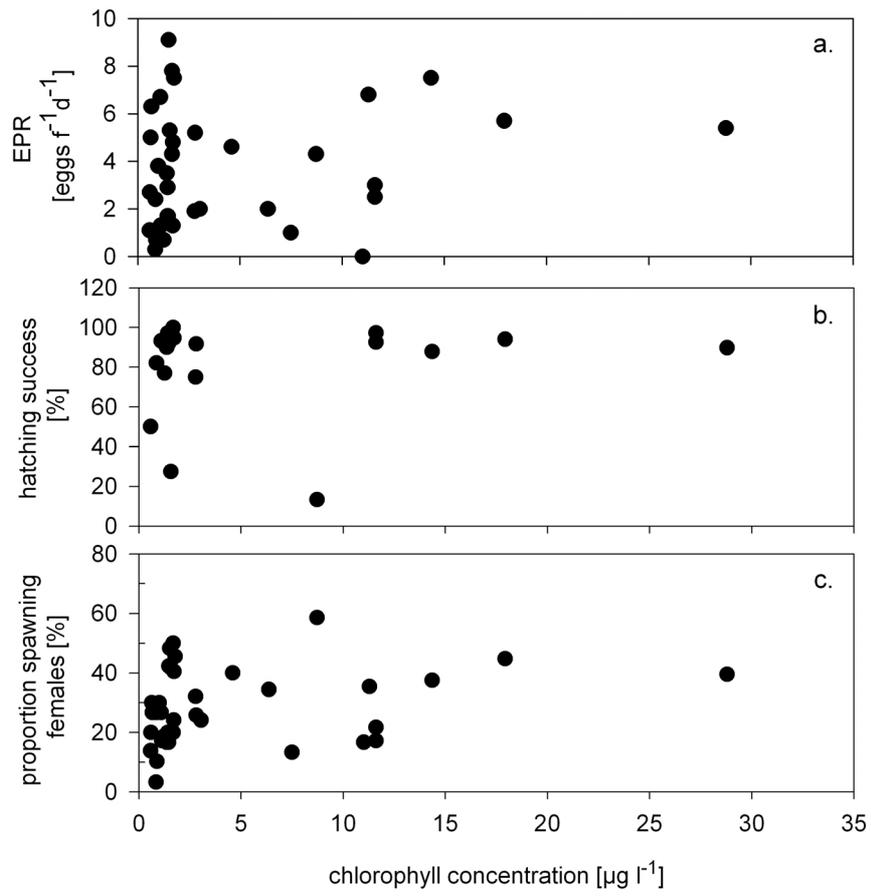


Fig. 8

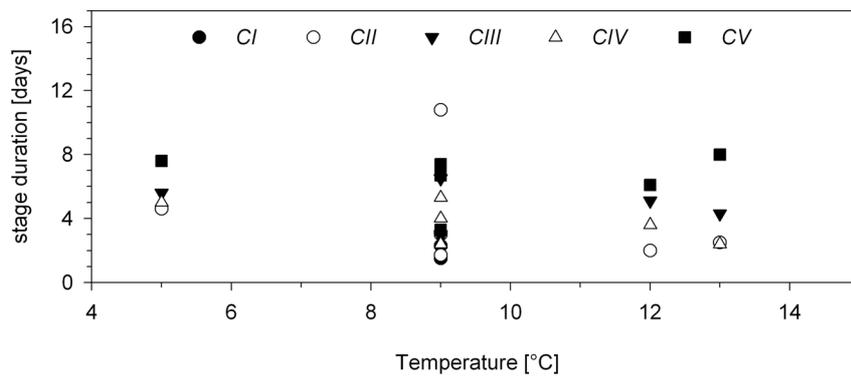
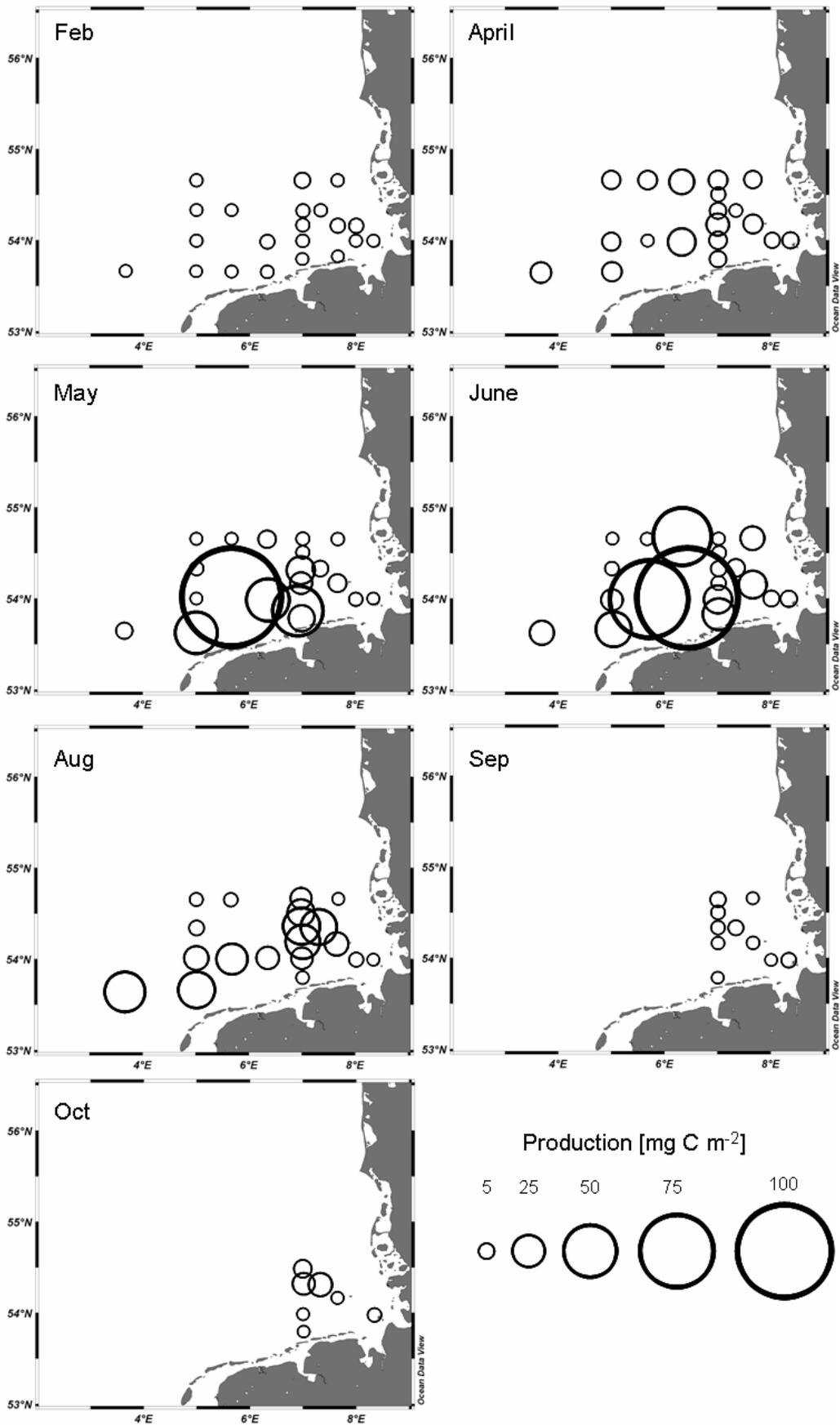


Fig. 9



## 7 References

- Ackefors H (1966) Plankton and hydrography of the Landsort Deep. Veröffentl Inst Meeresforsch Bremerhaven, Sonderbd 2: 381-385
- Ackefors H (1969) Ecological zooplankton investigations in the Baltic proper, 1963-1965. Rep Inst Mar Res Lysekil, Ser Biol 18: 1-139
- Afrikova SG (1975) Distribution of *Pseudocalanus elongatus* (Boeck) in the Black Sea. *Gidrobiologicheskii Zh* 11: 92-97 (in Russian)
- Alheit J, Möllmann C, Dutz J, Kornilovs G, Loewe P, Mohrholz V, Wasmund N (2005) Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES J Mar Sci* 62: 1205-1215
- Auel H, Hagen W (2005) Body mass and lipid dynamics of Arctic and Antarctic deep-sea copepods (Calanoida, *Paraeucope*): ontogenetic and seasonal trends. *Deep Sea Res I* 52: 1272-1283
- Båmstedt U, Håkanson JL, Brenner-Larsen J, Bjørnsen PK, Geertz-Hansen O, Tiselius P (1990) Copepod nutritional condition and pelagic production during autumn in Kosterfjorden, western Sweden. *Mar Biol* 104: 197-208
- Banner FT, Collins MB, Massie KS (1980) The north-west European Shelf seas: the sea bed and the sea in motion. II. Physical and chemical oceanography, and physical resources. Elsevier Scientific Publishing Company, New York
- Barz K (2006) Influence of pelagic invertebrate predators on the zooplankton in the Baltic Sea and the North Sea. PhD Thesis, University of Bremen, Germany
- Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the North-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fish Oceanogr* 12: 270-283
- Beaugrand G (2004) The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progr Oceanogr* 60: 245-262
- Becker GA, Prahm-Rodewald G (1980) Fronts in the Sea: Salinity Fronts in the German Bight. *Seewart* 41: 12-21
- Becker GA, Fiuza AFG, James ID (1983) Water mass analysis in the German Bight during MARSEN, Phase I. *J Geophys Res* 88: 9865-9870
- Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. *Mar Biol* 99: 341-352
- Bergström S, Carlsson B (1994) River runoff to the Baltic Sea: 1950-1990. *Ambio* 23: 280-287
- Bollens SM, Frost BW (1989) Predator-induced diel vertical migration in a planktonic copepod. *J Plankton Res* 11: 1047-1065
- Bossicart M (1980) Population dynamics of copepods in the Southern Bight of the North Sea (1977-1979), use of a multicohort model to derive biological parameters. *ICES CM L:24*

- Böttger R, Schnack D (1986) On the effect of formaldehyde fixation on the dry weight of copepods. *Meeresforschung/Rep Mar Res* 31: 141-152
- Bucklin A, Frost BW, Bradford-Grieve J, Allen LD, Copley NJ (2003) Molecular systematic and phylogenetic assessment of 34 calanoid copepod species of the Calanidae and Clausocalanidae. *Mar Biol* 142: 333-343
- Bunker AJ, Hirst AG (2004) Fecundity of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature and body weight. *Mar Ecol Prog Ser* 279: 161-181
- Cairns AA (1967) The zooplankton of Tanquary Fjord, Ellesmere Island, with special reference to the calanoid copepods. *J Fish Res Board Can* 24: 555-568
- Chisholm LA, Roff JC (1990a) Size-weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. *Mar Biol* 106: 71-77
- Chisholm LA, Roff JC (1990b) Abundances, growth rates, and production of tropical neritic copepods off Kingston, Jamaica. *Mar Biol* 106: 79-89
- Clarke KR (1993) Non-parametric multivariate analyses of change in community structure. *Austral J Ecol* 18: 117-143
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Bourne Press Limited, Plymouth
- Colebrook JM (1979) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north Atlantic Ocean and the North Sea. *Mar Biol* 51: 23-32
- Conover RJ (1967) Reproductive cycle, early development, and fecundity in laboratory populations of the copepod *Calanus hyperboreus*. *Crustaceana* 13: 61-72
- Conover RJ (1988) Comparative histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167/168: 127-142
- Conover RJ, Siferd TD (1993) Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. *Arctic* 46: 303-311
- Corkett CJ, McLaren IA (1970) Relationships between development rate of eggs and older stages of copepods. *J Mar Biol Ass UK* 50: 161-168
- Corkett CJ, McLaren IA (1978) The biology of *Pseudocalanus*. *Adv Mar Biol*: 1-231
- Cotonnec G, Brunet C, Sautour B, Thoumelin G (2001) Nutritive Value and Selection of Food Particles by Copepods During a Spring Bloom of *Phaeocystis* sp. in the English Channel, as Determined by Pigment and Fatty Acid Analyses. *J Plankton Res* 23: 693-703
- Cushing DH (1982) The North Sea. In: *Climate and fisheries*, Academic press, London, pp 373
- Dahmen K (1995) Vertikalverteilung und produktionsbiologische Bedeutung des Mesozooplanktons im Bornholm-Becken (Südliche Ostsee). *Berichte aus dem Institut für Meereskunde an der Universität Kiel* 273: pp 175
- Davis CC (1976) The pelagic Copepoda of the north-eastern Pacific Ocean. University of Washington Publications in Biology, Seattle 14: 1-117
- Davis CS (1984a) Predatory control of copepod seasonal cycles on Georges Bank. *Mar Biol* 82: 31-40

- Davis CS (1984b) Food concentrations on Georges Bank: non-limiting effect on development and survival of laboratory reared *Pseudocalanus* sp. & *Paracalanus parvus* (Copepoda, Calanoida). *Mar Biol* 82: 41-46
- Dickmann M (2005) Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the Baltic Sea and the North Sea. PhD Thesis, University Rostock, Germany
- Dietrich G, Kalle K, Krauss W, Siedler G (1975) Allgemeine Meereskunde. Eine Einführung in die Ozeanographie. Gebrüder Bornträger, Berlin, pp 593
- Digby PSB (1950) The biology of small planktonic copepods of Plymouth. *J Mar Biol Ass UK* 29: 393-438
- Dippner JW, Kornilovs G, Sidrevics L (2000) Long-term variability of mesozooplankton in the central Baltic Sea. *J Mar Syst* 25: 23-31
- Dippner JW, Hänninen J, Kuosa H, Vuorinen I (2001) The influence of climate variability on zooplankton abundance in the Northern Baltic Archipelago Sea (SW Finland). *ICES J Mar Sci* 58: 569-578
- Drebes G (1972) Entwicklung des Ektoparasiten *Dissodinium pseudocalani* (Dinophyceae). Accompanying pamphlet for scientific film C 1069/1971, Institut für den wissenschaftlichen Film, Göttingen
- Durbin EG, Durbin AG, Smayda TJ, Verity PG (1983) Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. *Limnol Oceanogr* 28: 1199-1213
- Edwards M, Reid PC, Planque B (2001) Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES J Mar Sci* 58: 39-49
- Eiane K, Ohman MD (2004) Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. *Mar Ecol Prog Ser* 268: 183-193
- Eriksson S (1973) Abundance and composition of zooplankton on the west coast of Sweden. *Zoon* 1: 113-123
- Evans F (1977) Seasonal density and production estimates of the commoner planktonic copepods of Northumberland coastal waters. *Est Coast Mar Sci* 5: 233-241
- Farran GP (1920) On the local and seasonal distribution of the pelagic copepoda of the south-west of Ireland. *Publs Circonst Cons Perm Int Expl Mer* 73
- Feistel R, Nausch G, Matthaus W, Hagen E (2003) Temporal and spatial evolution of the Baltic deep water renewal in spring 2003. *Oceanologia* 45: 623-642
- Fransz HG, Arkel W van (1983) Fluctuation and succession of common pelagic copepod species in the Dutch Wadden Sea. *Oceanologia Acta*: 87-91
- Fransz HG, Miquel JC, Gonzalez SR (1984) Mesozooplankton composition, biomass and vertical distribution, and copepod production in the stratified Central North Sea. *Neth J Sea Res* 18: 82-96
- Fransz HG, Colebrook JM, Gamble JC, Krause M (1991) Zooplankton of the North Sea-Review. *Neth J Sea Res* 28: 1-52

- Fraser AJ, Sargent JR, Gamble JC (1989) Lipid class and fatty acid composition of *Calanus finmarchicus* (Gunnerus), *Pseudocalanus* sp. and *Temora longicornis* Müller from a nutrient-enriched seawater enclosure. *J Exp Mar Biol Ecol* 130: 81-92
- Frost BW (1969) Distribution of the oceanic, epipelagic copepod genus *Clausocalanus* with an analysis of sympatry of North Pacific Species. PhD Thesis, Scripps Institute of Oceanography, University of California, San Diego, USA
- Frost BW (1985) Food limitation of the planktonic marine copepods *Calanus pacificus* and *Pseudocalanus* sp. in a temperate fjord. *Arch Hydrobiol Beih Ergeb Limnol* 21: 1-13
- Frost BW (1989) A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can J Zool* 67: 525-551
- Glover RS, Robinson GA, Colebrook JM (1972) Plankton in the North Atlantic- an example of the problems of analysing variability in the environment. In: Ruivo M (ed.) *FAO: Marine pollution and sea life*. Fishing News (Books), Surrey, London
- Grant GC (1988) Seasonal occurrence and dominance of *Centropages congens* in the Middle Atlantic Bight, USA. *Hydrobiologia* 167/168: 227-237
- Greve W, Reiners F, Nast J (1996) Biocoenotic changes of the zooplankton in the German Bight: the possible effects of eutrophication and climate. *ICES J Mar Sci* 53: 951-956
- Greze VN (1978) Production in Animal Populations. In: Kinne O (1978) (ed.) *Marine Ecology. A comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters. Vol. IV Dynamics*. Wiley, New York, pp 89-115
- Hänninen J, Vuorinen I, Hjelt P (2000) Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnol Oceanogr* 45: 703-710
- Hairton NG Jr, Twombly S (1985) Obtaining life table data from cohort analysis: a critique of current methods. *Limnol Oceanogr* 30: 886-893
- Halliday NC (2001) A comparison of morphometric and geometric methods for the estimation of individual zooplankton volumes. *Sarsia* 86: 101-105
- Hansen K vagn (1969) Investigations on the quantitative and qualitative distribution of zooplankton in the southern part of the Norwegian Sea. *Medd Danmarks Fiskeri- og Havunders. NS 2 (53):* 1-53
- Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds) (2000) *Zooplankton Methodology Manual*. Academic Press, pp 410-412
- Hattori H, Saito H (1997) Diel changes in vertical distribution and feeding activity of copepods in ice-covered Resolute Passage, Canadian Arctic, in spring 1992. *J Mar Syst* 11: 205-219
- Hay SJ, Evans GT, Gamble JC (1988) Birth, growth and death rates for enclosed populations of calanoid copepods. *J Plankton Res* 10: 431-454
- Hays GC, Carr MR, Taylor AH (1993) The relationship between Gulf Stream position and copepod abundance derived from the Continuous Plankton Recorder survey: Separating biological signal from sampling noise. *J Plankton Res* 15: 1359-1373
- Herrnroth L, Ackefors H (1979) The zooplankton of the Baltic proper: a long-term investigation of the fauna, its biology and ecology. *Report Fish Bd Sweden, Inst Mar Res* 2: 1-160

- Hernroth L (1985) Recommendations on methods for marine biological studies in the Baltic Sea: Mesozooplankton Biomass Assessment. *Baltic Mar Biol* 10: 1-32
- Hinrichsen HH, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. *Can J Fish Aquat Sci*: 1858-1873
- Hinrichsen HH, Lehmann A, Möllmann C, Schmidt J (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. *Fish Oceanogr* 12: 425-433
- Hirche HJ (1996) Diapause in the marine copepod, *Calanus finmarchicus* - a review. *Ophelia*: 129-143
- Hirche HJ (1998) Dormancy in three *Calanus* species (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*) from the North Atlantic. In: Brendonck L, De Meester L, Hairston N Jr (eds) Evolutionary and ecological aspects of crustacean diapause, Stuttgart. *Adv Limnol* 52: 359-369
- Hirche HJ, Brey T, Niehoff B (2001) A high-frequency time series at Ocean Weather Ship Station M (Norwegian Sea): Population dynamics of *Calanus finmarchicus*. *Mar Ecol Prog Ser* 219: 205-219
- Hirst AG, Lampitt RS (1998) Towards a global model of in situ weight/specific growth in marine planktonic copepods. *Mar Biol* 132: 247-257
- Hirst AG, Bunker AJ (2003) Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnol Oceanogr* 48: 1988-2010
- Huntley ME, Lopez MDG (1992) Temperature-dependent production of marine copepods: A global synthesis. *Am Nat*: 201-242
- Hurrell JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269: 676-679
- Ianora A, Poulet SA, Miralto A, Grotoli R (1996) The diatom *Thalassiosira rotula* affects reproductive success in the copepod *Acartia clausi*. *Mar Biol* 125: 279-286
- Jarre-Teichmann A, Wieland K, MacKenzie BR, Hinrichsen HH, Plikshs M, Aro E (2000) Stock-recruitment relationships for cod (*Gadus morhua callarias* L.) in the central Baltic Sea incorporating environmental variability. *Arch Fish Mar Res* 48: 97-123
- Jónasdóttir SH (1989) Effects of food concentration on egg-production rates of two species of *Pseudocalanus*: Laboratory observations. *J Exp Mar Biol Ecol* 130: 33-43
- Kaipris K, Miliou H, Moraitou-Apostolopoulou M (1997) Effects of formaldehyde preservation on biometrical characters, biomass and biochemical composition of *Acartia clausi* (Copepoda, Calanoida). *Helgoländer Meeresunters* 51: 95-106
- Kane J (1984). The feeding habits of co-occurring cod and haddock larvae from Georges Bank. *Mar Ecol Prog Ser* 16: 9-20
- Kimmerer WJ, McKinnon D (1987) Growth, mortality, and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. *Limnol Oceanogr* 32: 14-28
- Kinne O (1963) The effects of temperature and salinity on marine and brackish water animals. I. Temperature. *Oceanogr Mar Biol Ann Rev* 1: 301-340

- Kinne O (1978) (ed) Marine Ecology. A comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters. Vol. IV Dynamics. Wiley, New York, pp 746
- Kjørboe T, Møhlenberg F, Tiselius P (1988) Propagation of planktonic copepods: production and mortality of eggs. *Hydrobiologia* 167/168: 219-225
- Kjørboe T, Nielsen TG (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 1. Copepods. *Limnol Oceanogr* 39: 493-507
- Kjørboe T, Sabatini M (1995) Scaling of fecundity, growth and development in marine planktonic copepods. *Mar Ecol Prog Ser* 120: 1-3
- Klein-Breteler WCM, Gonzalez SR (1982) Influence of cultivation and food concentration on body length of calanoid copepods. *Mar Biol* 71: 157-161
- Klein Breteler WCM, Gonzalez SR, Schogt N (1995) Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. *Mar Ecol Prog Ser* 119: 99-110
- Klein Breteler WCM, Gonzalez SR, Schogt N, Franz HG (1998) Feasibility of incubation experiments to estimate moulting rates in marine copepods. *J Plankton Res* 20: 257-269
- Kononen K, Kuosa H, Leppänen J, Olsonen R, Kuparinen J, Postel L, Behrends G (1996) Overall assessment. Pelagic Biology. HELCOM 1996: Baltic Sea Envir Proc 64B: 215-222
- Kornilovs G, Sidrevics L, Dippner JW (2001) Fish and zooplankton interaction in the Central Baltic Sea. *ICES J Mar Sci* 58: 579-588
- Koski M, Breteler WK, Schogt N (1998) Effect of food quality on rate of growth and development of the pelagic copepod *Pseudocalanus elongatus* (Copepoda, Calanoida). *Mar Ecol Prog Ser* 170: 169-187
- Köster FW, Hinrichsen HH, St.John MA, Schnack D, MacKenzie BR, Tomkiewicz J, Plikshs M (2001) Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. *Can J Fish Aquat Sci* 58: 1535-1557
- Kraefft F (1910) Über das Plankton in Ost- und Nordsee und den Verbindungsgebieten mit besonderer Berücksichtigung der Copepoden. *Wiss Meeresunters der Kommission zur Wiss Unters dt Meere, Abt Kiel* 11: 29-107
- Krause M, Trahms J (1983) Zooplankton dynamics during FLEX'76. In: Sündermann J and Lenz W. North Sea dynamics. Springer Verlag, Berlin: 632-661
- Krause M, Dippner J, Beil J (1995) A review of hydrographic controls on the distribution of zooplankton biomass and species in the North Sea with particular reference to a survey conducted in January-March 1987. *Prog Oceanogr* 35: 81-152
- Künne C (1952) Untersuchung über das Grossplankton in der Deutschen Bucht und im Sylter Wattenmeer. *Helgoländer Wiss Meeresunters* 4: 1-54
- Lalli CM, Parsons TR (eds) (1993) Biological Oceanography-An Introduction. The Open University, Butterworth and Heinemann, Linacre House, Oxford, pp314
- Landry MR (1978) Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. *Int Rev Ges Hydrobiol* 63: 77-119

- Lee HW, Ban S, Ikeda T, Matsuishi T (2003) Effect of temperature on development, growth and reproduction in the marine copepod *Pseudocalanus newmani* at satiating food condition. J Plankton Res 25: 261-271
- Lischka S, Hagen W (2005) Life histories of the copepods *Pseudocalanus minutus*, *P. acuspes* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). Polar Biol 28: 910-921
- Lücke F (1912) Quantitative Untersuchung an dem Plankton bei dem Feuerschiff 'Borkumriff' im Jahre 1910. Wiss Meeresunters Kiel 14: 101-128
- Macus N (1984) Variation in the diapause response of *Labidocera aestiva* (Copepoda, Calanoida) from different latitudes and its importance in the evolutionary process. Biol Bull 166: 127-139
- Marshall SM (1949) On the biology of the small copepods in Loch Striven. J Mar Biol Ass UK 28: 45-122
- Matthäus W, Franck H (1992) Characteristics of major Baltic inflows - a statistical analysis. Cont Shelf Res 12: 1375-1400
- Matthäus W, Schinke H (1994) Mean atmospheric circulation patterns associated with major Baltic inflows. Dtsch Hydrogr Z 46: 321-339
- Mauchline J (1995) Bathymetric adaptations of life history patterns of congeneric species (Euchaeta: Calanoida) in a 2000m water column. ICES J Mar Sci 52: 511-516
- Mauchline J (1998) The biology of calanoid copepods. In: Blaxter JHS, Southward AJ, Tyler PA (eds) Adv Mar Biol, Academic Press, San Diego, pp 710
- McGillcuddy DJ Jr, Lynch DR, Moore AM, Gentleman WC, Davis CS, Meise J (1998) An adjoint data assimilation approach to diagnosis of physical and biological controls on *Pseudocalanus* spp. in the Gulf of Maine-Georges Bank region. Fish Oceanogr 7: 205-218
- McLaren IA (1963) Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J Fish Res Board Can 20: 685-727
- McLaren IA (1969) Population and production ecology of zooplankton in Ogac Lake, a landlocked fjord on Baffin Island. J Fish Res Board Can 26: 1485-1559
- McLaren IA, Laberge E, Corkett CJ, Sevigny JM (1989a) Life cycles of four species of *Pseudocalanus* in Nova Scotia. Can J Zool 67: 552-558
- McLaren IA, Sevigny JM, Corkett CJ (1989b) Temperature-dependent development in *Pseudocalanus* species. Can J Zool 67: 559-564
- McLaren IA, Avendaño P. (1995). Prey field and diet of larval cod on Western Bank, Scotian Shelf. Can J Fish Aquat Sci 52: 448-463
- Miller CB (2004) (ed) Biological Oceanography. Blackwell Publishing, pp 402
- Minoda T (1971) Pelagic Copepoda in the Bering Sea. Mem Fac Fish Hokkaido Univ 18: 1-74
- Mohrholz V, Dutz J, Kraus G (2006) The impact of exceptionally warm summer inflow events on the environmental conditions in the Bornholm Basin. J Mar Syst 60: 285-301
- Möllmann C, Köster FW (1999) Food consumption by clupeids in the Central Baltic: evidence for top-down control? ICES J Mar Sci 56: 100-113

- Möllmann C, Kornilovs G, Sidrevics L (2000) Long-term dynamics of main mesozooplankton species in the central Baltic Sea. *J Plankton Res* 22: 2015-2038
- Möllmann C, Köster FW, Kornilovs G, Sidrevics L (2002) Long-term trends in abundance of cladocerans in the Central Baltic Sea. *Mar Biol* 141: 343-352
- Möllmann C, Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. *J Plankton Res* 24: 959-978
- Möllmann C, Kornilovs G, Fetter M, Köster F, Hinrichsen H (2003) The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. *Fish Oceanogr* 12: 360-368
- Napp JM, Hopcroft RR, Baier CT, Clarke C (2005) Distribution and species-specific egg production of *Pseudocalanus* in the Gulf of Alaska. *J Plankton Res* 27: 415-426
- Niehoff B, Klenke U, Hirche HJ, Irigoien X, Head R, Harris R (1999) A high frequency time series at Weathership M, Norwegian Sea, during the 1997 spring bloom: The reproductive biology of *Calanus finmarchicus*. *Mar Ecol Prog Ser* 176: 81-91
- Norrbin MF, Olsen RE, Tande KS (1990) Seasonal variation in lipid class and fatty acid composition of two small copepods in Balsfjorden, northern Norway. *Mar Biol* 105: 205-211
- Norrbin F (1992) Overwintering strategies of small copepods in high latitude marine environments. Dissertation, Faculty of Natural Sciences, Göteborg, Sweden
- Ohman MD (1985) Resource satiated population growth of the copepod *Pseudocalanus* sp. *Adv Limnol* 21: 15-32
- Ohman MD, Aksnes DL, Runge JA (1996) The interrelationship of copepod fecundity and mortality. *Limnol Oceanogr* 41: 1470-1477
- Ojaveer E, Lumberg A, Ojaveer H (1998) Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). *ICES J Mar Sci* 55: 748-755
- Østvedt W (1955) Zooplankton investigation from Weather Ship 'M' in the Norwegian Sea, 1948-1949. *Hvalradets Skr* 40: 1-93
- Pertsova NM (1981) Number of generations and their life span in *Pseudocalanus elongatus* (Copepoda, Calanoida) in the White Sea (in Russian). *Zool Zh* 60: 673-684
- Paffenhöfer GA, Harris RP (1976) Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus* Boeck. *J Mar Biol Assoc UK* 56: 327-344
- Paffenhöfer GA (1991) Some characteristics of abundant subtropical copepods in estuarine, shelf and oceanic waters. *Bull Plankton Soc Japan Spec Vol* 1991: 201-216
- Peters J, Renz J, van Beusekom J, Boersma M, Hagen W (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin): evidence from lipid composition. *Mar Biol* DOI 10.1007/s00227-006-0290-8
- Planque B, Fromentin JM (1996) *Calanus* and environment in the eastern North Atlantic. 1. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. *Mar Ecol Prog Ser* 134: 101-109

- Reid PC, Planque B, Edwards M (1998) Is observed variability in the long-term results of the Continuous Plankton Recorder survey a response to climate change? *Fish Oceanogr* 7: 282-288
- Reid PC, Edwards M (2001) Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenbergiana Maritima* 31: 107-115
- Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fish Oceanogr* 12: 260-269
- Renz J, Hirche HJ (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I: Seasonal and spatial distribution. *Mar Biol* 148: 567-580
- Rigler FH, Downing JA (1984) The calculation of secondary productivity. In: Downing JA, Rigler FH (eds) *A manual on methods for the assessment of secondary productivity in fresh waters*. Blackwell Science, Oxford, pp19-58
- Rothschild BJ (1998) Year class strengths of zooplankton in the North Sea and their relation to cod and herring abundance. *J Plankton Res* 20: 1721-1741
- Runge JA, Roff C (2000) The measurement of growth and reproductive rates. In: Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds), *Zooplankton Methodology Manual*, Academic Press, London, pp 401-444
- Saito H, Hattori H (1997) Diel vertical migration and feeding rhythm of copepods in a shallow, food-abundant embayment. *Plankton Biol Ecol* 44: 13-29
- Schnack S (1975) Studies on the feeding biology of copepods (Crustacea) in the Kiel Bight (in German). PhD Thesis, University Kiel, Germany
- Sekiguchi H, McLaren IA, Corkett CJ (1980) Relationship Between Growth Rate and Egg Production in the Copepod *Acartia clausi hudsonica*. *Mar Biol* 58: 133-138
- Sell AF, van Keuren D, Madin LP (2001) Predation by omnivorous copepods on early developmental stages of *Calanus finmarchicus* and *Pseudocalanus* spp. *Limnol Oceanogr* 46: 953-959
- Sewell RBS (1948) The free swimming planktonic copepoda. Geographical distribution. John Murray Expedition. *Sci Rep BM* 8: 317-592
- Sewell RBS (1951) The epibionts and parasites of the planktonic Copepoda of the Arabian Sea. John Murray Expedition. *Sci Rep BM* 9: 255-394
- Sullivan BK, Meise CJ (1996) Invertebrate predators of zooplankton on Georges Bank, 1977-1987. *Deep-Sea Res II* 43: 1505-1519
- Taylor AH (1995) North-South shifts of the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. *ICES J Mar Sci* 52: 711-721
- Thompson BM (1976) The biology of *Pseudocalanus elongatus* (Boeck). PhD Thesis, University of East Anglia, Norwich, Great Britain
- Tønnesson K, Tiselius P (2005) Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. *Mar Ecol Prog Ser* 289: 177-190

- 
- Viitasalo M (1992) Mesozooplankton of the Gulf of Finland and northern Baltic proper - A review of monitoring data. *Ophelia* 35: 147-168
- Vinogradov ME, Flint MV, Shushkina EA (1985) Vertical distribution of mesoplankton in the open area of the Black Sea. *Mar Biol* 89: 95-107
- Voss R (2002) Recruitment processes in the larval phase: the influence of varying transport on cod and sprat larval survival. PhD Thesis, University Kiel, Germany
- Vuorinen I (1987) Vertical migration of *Eurytemora* (Crustacea, Copepoda): a compromise between the risks of predation and decreased fecundity. *J Plankton Res* 9: 1037-1046
- Vuorinen I, Ranta E (1987) Dynamics of marine meso-zooplankton at Seili, northern Baltic Sea, in 1967-1975. *Ophelia* 28: 31-48
- Vuorinen I, Hänninen J, Viitasalo M, Helminen U, Kuosa H (1998) Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. *ICES J Mar Sci* 55: 767-774
- Walve J, Larsson U (1999) Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: implications for nutrient recycling. *J Plankton Res* 21: 2309-2321
- Wiborg KF (1954) Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway. *Fiskeridirektoratets Skr, Ser Havundersøkelser* 11: 1-246
- Williams R, Robins DB (1982) Effects of preservation on wet weight, dry weight, nitrogen and carbon contents of *Calanus helgolandicus* (Crustacea: Copepoda). *Mar Biol* 71: 271-281
- Wimpenny RS (1933) Variations in the North Sea plankton 1923-4. *Min Agric Fish, Fish Invest Ser II*, 8

## 8 Acknowledgements

Diese Arbeit wäre nicht ohne die Unterstützung vieler Menschen möglich gewesen, denen ich im Folgenden meinen Dank aussprechen möchte.

Ein herzlicher Dank geht an Herrn Prof. Dr. Wilhelm Hagen für die Betreuung und die Begutachtung dieser Arbeit.

Ein herzlicher Dank auch an Frau Prof. Dr. Sigrid Schiel für die Begutachtung der Arbeit und die konstruktive Diskussion.

Bei Herrn Dr. Hans-Jürgen Hirche bedanke ich mich für die Zusammenarbeit am Alfred-Wegener-Institut, die Betreuung der Arbeit und die kritische Durchsicht der Manuskripte.

Ein Dank an Herrn Prof. Dr. Gunter-Otto Kirst, der sich bereit erklärt hat, meiner Prüfungskommission beizusitzen.

Ein ganz großes Danke geht an meine vielen GLOBEC Kollegen für die tolle Zusammenarbeit im Projekt. Mölli, Rudi, Gerd, Hans-Harald, Jörn, Jörg, Frank, Laura, Rosie, Susanna.... Ihr seid einfach klasse! Janna- wenn es dich nicht gegeben hätte! Einen ganz lieben Dank an dich für viele gemeinsame Stunden des Planktontsrierens und Experimentierens auf all den Seereisen, lange durcharbeitete Nächte und die kreative Zusammenarbeit und Diskussion zwischen AWI und Uni Bremen.

Meinen herzlichen Dank an die Offiziere und Mannschaften der Forschungsschiffe Alkor, Heincke und Alexander von Humboldt für die großartige Unterstützung auf all den Ausfahrten.

Vielen Dank an Ruth Alheit für die Korrektur des englischen Textes.

Ein 1000-facher allerliebster Dank an meine wunderbare und einzigartige Arbeitsgruppe: Kristina, Dirk, Jan, Anne, Adrian, Marcus. Danke fürs Korrekturlesen in den letzten Tagen, unzählige Kaffeepausen, die vielen gemeinsamen Reisen mit AWI-Tours, unermüdliche Einsätze in allen Krisen und eine tolle Zeit am AWI. Ulrike, dir danke ich besonders für die 2 gemeinsamen Jahre im Büro und deine Unterstützung bei all den logistischen Problemen.

Miriam, Katrin, Michael, Jan- Euch möchte ich für die Grillabende, Skatingnachmittage, Brunch-, Koch-, und Kneipeneinsätze in den letzten Wochen vor der Abgabe danken, ohne die die Schlussphase dieser Arbeit wohl kaum zu ertragen gewesen wäre.

Mein abschließender und ganz besonderer Dank gilt meiner Familie für ihre Liebe und unermüdliche Unterstützung. Steffen, dir danke ich für deine Liebe, deine unglaubliche Geduld und deine Fähigkeit, das Chaos der letzten Wochen immer wieder zu lichten.

---

## Abbreviations

ANOVA	Analysis of variances
AF	Adult females
AM	Adult males
B	Biomass
BB	Bornholm Basin
C	Carbon
CCW	Continental Coastal Water
Chl	Chlorophyll
CI-CVI	Copepodite stages I-VI
D	Stage duration
DM	Dry mass
EPR	Egg production rate
Ex	Exuviae
f	Female
g	Growth rate
GB	Gotland Basin
MBI	Major Baltic Inflow
MDS	Multi-dimensional scaling
MR	Moulted rate
Moult	Moulted
NI-NVI	Nauplii stages I-VI
NAO	North Atlantic Oscillation
n	Number of individuals
P	Production
P/B	Productivity
PL	Prosome length
Rep	Reproduction
T	Temperature (°C)
TL	Total length
Tukey's hsd	Tukey's honestly significant differences
SEPR	Specific egg production rate
sta	Station
W	Mass
WMD	Weighted Mean Depth
X	Abundance

Anlage zur Dissertation

Jasmin Renz  
Preßburger Straße 2  
27568 Bremerhaven

### **Erklärung gem. § 6 (5) Nr. 1-3 Promotionsordnung**

Ich erkläre hiermit, dass ich

1. die Arbeit ohne unerlaubte fremde Hilfe angefertigt habe,
2. keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe

und

3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Jasmin Renz