Food and climate effects on copepod reproduction in the North and Baltic Seas

DISSERTATION

Zur Erlangung des Doktorgrades

der Mathematisch –Naturwissenschaftlichen Fakultät

der Christian-Albrechts-Universität zu Kiel

vorgelegt von

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Kiel 2006

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Tag der mündlichen Prüfung: 06.07.2006

Zum Druck genehmigt:

Kiel, den

Das schönste Glück des denkenden Menschen ist,

das Erforschliche erforscht zu haben und das

Unerforschliche zu verehren.

Johann Wolfgang von Goethe

Für meine Mutter Brigitte

CONTENTS

I. GENERAL INTRODUCTION

Zooplankton is a group of key organisms in aquatic food webs, both as mediators of energy to higher trophic levels, such as fish (Cushing 1995, Gowen et al. 1999, Möllmann et al. 2000, deYoung et al. 2004, Malzahn et al. *in prep.*), as well as selective predators and nutrient regenerators structuring the phytoplankton community (Riegman et al. 1993, Banse 1995a, Verity & Smetacek 1996, Gismervik & Andersen 1997, Bathmann et al. 2001). According to the classical food chain theory (Steele 1974), copepods are the main grazers on larger phytoplankton, such as diatoms, but it has become increasingly clear that heterotrophic protists such as dinoflagellates and ciliates play a larger role as grazers on the generally more abundant smaller phytoplankton in marine planktonic food webs (e.g. Azam et al. 1983, Pierce & Turner 1994, Banse 1995b, Waterhouse & Welschmeyer 1995), although recent integrated calculations of respiration suggest that feeding of mesozooplankton may be underestimated on a global scale (Hernández-León & Ikeda 2005). Heterotrophic protists themselves are an important food source for copepods in brackish and marine systems (Stoecker & Capuzzo 1990, Gifford 1993, Kleppel 1993), and may support a significant fraction of copepod respiration and egg production (Atkinson 1994, Ohman & Runge 1994, Atkinson 1996, Calbet & Saiz 2005).

Copepods are the most abundant group of crustaceans among the zooplankton. They are important components of the food web also in brackish and shallow coastal marine waters (Hansson et al. 1990, Tester & Turner 1991). The wide distribution and abundance of such copepods is facilitated by adaptation of life history traits to match specific physical and chemical constraints of the environment (Uye 1985, Båmstedt 1988, Villar-Argaiz et al. 2002, Gislason 2003). Population dynamics in marine copepods can be influenced by climate forcing through several physical and chemical factors, such as temperature (Halsband & Hirche 2001, Halsband-Lenk et al. 2002, Maps et al. 2005), light (Alcaraz et al. 1994, Williamson et al. 1994, Naganuma et al. 1997, Chinnery & Williams 2003), turbulence (Saiz et al. 1992, Alcaraz et al. 1994, Saiz et al. 2003) and oxygen concentration (Bakker & Rijswijk 1989, Kuosa 1989, Marcus et al. 2004).

Temperature has been suggested to be the main abiotic factor controlling copepod population dynamics (Huntley and Lopez 1992), and some more recent investigations have also shown strong effects of temperature on egg production of copepods (Koski et al. 1998, Halsband & Hirche 2001, Halsband-Lenk et al. 2002, Devreker et al. 2005, Maps et al. 2005). However, there are also critics of the general theory on temperature and growth (Kleppel et al. 1996b), and there are a number of field studies where no correlation could be observed between egg production and temperature (e.g. Lawrence & Sastry 1985, Williamson & Butler 1987, Bautista et al. 1994, Hay 1995b). Thus, it appears that although temperature may have a strong influence on the metabolism, development times and sizes of copepods other factors may override the temperature effects at times, directly or indirectly (Dagg 1978, Uye & Shibuno 1992, Ban 1994, Koski & Kuosa 1999, Lee et al. 2003).

In brackish ecosystems like the Baltic Sea, salinity is one of the physical factors that may strongly affect population dynamics (Hansen et al. 2004, Holste & Peck 2006). The low salinity might be one of the mechanisms directly causing a shift in dominance of different calanoid copepod species in different areas of the Baltic Sea due to different tolerance of salinity in the later copepodite stages (Möllmann et al. 2000). A shift in salinity may also affect the copepod populations indirectly by controlling fecundity and body size (Remane & Schlieper 1958, Anger 2003, Castro-Longoria 2003).

Although food is one of the most investigated factors affecting copepod growth and reproduction, still many questions about different aspects of the food are unresolved. It is known that biotic factors such as food and prey-predator interactions can strongly affect copepod reproduction. Obviously, food is necessary to maintain growth and reproduction (Raymont 1983). Thus food availability (quantity) compared to the food requirement of the copepod is one of the principal factors influencing reproduction in copepods (reviewed by Mauchline 1998), while it has become more and more clear that food quality also has to be taken into account when investigating the effect on reproduction (Kleppel 1993, Laabir et al. 1998, Guisande et al. 2000). A number of experimental studies have shown that reproduction is related to food quantity (Frost 1985, Durbin et al. 1992, Escribano et al. 1997, Hansen & Hairston 1998, Niehoff et al. 1999, Guisande et al. 2000, Kimmerer et al. 2005), but many field studies fail to show a direct correlation between food quantity and reproduction (Stearns et al. 1989, Bautista et al. 1994, Hay 1995b, Devreker et al. 2005, Poulet et al. 2006). As a result, many recent studies have focused on the role of the food quality for copepod growth and development. Food quality of algae exhibit a high temporal and spatial variability (Pond et al. 1996), which has been related to variation in e.g. nitrogen, phosphorus, silica and/or iron (Brett & Müller-Navarra 1997). The variation can be also caused by differential temperature (Brett & Müller-Navarra 1997) or grazing pressure (Kilham et al. 1997a, DeMott et al. 2001). Poor food quality may result in food limitation even if food concentrations are high (Durbin et al. 1983, Kleppel & Burkart 1995). The most widely used parameters to estimate food quality have been the ratios of the essential elements carbon, nitrogen and phosphorus (e.g. Debs

1984, Touratier et al. 1999, Elser et al. 2000, Jones et al. 2002, Poulet et al. 2006) and the content of essential biochemicals such as fatty acids (Jónasdóttir 1994, Kleppel et al. 1998, Becker et al. 2005, Klein Breteler et al. 2005), amino acids (Guisande et al. 2002) or sterols (Ederington et al. 1995, Von Elert et al. 2003, Klein Breteler et al. 2005), whereby most studies focused on fatty acids. Both the essential elements and biochemicals have been shown to vary in complex ways dependent or independent of each other (e.g. Kilham et al. 1997b, Sterner & Schulz 1998). The ratio of the essential elements carbon and nitrogen can vary widely according to the nutritional status of the phytoplankton (Touratier et al. 2001) and is known to be related to the reproduction of zooplankton (Sterner 1990, Urabe 1993). Fatty acids are the main component of lipids in organisms. Many of the highly unsaturated fatty acids are essential for heterotrophic organisms, i.e. they cannot be synthesised by the grazers but have to be ingested. In many cases phytoplankton is the only source of fatty acids in pelagic systems (Pohl & Zurheide 1979). Especially many of the n-3 and n-6 fatty acids are essential for the growth and reproduction in copepods.

Protists, such as diatoms, dinoflagellates and ciliates make up the majority of the food for calanoid copepods. However the role of these different prey types as food for copepods is debated, especially if some of these common species may have toxic effects on the grazer and its reproduction or if they merely have a strongly variable nutritional value (e.g. Ban et al. 1997, Miralto et al. 1999, Irigoien et al. 2002, Turner et al. 2002, Thomas et al. 2003, Ianora et al. 2004, Paffenhöfer et al. 2005).

The most important parameter to assess population dynamics is the (individual and population) growth rate (Sommer 1998). The specific growth rate of calanoid copepods is closely related to specific egg production, because after moulting adult females do not grow further (Hay 1995b). Therefore reproduction can be seen as an index of copepod population response (Hay 1995b, Harris et al. 2000). Reproduction is mainly measured as egg production rate (*EPR*), which is one of the most studied vital rates in copepods (Harris et al. 2000, Castellani & Altunbas 2006).

In this thesis the importance of the different factors potentially controlling the reproduction in calanoid copepods such as *Temora longicornis* and *Acartia* spp. is assessed.

1.1. The study areas

The Baltic and the North Seas are marginal seas in the temperate northern hemisphere. Both systems are influenced by the Northern Atlantic climate system. The temperature follows a seasonal rhythm forced by large-scale weather systems (Janssen et al. 1999, Alheit et al. 2005). Thermal stratification can occur in both systems whereas permanent vertical stratification caused by salinity exists only in the Baltic Sea (Janssen et al. 1999).

The nutrient concentrations vary in a seasonal cycle with high concentrations during the winter and a rapid decrease in the spring during the phytoplankton bloom (van der Zee & Chou 2005). Over an annual cycle, the phytoplankton composition shows a succession with diatoms dominating during the spring bloom (Mills et al. 1994, Wiltshire & Manly 2004). In summer, protozoan such as flagellates and ciliates are often abundant and available as food for copepods and other mesozooplankton (Andersson et al. 1994, Sommer et al. 2002). There can also be a second smaller bloom of diatoms in autumn in both areas, which is accompanied by high abundances of dinoflagellates (Wasmund et al. 2004).

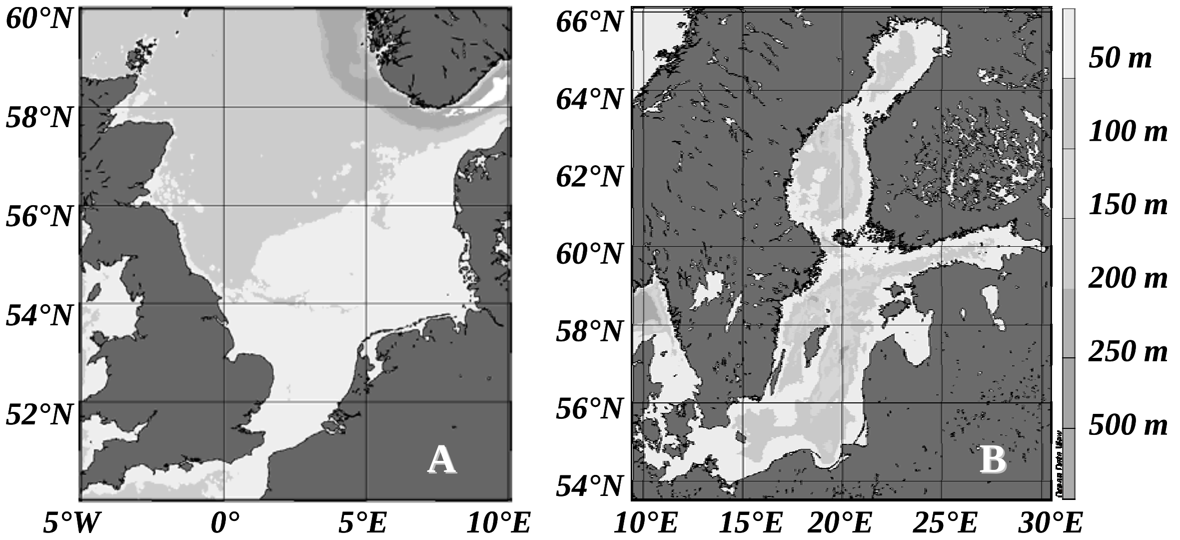


Figure 1. Topographical map of A) the North Sea and B) the Baltic Sea. The water depth is indicated by the grey scale on the right side of Panel B.

The shallow sheltered North Sea is strongly influenced by the coastal areas with large rivers such as the Rhine and the Elbe (Allen 1981, van der Zee & Chou 2005) and it is connected to the Northern Atlantic at the English channel and between Scotland, Shetland and Norway (Reid et al. 2003). From the long time series of investigations on the Helgoland Roads in the

German Bight (Franke et al. 2004), it is clear that the temperature has significantly increased over the last years and caused shifts in the phytoplankton species succession (Wiltshire & Manly 2004). Typical for a phytoplankton succession in the North Sea is that after a diatom bloom in spring high abundances of *Phaeocystis globosa* occur regularly (Riegman et al. 1992, Mills et al. 1994, Riegman & van Boekel 1996, Stelfox-Widdicombe et al. 2004).

The Baltic Sea is a semi-enclosed brackish water body, which in its southwest opening is influenced by water from the North Sea (salinity of 34-35), but in the north and eastern ends is nearly fresh (salinity of 1-2), due to a strong influence by freshwater run-off from land and direct rainfall. The central area of the Baltic Sea, called the Baltic Proper, is stratified. Nutrient limitation occurs regularly in the upper layer. Nitrogen limitation occurs in the central parts of the Baltic Sea whereas phosphor can become limited in the coast areas (Thomas et al. 2003). In the succession of the phytoplankton in summer a bloom of nitrogen fixing cyanobacteria in the central nitrogen depleted areas can occur (Nausch et al. 2004) and heterotrophic protozoa, mostly ciliates, can reach high abundances (Johansson et al. 2004, Höglander 2005).

1.2. The study organisms

Among the zooplankton the largest group is the crustacean order Copepoda with more than 5,000 species. Copepoda are widely distributed from marine to brackish and freshwater, with a few species even living in damp environments on land and many other as specialized parasites. Their size ranges from a few hundred µm up to a few cm. Most adult free living aquatic species range between 0.5-2 mm (Mauchline 1998). In marine and coastal water systems they represent a main part of the biomass (Legendre & Rassoulzadegan 1995, Bonnet et al. 2005). The calanoid copepod species focused on in this thesis, *Acartia* spp. and *Temora longicornis*, are among the most abundant in the investigated areas (Hickel 1975, Greve et al. 2004, Alheit et al. 2005, Hansen et al. 2006) and are known to have a largely omnivore feeding strategy (Cotonnec et al. 2001).

Acartia tonsa (Dana 1849)

Acartia tonsa has been found in the coastal areas of North and South America, the Mediterranean, the Black Sea and in European coastal waters from the Gulf of Finland to the Bay of Biscay and including British coastal waters (Bradford-Grieve 1999). The native distribution was described as Indo–Pacific, but through ballast waters of ships the species now shows a cosmopolitan distribution in temperate estuaries and costal areas. In the Baltic and the North Sea *A. tonsa* is seen as an invading species (Leppäkoski et al. 2002). *A. tonsa* is euryhaline (Cervetto et al. 1999, Lawrence et al. 2004) and eurythermic (Kimmel & Roman 2004, Holste & Peck 2006). *A. tonsa* is easy to maintain in laboratory cultures (Støttrup 2000). Because of its wide distribution it has become one of the most intensively studied calanoid species (Mauchline 1998). Previous investigations on this species have quantified the effects of temperature and/or feeding on growth and egg production (e.g. Corkett & Zillioux 1975, Roman 1977, Stoecker & Sanders 1985, Ambler 1986, Berggreen et al. 1988, Kleppel 1992, Jónasdóttir 1994, Broglio et al. 2003, Holste & Peck 2006).

Acartia clausii (Giesbrecht 1889)

Acartia clausii was described in 1889 by Giesbrecht, but many studies refer to the citation of Giesbrecht from 1892, where it was named *Acartia clausi*. In this study the original name will be used following the rules of the nomenclature (ICZN 1999). *A. clausii* occurs in abundant numbers in the central North Sea (Hickel 1975, Halsband & Hirche 2001). Further areas of distribution are the Black Sea, Atlantic Ocean, Indian Ocean and the Mediterranean Sea (Breemen 1964, Bradford-Grieve 1999). This species co-occurs with *A. tonsa* (Lee & McAlice 1979).

Acartia longiremis (Lilljeborg 1853)

Acartia longiremis is widely distributed in the polar seas, Northern Atlantic and across the Baltic Sea up to the subarctic areas (Norrbin 2001). In subarctic marine areas the copepod is well adapted to the environment and reproduces even during winter, producing subitaneous eggs rather than dormant ones. *A. longiremis* is an omnivorous feeder and can be important for the efficiency of the trophic coupling in the food web (Levinsen et al. 2000). In the Baltic Sea *A. longiremis* can dominate in spring and summer (Yurkovskis et al. 1976). There are many investigations on the distribution of this species but only a few laboratory studies have been done. In this study *A. longiremis* was successfully maintained in culture.

Temora longicornis (Müller 1792)

Temora longicornis is a cold-temperate and euryhaline species, which is present in the epipelagial or in neritic areas from the coast of Portugal to northern Norway, the Barents Sea, western Spitzbergen, including the North Sea and the Baltic Sea (reviewed by Halsband-Lenk 2001). This species coexists with *Acartia* spp. and is abundant during all seasons (Hickel 1975). Especially in the Baltic Sea *T. longicornis* is a favoured prey for juvenile and adult sprat and herring (Hinrichsen et al. 2002, Möllmann & Köster 2002, Möllmann et al. 2004).

T. longicornis mainly feed on dinoflagellates and diatoms whereas *A. clausii* was found to feed mostly on chlorophytes and diatoms (Guisande et al. 2002).

1.3. Focus and outline of the thesis

The aim of the work for this thesis was to increase the quantitative knowledge about the phytoplankton and zooplankton interactions in the North and Baltic Seas. The present study examines different factors controlling the reproduction and survival in some dominant copepod species, which is essential for copepod recruitment and thus the prey field for higher trophic levels such as fish populations. In this study, the influence of food quality is investigated in relation to other potentially important factors such as temperature and salinity in pelagic food webs of the two temperate areas, the Baltic and the North Seas.

In the following chapters several studies are described that investigate the expected major controlling factors and their combinations. Chapter II and III present studies investigating effects of food quality in controlled laboratory experiments with simple prey-predator interactions. For these simplified food web experiments, well established cultures of the cryptophyte *Rhodomonas* sp. and the calanoid copepod *Acartia* spp. were used. Several investigations have shown that food quality can have an impact on copepod reproduction, but there are only a few experimental studies reporting responses to single changes in nutritional condition of the food. In Chapter II the impact of decreased availability of nutrients such as nitrogen in a food chain between *Rhodomonas* sp. and *Acartia* spp. were investigated, whereas in chapter III the role of protists added to this simple food chain was observed. Recent investigations have shown that heterotrophic Protists may play an important role in the food web as a food quality upgrading trophic link between phytoplankton and copepods. Since the nutritional condition of phytoplankton may directly influence copepod reproduction, microzooplankton might be a necessary supplement in the food composition for copepods. Because microzooplankton feed on various phytoplankton, they may become more nutritionally balanced and rich in proteins than their individual prey algae and may thus be a more suitable food source for copepods. However, it is still not clear, how important heterotrophic protists are for the nutritional composition of the food for copepods. To understand the phytoplankton-zooplankton interactions both laboratory and field experiments were conducted. These investigations (Chapter IV and V) were done by combining investigations on copepod cultures and copepods in the field (cruises in the Baltic Sea and investigations on a permanent station in the North Sea, the Helgoland Roads).

Besides food quality there are also other factors that can control the egg production in copepods, which have been taken into account in Chapter IV. In the Baltic Sea especially the temperature and salinity is believed to cause the considerable temporal and spatial variation in abundance and distribution observed in calanoid copepods. Such variations in copepod abundance have been explained by variations in abiotic climatic factors such as salinity and temperature alone (Stenseth et al. 2002), while others have shown that biotic variables such as food concentration and avoidance of predation pressure may explain variations in copepod abundance (Hays 2003, Kimmerer et al. 2005).

In Chapter V experiments were conducted over a seasonal cycle to generate more complete functional responses of reproductive success in relation to environmental factors, copepod size, food quality and food quantity. This study was done on the Helgoland Roads where it could be linked to an existing long-term data series (Greve et al. 2004, Wiltshire & Durselen 2004).

This thesis is aimed to be a step toward a better understanding of the zooplankton population dynamics and interactions within the food web by addressing the role of food quality and quantity in combination with other environmental factors for copepod reproduction in laboratory and field studies.

II. EFFECTS OF NITROGEN STRESSED ALGAE ON DIFFERENT *ACARTIA* SPECIES

2.1. Introduction

Copepod ingestion and production rates are influenced by physical and biological environmental factors (Runge 1984, Ambler 1986, Rothschild & Osborn 1988). A considerable body of literature already exists on the influence of the feeding environment on the growth and reproduction of a wide number of zooplankton species (e.g. Mayzaud et al. 1998, Gomez-Gutierrez & Peterson 1999, Nejstgaard et al. 2001, Turner 2004). Based on these findings, it has become increasingly clear, that not only food quantity determines the success of zooplankton in their environment, but that differences in food quality may be just as important (Kiørboe et al. 1985, Houde & Roman 1987, Støttrup & Jensen 1990, Kleppel & Burkart 1995, Koski et al. 1998, Khanaychenko 1999, Klein Breteler & Koski 2003, Jones & Flynn 2005).

One of the main aspects of food quality currently researched in marine systems is the biochemical composition of the food or more specifically the fatty acid spectrum of the different algal groups (Klein Breteler & Gonzalez 1988, Jónasdóttir et al. 1995, Kleppel & Burkart 1995, Müller-Navarra 1995). Other food quality factors that have been investigated, especially in freshwater systems, include the nutrient content of the food, or more specifically the C:N:P stoichiometry, the morphology and biochemical components such as amino acids and sterols (Urabe & Watanabe 1992, Ederington et al. 1995, Frost et al. 2005). In fact, several authors have shown that even within a single algal species the quality as food for zooplankton can vary dramatically as a result of differences in growth conditions (Jónasdóttir 1994, Jónasdóttir & Kiørboe 1996, Urabe & Sterner 2001, Boersma & Kreutzer 2002, Jones et al. 2002, Villar-Argaiz & Sterner 2002, Jones & Flynn 2005).

In the field, several studies have followed growth and reproduction of copepods throughout blooms of phytoplankton, during which growth conditions of the algae change dramatically as a result of nutrient and/or light depletion (Fransz 1976, Tang & Dam 1999, Kleppel & Hazzard 2000). Typically, the carbon-to-nutrient ratios in the algae continually increase throughout the bloom (Ambler 1986, Båmstedt 1988, Jónasdóttir et al. 1998, Touratier et al. 1999, Van Nieuwerburgh et al. 2004). However, during a phytoplankton bloom factors may change both independently or in correlation with others, it is thus difficult to link changes in egg production of consumers to any single specific factor in complex natural systems.

It is often argued that macronutrient stoichiometry of the food is an important factor for the trophic transfer in marine food webs (Burdloff et al. 2002, Jones et al. 2002, Klein Breteler & Koski 2003, Anderson et al. 2004, Jones & Flynn 2005, Mitra & Flynn 2005). However, the effect of algae growth conditions on the growth and reproduction of zooplankton is rarely studied directly in laboratory settings. This study seeks to fill this gap in our knowledge, which is especially important for the development of more realistic ecosystem models, as they often do not include different quality values of food (Checkley 1980a, Mitra & Flynn 2005).

Copepods of the genus *Acartia* are distributed worldwide. They do not have large lipid reserves and hence usually react rapidly to experimental treatments (Kiørboe et al. 1985). Moreover, many species can be found with overlapping distributions and slightly different phenology or habitat preferences. For example, adult *A. clausii* is found in the mouth of rivers, whereas *A. tonsa* is mainly restricted to the upper reaches of estuaries (Chinnery & Williams 2004). The species co-occur in the Maine Estuary (Lee & McAlice 1979), in the Gullmarfjord (Tiselius 1998) and in the Wadden Sea (Klein Breteler & Gonzalez 1982). In our experiments, we used *A. clausii* and *A. tonsa*, as they both are found in the North Sea and their abundances differ with the time of year. *A. tonsa* mainly occurs in summer-autumn, whereas *A. clausii* dominates in winter-spring (see also Lee & McAlice 1979), which could cause the species to have different strategies to deal with nitrogen depletion of the food. *Acartia* species are known to distinguish between different nutritional microcapsules (Poulet & Marsot 1978) and single algal species with different nutrient content (Houde & Roman 1987, Cowles et al. 1988). This suggests that differences in nutritional content of the algae can be of importance in its natural environment (Timmermans et al. 2004). Based on their phenology, we hypothesize that *A. tonsa* and *A. clausii* have different strategies in dealing with phytoplankton blooms. Hence, to determine the effects of different growth conditions of the algae on life history parameters of these copepods, we compared the reproductive responses to a model prey algae, *Rhodomonas* sp., in nitrogen sufficient (beginning of bloom) and nitrogen limited (end of bloom) culture conditions. Ingestion rates, egg production, egg size, egg hatching and resting egg production were measured.

2.2. Material and methods

A. tonsa and *A. clausii* were reared in 5 l beaker batch cultures under 16:8 h light: dark cycle and a temperature of 15 - 16 °C. They were supplied in excess (> 300 µg C l^{-1} day^{-1}) with batch cultures of the cryptophyte algae *Rhodomonas* sp. The different *Rhodomonas* cultures were kept in 5 l bottles under similar conditions as the copepods. One set of cultures was kept in full f/2 medium (Guillard 1975a) and the other one in f/2 medium without nitrogen. Both cultures were started with the same cell concentration originating from the same stock culture. After 3 days the algae culture in low nitrogen medium showed signs of nitrogen limitation, visible as changes in the colour (from red to green) and decreased growth (Fig. 1a). Furthermore, C:N ratios of the nitrogen depleted cells increased steadily, whereas the *Rhodomonas* sp. cultures that received nitrogen showed relatively constant C:N ratios (Fig. 1b). The particulate carbon and nitrogen content of the algae was measured with a Fison EA 1108 CHN analyser after filtering 30 to 50 ml of the algal culture onto a combusted Whatman GF/C filter and storing at –20 °C. Based on this, nitrogen depleted and nitrogen sufficient *Rhodomonas* sp. cultures were timed so that the nitrogen limited culture was on the verge of crashing at the beginning of the experiment while the nitrogen sufficient culture was still growing fast (after four days). The C:N ratio (molar) of nitrogen depleted cells was 9.05 (± 0.8 SD; n = 6) after four days, whereas the C:N ratio of algae in the medium with nitrogen was 4.49 (± 0.2 SD; n = 6). The C:N ratios were similar in all the three experiments.

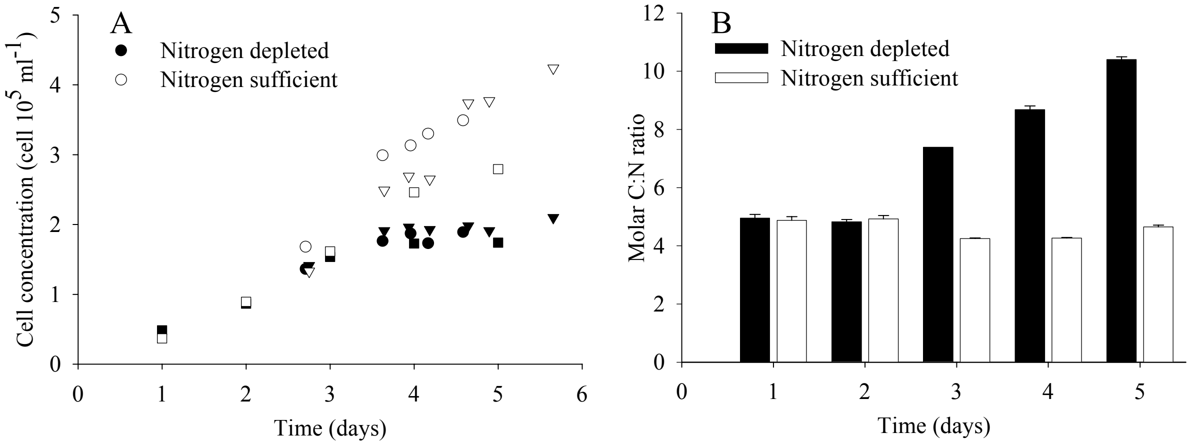


Figure 1. *Rhodomonas* sp. Development of cell densities (panel A) and molar C:N ratios (panel B) in cultures grown in different media; nitrogen depleted (filled symbols) and nitrogen sufficient (open symbols); Different symbol shapes represent different experiments. Error bars denote standard error of the mean.

Groups of 10 adult female copepods and 4 adult males were selected gently and placed into 1140 ml bottles, which were filled with 0.45 µm filtered artificial sea water. The artificial sea water was made up with commercial sea salt (Aqua Marin) and distilled water with a final salinity of 32-33. This solution contained no additional nitrogen to prevent nitrogen deficient algal cultures from receiving nitrogen during the incubations. The cell concentration in the cultures was determined with a CASY particle counter (Schärfe Systems, Reutlingen, Germany) and was adjusted to a concentration of 13000 cells ml^{-1} (corresponding to about 500 µg C l^{-1}) in the incubation bottles. This is a non limiting food concentration for the copepods (Roman 1977, Kiørboe et al. 1985). To prevent sedimentation of the food, the bottles were mounted on a plankton wheel and rotated with 1 rpm at 15 °C in a temperature controlled room. Every day, the copepods were transferred gently with a pipette into new bottles with fresh *Rhodomonas*. After two days of incubation, the egg production per female during the previous 24 hours was determined by carefully filtering the water through a submerged 50 µm sieve and rinsing the eggs into small Petri dishes. The copepods were counted and transferred to incubation bottles with fresh medium. The eggs were counted and transferred into fresh artificial sea water. To determine hatching success, the eggs were kept at 15 °C, in a light:dark cycle of 16:8 h and recounted after 4 days of incubation. Total duration of the experiment was three days. The whole experiment was carried out three times during 6 months to test for the robustness and repeatability of the observed responses.

The core program of the three experiments to measure egg production and hatching success was identical, but small modifications were made to investigate additional aspects. In two experiments, we measured the ingestion rates of the copepods using the equations by Frost (1972) to investigate whether the reactions to the different algae were caused by differences in ingestion. This was done with three replicates of the bottles with copepods and three replicate controls without animals. Furthermore, we investigated whether the response is dependent on the quantity of the food by adding an extra algae treatment with only half of the algal biomass in one experiment. In another experiment, we determined the average egg sizes by measuring 30 eggs from each treatment using a SIS video imaging system. We kept the unhatched eggs of this experiment for a period of three weeks at the same temperature to establish the percentage of the eggs that can be considered resting eggs. Those that were still intact after three weeks were considered to have entered a dormancy period, other eggs disintegrate after this period. Normally at 17 °C, eggs of *Acartia tonsa* hatch within 2 days, or disintegrate (Ambler 1986).

2.3. Results

The copepods showed significant feeding in all experiments (Fig. 2): the 95% confidence interval of the mean did not include zero. At the low food concentration (250 µg C l^{-1}) there were no significant differences in ingestion rates between the nutrient depleted and sufficient diets (ANOVA $F_{1,8}$= 0.78, p = 0.402) or between the species ($F_{1,8}$ =1.05; p = 0.335; Fig. 2a). At the higher concentration (500 µg C l^{-1}) the ingestion rates were significantly different between the diets (ANOVA $F_{1,16}$ = 11.20; p = 0.004) and between the species $F_{1,16}$ = 5.02; p = 0.040, Fig. 2b).

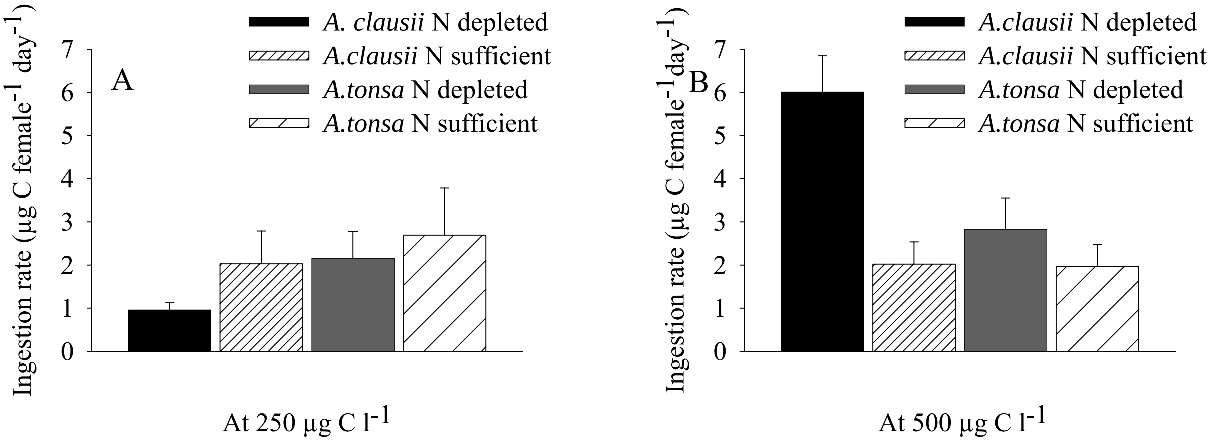


Figure 2. *Acartia tonsa* and *Acartia clausii*. Ingestion rates of nitrogen depleted and nitrogen sufficient *Rhodomonas* sp.; error bars denote the standard error of the mean at algae concentration of 250 µg C l^{-1} (panel A) and at 500 µg C l^{-1} (panel B).

A Tukey post hoc test (Table I) revealed that the difference was due to the higher ingestion rate of *A. clausii* feeding on nitrogen depleted food. The amount of carbon ingested was in the range of 1 to 6 µg C female^{-1} day^{-1} in all experiments.

Table I. *Acartia clausii* (*A.c.*) and *Acartia tonsa* (*A.t.*). Tukey post hoc test: effect of nutritional conditions on the ingestion rates per female and day at the 500 µg C l^{-1}, (significant values are in bold).

	A.c. N sufficient	*A.c.* N depleted	*A.t.* N sufficient
A.c. N depleted	**0.006**		
A.t. N sufficient	1.000	**0.006**	
A.t. N depleted	0.862	**0.031**	0.838

When incubated with high food concentrations (500 µg C l^{-1}), *A. clausii* generally produced eggs at a lower rate than *A. tonsa*, but both species increased their egg production rates significantly in nitrogen depleted food, relative to when feeding nitrogen sufficient *Rhodomonas* (Fig. 3). Although there was a difference in magnitude of the response between the experiments causing a significant experiment effect in the ANOVA (Table II), the patterns observed in the different experiments were robust.

Table II. *Acartia clausii* and *Acartia tonsa*. ANOVA: testing the effect of nutritional conditions on the egg production rates per female and day in three experiments. (significant values are in bold).

Effect	Degree of freedom $_{\text{effect}}$	Mean squares	Variance ratio	p
Species	1	1086.81	51.42	< **0.001**
Nutritional condition	1	468.08	22.14	< **0.001**
Experiment	2	79.39	3.76	**0.034**
Species vs. Nutrition	1	0.16	0.01	0.932
Species vs. Experiment	2	388.97	18.40	< **0.001**
Nutrition vs. Experiment	2	118.52	5.61	**0.008**
3-way	2	16.23	0.77	0.472
Error	32	21.14		

This pattern was also visible when the females were fed the lower concentration (250 µg C l^{-1}); a highly significant effect between food types ($F_{1,8}$ = 11.26; *p* = 0.009), and a significant species effect ($F_{1,8}$ =12.16; *p* = 0.008), with a marginally significant interaction between species and food type indicating that the species reacted in a similar way ($F_{1,8}$ = 5.31; *p* = 0.050) (Fig. 4).

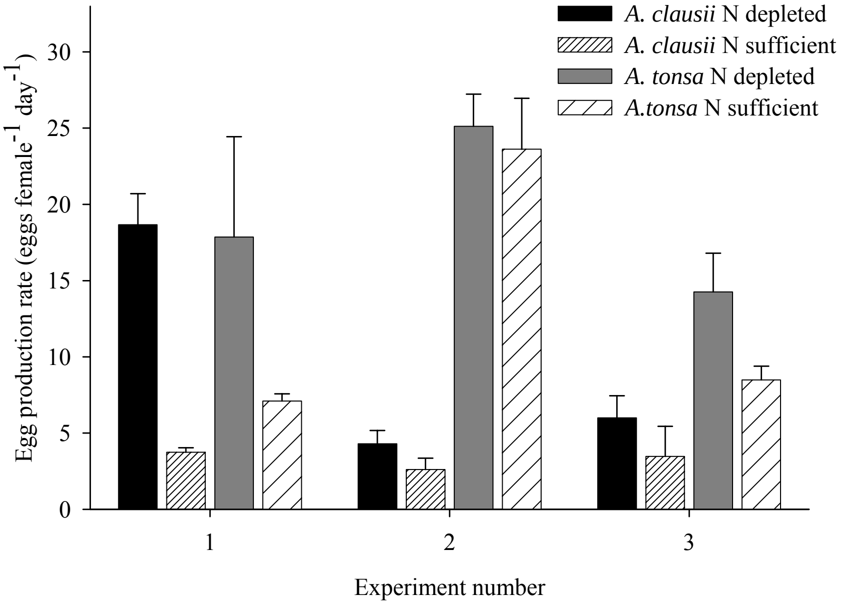


Figure 3. ***Acartia clausii*** **and** ***Acartia tonsa*****. Egg production rates after 48 h incubation in either nitrogen depleted, or nitrogen sufficient** ***Rhodomonas*** **sp. cultures at a food concentration of 500 µg C l^{-1}; error bars denote standard error of the mean.**

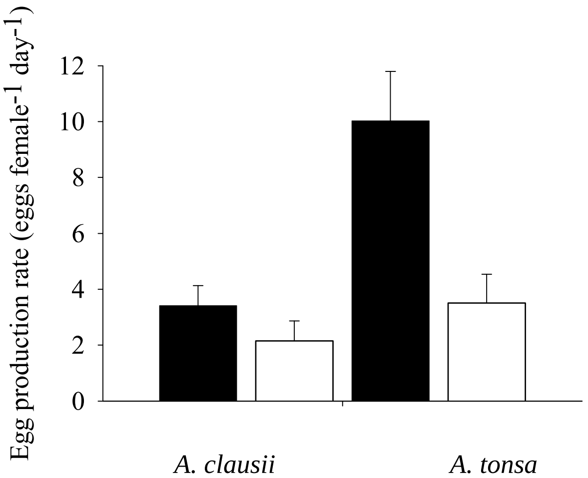


Figure 4. ***Acartia clausii*** **and** ***Acartia tonsa.*** **Egg production rates after 48 h incubation in 250 µg C l^{-1} of nitrogen depleted** ***Rhodomonas*** **sp. (filled bars) or nitrogen sufficient** ***Rhodomonas*** **sp. cultures (open bars); error bars denote standard error.**

Hatching success was not significantly affected by the type of food. Both species showed similar levels of hatching, ranging from 40-100% in the different experiments but with no significant differences between the treatments (Fig. 5).

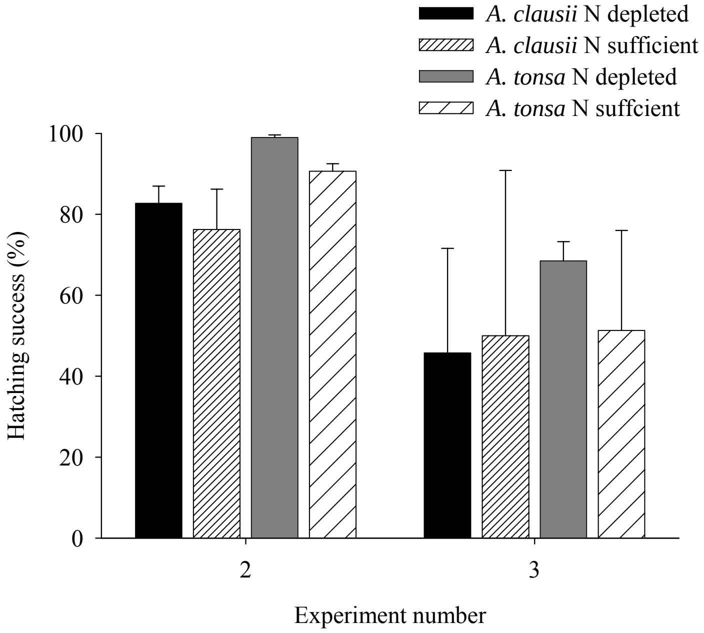


Figure 5. *Acartia clausii* and *Acartia tonsa.* Hatching success after feeding nitrogen depleted or nitrogen sufficient *Rhodomonas* sp.; **error bars denote standard error.**

A. tonsa always produced a certain percentage of resting eggs, whereas we did not observe resting egg production by *A. clausii.* Between the two food types the difference in the percentage of resting eggs produced was, however, not significant (χ^2 = 0.045; n = 134; *p* = 0.83, Fig. 6).

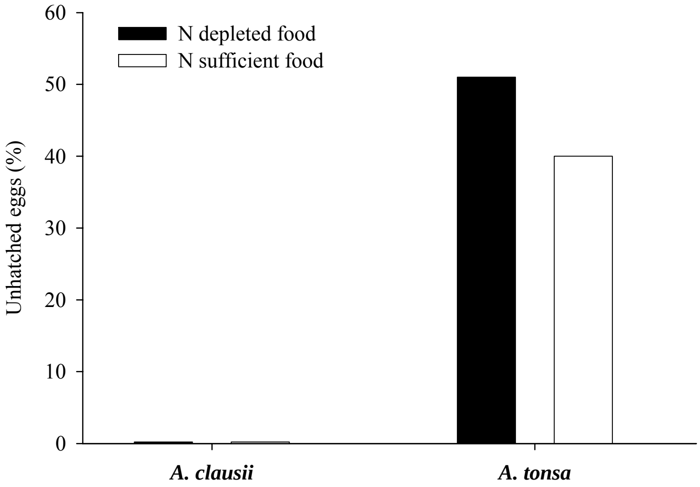


Figure 6. *Acartia clausii* and *Acartia tonsa,* experiment 1. **Production of resting eggs after feeding nitrogen depleted or nitrogen sufficient *Rhodomonas* sp.**

We did observe differences in the size of the eggs produced by both species in the different food treatments. While *A. clausii* decreased the size of the eggs slightly under nitrogen limitation, the opposite was found for *A. tonsa,* although both differences were small (ANOVA: Interaction Species*Nitrogen treatment, $F_{1,116} = 4.27$; $p = 0.041$).

2.4. Discussion

It is well established that egg production rates and abundances of copepods generally increase during blooms of phytoplankton (Bautista et al. 1994, Schmidt et al. 1998, Titelman & Tiselius 1998). However, since many factors change simultaneously it is not well understood what directly causes these changes during such blooms. Food availability and quality are key factors determining secondary production (Klein Breteler & Gonzalez 1988, Kleppel 1992), but copepods also react to the increase in temperature during spring blooms in temperate regions (Halsband & Hirche 2001). Here we focus on the effects of nitrogen limitation of the food on egg production of two copepods.

Both species of *Acartia* showed higher egg production when feeding *Rhodomonas* sp. grown under nitrogen limitation, not only when food concentrations were high (500 µg C l^{-1}), but also when the animals were supplied with lower (250 µg C l^{-1}) algae concentrations. This was surprising, as previous work in marine and freshwater systems has indicated that nitrogen limited food has a lower quality than food with higher nitrogen content (Checkley 1985, Anderson & Hessen 1995, Müller-Navarra 1995, van Donk & Hessen 1995, Jones et al. 2002, Jones & Flynn 2005). As there was only one case of a significantly different feeding rate (higher ingestion for *A. clausii* feeding on nitrogen limited algae at high concentrations, Fig. 2b, Table I, see also (Plath & Boersma 2001)), the significant differences in egg production between the algae treatments and copepod species (Table II) can not be explained by differences in C-ingestion rates, especially since ingestion by *A. clausii* of nitrogen limited algae in the lower concentration (250 µg C l^{-1}) showed the opposite trend compared to the higher concentration (Fig. 2). Several reports (e.g. van Donk et al. 1997) have shown that both phosphorus limited and nitrogen limited algae may be more difficult to digest than algae grown under balanced nutrient conditions, because the former may increase the thickness of their cell wall. This, however, is less likely to happen with a cryptophyte as they do not have such a cell wall, but a periplast only (Lichtle 1979).

A decrease in reproductive output is often explained by a direct limitation of the nutrient under study, or by a concordant change in the biochemical composition of the algae (Lacoste et al. 2001, Jones & Flynn 2005). The fatty acid spectrum of algae changes under nitrogen limitation, with a lower percentage of highly unsaturated fatty acids (HUFA) in nitrogen limited algae (Reitan et al. 1994). These fatty acids are essential to many consumers and hence a decrease in their content in the algae would cause a decrease in their quality as food for zooplankton (Elser et al. 2001). Most likely, however, the HUFA content of cryptophytes is high enough to meet the nutritional requirements of the copepods, even when the algae are nitrogen limited (Koski et al. 1998), as the saturation thresholds for fatty acids are very low for most zooplankton species (Becker et al. 2004).

Copepod eggs may also have a higher C:N ratio than body tissue as a result of the higher lipid content of the eggs (Pond et al. 1996). Hence, it could be that under nitrogen limitation (carbon surplus) the best strategy for a copepod is to produce more eggs to decrease the excess carbon (but see (Jones & Flynn 2005, Klein Breteler et al. 2005)). Such excess carbon eggs could have a different size or be of lower quality (Guisande & Harris 1995, Kleppel & Hazzard 2000), but then one would expect differences in hatching success, which we did not observe, neither was there a consistent pattern in egg sizes between the treatments.

The C:N content of the algae increased from 5 to 10 under nitrogen limitation. Although this increase is substantial, even under nitrogen limitation the C:N content of the algae is still fairly close to the Redfield ratio and hence it is likely that the animals were at least not very nitrogen limited even when feeding on the nitrogen limited algae. In fact, a recent study by Boersma and Elser (2006) argues that the response of animals to changes in carbon-to-nutrient ratios in their food should be unimodal, with a maximum at the threshold elemental ratio. One explanation for our results could hence be that the decrease in nitrogen content of the algae brought it closer to this ratio, as with a copepod C:N ratio around 5, assuming 30% gross growth efficiency for carbon, the theoretical threshold for nitrogen limitation for copepods could be as high as 15 (Urabe & Watanabe 1992). Accordingly, a dynamic energy budget model (Kuijper et al. 2004) showed a dome-shaped reaction to prey C:N ratio with a gross growth efficiency (egg production) for N increasing from prey with a C:N ratio at 5, peaking between 10 and 15 and decreasing again at higher ratios. Thus the results presented here strongly support the results of Urabe and Kuijper (Urabe & Watanabe 1992, Kuijper et al. 2004), and Boersma and Elser (Boersma and Elser, in press) suggesting a higher egg production at a prey C:N ratio of 9.05 compared to at 4.49, due to a combination of different C and N requirements for maintenance and reproduction.

General life history theory predicts that reduced life expectancy should change resource allocation decisions in favour of increased reproductive effort (Clutton-Brock 1984, Bollens & Stearns 1992). However, the dependence of reproductive investment on cues of low life expectancy has rarely been recorded. It could be that our observation of changing reproductive effort as a result of nitrogen depletion is such a response to a change in life expectancy, as this might mean that the bloom is reaching its end. Although not visible as a significant interaction between species and food type *A. tonsa* seems to be the more responsive species of the two. Interestingly, *A. tonsa* also increased the proportion of eggs that might be resting eggs as well as the size of the eggs produced, which could be a precaution against potential deteriorating food conditions. These were the only differences we observed between the two species under study with respect to the reaction to the differences in feeding conditions.

In conclusion, we show that both *Acartia* species reacted to *Rhodomonas* prey grown in nitrogen depleted cultures with an increase in egg production. This was explained by a better fit with the total nutritional C and N requirements of the copepods for maintenance and egg production on the N depleted algae prey with a C:N ratio of ca 9.1, compared to the N-replete cultures with a C:N ratio of ca 4.5. Further research, especially with longer incubations, is necessary to differentiate potential physiological reactions from using nitrogen depletion as information on bloom development. In the meantime, we can only stress the points made by Mitra and Flynn (2005) that it is essential to incorporate nutrient stoichiometry of the food when studying copepod production.

III. EFFECTS OF FOOD QUALITY UNDER NITROGEN DEPLETED CONDITION ON *ACARTIA LONGIREMIS*

3.1. Introduction

Heterotrophic protists are an important trophic link between phytoplankton and zooplankton in marine food webs. Many heterotrophic protists show strong seasonal variation in abundance (Riegman et al. 1993, Calbet et al. 2003, Hansen et al. 2003, Setaelae & Kivi 2003, Bojanic et al. 2005) and may control phytoplankton blooms (Maar et al. 2002, Johansson et al. 2004, Tillmann 2004, Zhang et al. 2006). They are an important component of the diet of many marine copepods (Stoecker & Capuzzo 1990, Calbet & Saiz 2005). Copepods have been shown to feed selective on heterotrophic protists such as ciliates and dinoflagellates (Jonsson & Tiselius 1990, Turner et al. 2001, Sommer et al. 2005). These organisms on the other hand graze on bacteria and phytoplankton at relatively high rates (Hansen et al. 1997, 2000), which results in rapid regeneration and cycling of nutrients (Flynn & Fielder 1989). In general, under circumstances of nitrogen limitation of phytoplankton, protists might be a particularly rich source of protein and amino acids, compared to phytoplankton and detritus (Stoecker & Capuzzo 1990).

Heterotrophic protists feed on phytoplankton and are themselves ingested by secondary consumers such as copepods. They may improve the food value for these animals. This so called trophic upgrading is attributed to more suitable sizes of the protists prey for copepods, but also to changes in the composition of essential fatty acids (EFA) in the heterotrophic protists prey, compared to the phytoplankton (Klein Breteler et al. 1999, Tang & Taal 2005). The content of fatty acids is often reported as one of the main factors influencing food quality in phytoplankton-zooplankton interactions (e.g. Hessen et al. 1997, Sterner & Schulz 1998, Müller-Navarra et al. 2000, Paffenhöfer et al. 2005). Recent literature has shown that among the EFA mainly essential long chained n-3 polyunsaturated fatty acids like docosahexanoic acid (DHA) and eicosapentanoic (EPA) influence the reproduction of copepods (Kleppel et al. 1998, Koski et al. 1998, Hazzard & Kleppel 2003, Shin et al. 2003, Tang & Taal 2005). At the same time, algae grown under nutrient limitation are often a food of lower quality for zooplankton, as not only their nutrient content changes, but also the relative content of many essential fatty acids. Hence, given the observation by (Stoecker & Capuzzo 1990) that protists are potentially a food source of high in nitrogen content and upgrade certain fatty acids, we combined in this study nutrient limitations in primary producers with the addition of heterotrophic protists and fed these to copepods. This has not been done to date.

In the Baltic Sea nitrogen becomes limiting for phytoplankton growth across wide areas in summer (Thomas et al. 2003, Nausch et al. 2004). At the same time after the spring bloom several species of the heterotrophic protists such as *Strombidium* sp. and *Strobilidium,* sp. (ciliates) can become abundant and act as important nutrient regenerators (Johansson et al. 2004). Therefore it is particularly relevant to study the interactions between copepods and smaller heterotrophic protists under nutrient limitation, especially since several studies in the Baltic Sea have shown that densities of microzooplankton and mesozooplankton are often closely correlated (Smetacek 1981, Heiskanen et al. 1996, Kivi et al. 1996, Uitto 1996).

Most laboratory experiments on the heterotrophic protists copepod link have been carried out with *Rhodomonas* sp. and *Oxyrrhis marina* (Dujardin 1841). These species are also found in the brackish waters of the Baltic Sea. In the same area *Acartia* spp. are abundant calanoid copepods, often found in the surface layer throughout the year (Adrian et al. 1999, Johansson et al. 2004). *Acartia longiremis* (Lilljeborg 1853) is widely distributed across the Baltic Sea and even found in subarctic areas (Norrbin 2001). Here, we investigated the effect of nitrogen depleted food on the reproduction of the common Baltic Sea copepod *A. longiremis*. Females were fed different combinations of the microzooplankton, *O. marina* or *Strombidium conicum* (Lohmann 1908), and one phytoplankter, *Rhodomonas* sp. that had grown under nitrogen sufficient and depleted conditions.

3.2. Material and methods

Feeding experiments were performed using the unicellular autotrophic phytoplankton *Rhodomonas* sp. (Cryptophyta), and two species of heterotrophic protists: the dinoflagellate *Oxyrrhis marina* and the ciliate *Strombidium conicum*. The phytoplankton were grown in batch cultures, under two different nutrient conditions, f/2 media (Guillard 1975a), and nitrogen depleted modified f/2 media, as described in Augustin & Boersma (2006). The dinoflagellate *O. marina* (Göttingen culture collection, Strain B21.89) was adapted from a salinity of 30 down to 10. The ciliate *S. conicum* was sampled at the Baltic Sea GLOBEC-Germany cruise in September 2002 (#AL219) at the central sampling station of the Bornholm Sea. After transport of the samples to the laboratory, individuals were isolated by dilution of the natural sample and pipetting under a microscope. *O. marina* and *S. conicum* were cultured under saturated concentrations of nitrogen sufficient *Rhodomonas* sp. and maintained in 0.45 µm filtrated North Sea water diluted to a salinity of 10.

A. longiremis females were collected at the same station as the ciliates. Copepods were sampled using a WP2-Plankton net equipped with a 10 l codend (mesh size 200 µm, vertically towed from the bottom to the surface with 0.2 m s^{-1}) and immediately sorted into filtered sea water and kept at *in situ* temperatures in gently aerated beakers. After transportation to the laboratory the copepods were cultured in temperature controlled rooms (10 °C, light:dark cycle of 16:8 h) in 0.45 µm filtrated North Sea water, which was diluted to a salinity of 10. The culture was maintained with *Rhodomonas* sp. as single food.

For each experiment, females from a single generation of *A. longiremis* were collected from the culture. The experiments were conducted in 1 l glass bottles (Schott) on a plankton wheel at 1 rpm, in the same temperature and light conditions as for the algae cultures. Every 24 hours the food suspension was renewed, and the copepod eggs were sampled from the old suspension and counted.

Experiment 1 and 2

To investigate the impact of different microzooplankton species on egg production, one microzooplankton species was added in combination with *Rhodomonas* sp. in each experiment. Each treatment was conducted in 3 replicates with 11 to 12 females and 2 males respectively. Based on cell counts, the total target food concentration was adjusted to 500 µg C l^{-1}, with the algae and microzooplankton making up 250 µg C l^{-1} each. Egg production rates were quantified from eggs sampled every 24 hours, and hatching success was estimated after 48 h incubation. All cell concentrations were measured with a CASY counter (Schärfe GmbH; Germany).

Experiment 3

Batch cultures of *Rhodomonas* sp. were grown under nitrogen depleted and sufficient conditions. During growth, cell number and fatty acid composition were measured daily. Both microzooplankton species *O. marina* and *S. conicum* cultured either with nitrogen depleted or sufficient *Rhodomonas* sp. were used as food in this experiment (Table I). The mixed food suspensions were made up as in Experiments 1 and 2. In addition, *Rhodomonas* sp. was fed to the copepods in single food suspensions at two concentrations, 250 and 500 µg C l^{-1}, respectively. The low concentration of *Rhodomonas* sp. corresponded to the amount of algae in the mixed suspensions, while the high concentration corresponded to the total food concentrations in the mixed suspensions. At the beginning of the experiment, samples were taken from the different stock cultures to measure fatty acid content, CN concentration and cell abundance. Carbon and nitrogen content was estimated with a Fison EA 1108 CHN analyser after filtering of 30 to 200 ml of the algal culture onto a combusted Whatman GF/C filter and storing at –20 °C.

Table I. Species of phytoplankton and heterotrophic protists used in this study.

	Nitrogen treatment	Size (µm)	Carbon content (pg C $cell^{-1}$)
Rhodomonas sp.	sufficient	8.73 ± 0.1	42.26
	depleted	9.09 ± 0.2	58.32
Strombidium conicum	sufficient	13.65 ± 0.1	1086.00
	depleted	14.09 ± 0.2	1004.83
Oxyrrhis marina	sufficient	19.97 ± 0.3	996.36
	depleted	18.27 ± 0.0	1327.18

Fatty acid samples were taken by filtrating 50-100 ml on pre-combusted GF/C filters (Whatman) at low pressure and stored at -80 °C until further analysis. Lipid extraction was performed with minor modifications as described in Folch et al. (1957) using ultrasonic disruption in dichloromethane:methanol (v/v:2/1) 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. An additional centrifugation step was carried out prior to the washing procedure to remove GF/C filter remains. For fatty acid analyses sub-samples of total lipids were hydrolyzed and fatty acids were converted to their methyl ester derivatives (FAME) in methanol containing 3 % concentrated sulphuric acid at 80 °C for 4 h (Kattner and Fricke 1986). After cooling, 2 ml of aqua bi-distilled was 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 programmable temperature vaporizer injector (solvent vent mode). The FAMEs and alcohols were detected by flame ionization and identified by comparing retention times with those derived from standards of known composition.

Results were tested with one way ANOVA followed by Tukey test.

3.3. Results

In the first two experiments the egg production rates of *A. longiremis* were measured for 4 days (Fig. 1). Egg production rates at day 1 varied between 2 and 3 eggs female^{-1} day^{-1}. In both experiments the females produced more eggs when they were fed on a mixed diet including heterotrophic protists than with the phytoplankton itself. The egg production rate after 4 days feeding on *Rhodomonas* sp. mixed with *S. conicum* or *O. marina* increased to 5 eggs Female^{-1} day^{-1}.

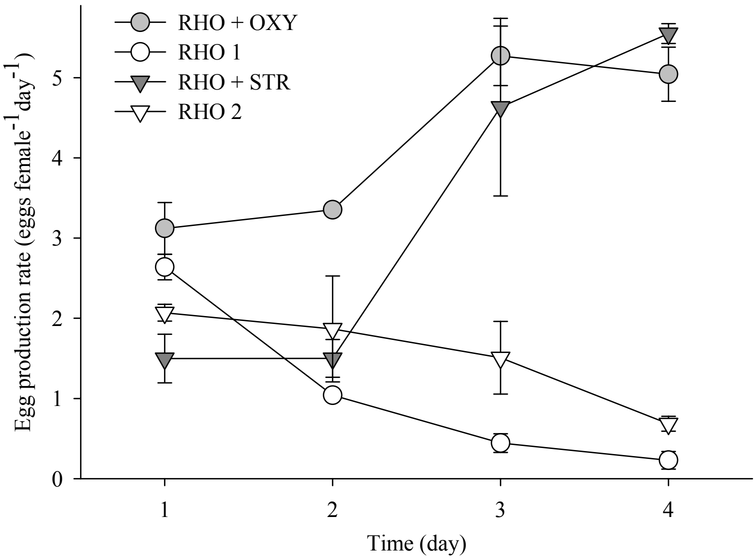


Figure 1. *A. longiremis*. Egg production rates over time at different food either containing single *Rhodomonas* sp. (open symbols) or *Rhodomonas* sp. and *O. marina* (filled symbols); Different shapes of the symbols present different experiments; Error bars indicate standard error of the mean.

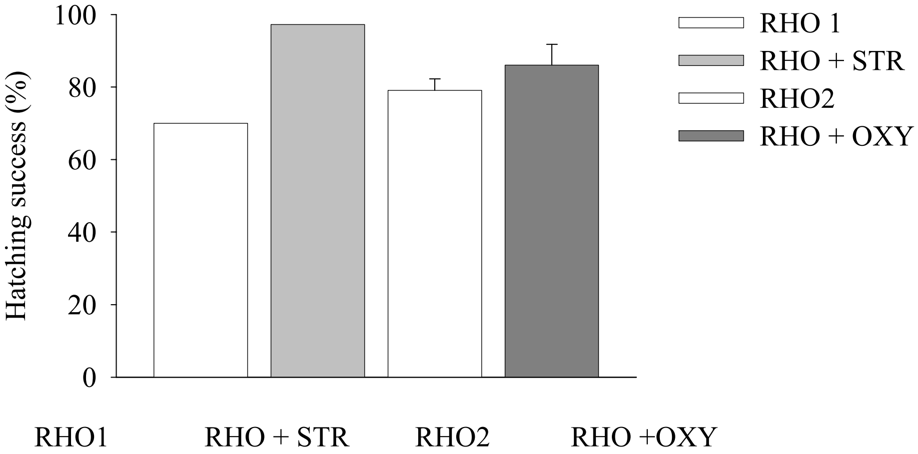


Figure 2. *A. longiremis*. Hatching success after incubation with single *Rhodomonas* sp. (open bars), *Rhodomonas* sp. and *O. marina* (dark grey bars) or *Rhodomonas* sp. and *S. conicum* (light grey bars); Error bars indicate standard error of the mean.

In contrast, a decrease to 1 egg female^{-1} day^{-1} was observed in the treatment with *Rhodomonas* sp. only. But there was no difference between the two heterotrophic protists.

The hatching success (Fig. 2) after feeding on *Rhodomonas* sp. and *S. conicum* was with 70 to 90 % in a similar range compared to eggs produced after feeding on *Rhodomonas* sp. and *O. marina* with 80 to 90 %.

The fatty acid contents of *Rhodomonas* sp. from the different nitrogen treatments differed significantly ($p < 0.01$, ANOVA). The amount of saturated fatty acids (SFAs) and monounsaturated fatty acids (MUFAs) in the cells increased from 20 to 115 and 200 to 400 pg FA cell^{-1} respectively compared to nitrogen sufficient phytoplankton (Fig. 3A, B).

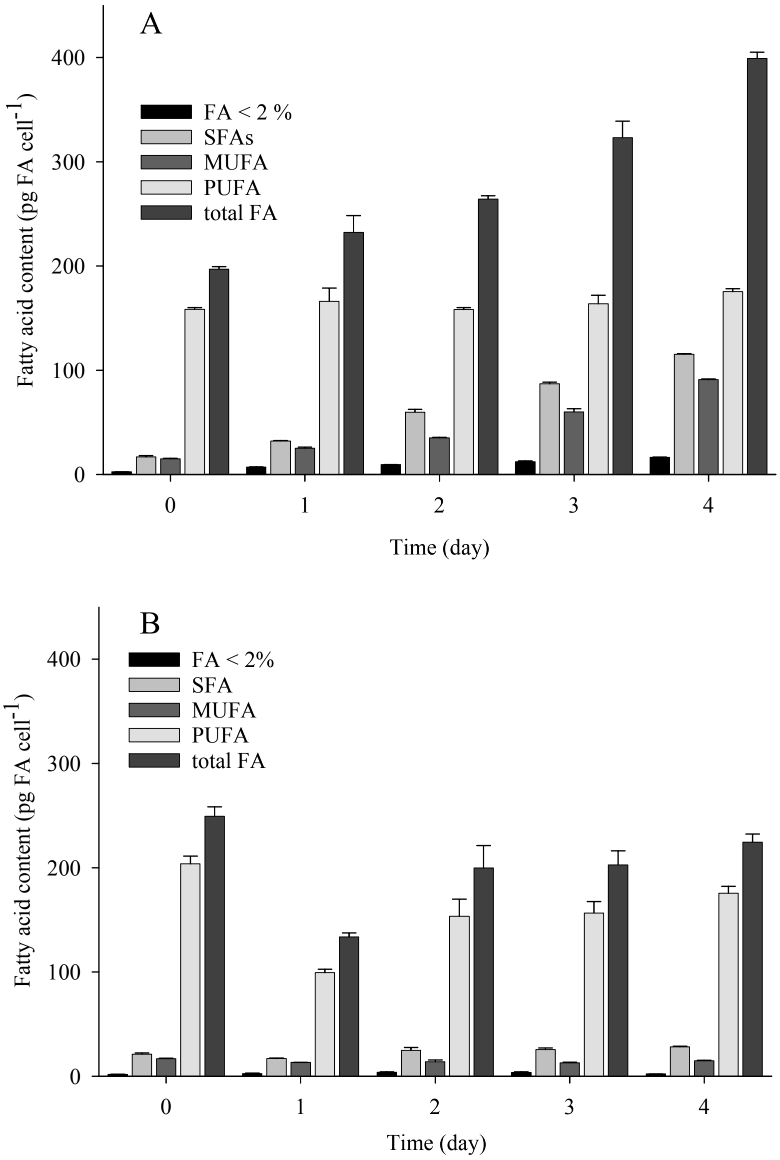


Figure 3. Fatty acid content (pg cell^{-1}) of *Rhodomonas* sp. over the time during growing in either nitrogen depleted (A) or nitrogen sufficient (B) media

The fatty acid content of polyunsaturated fatty acids (PUFAs) remained at around the same level in both treatments (Fig. 3A, B). On the other hand, the percentage of EPA and DHA from the total fatty acid content decreased rapidly when the phytoplankton became nitrogen depleted (Fig. 4). With the presence of heterotrophic protists the percentage of EPA and DHA to the total fatty acid was different (Fig. 5).

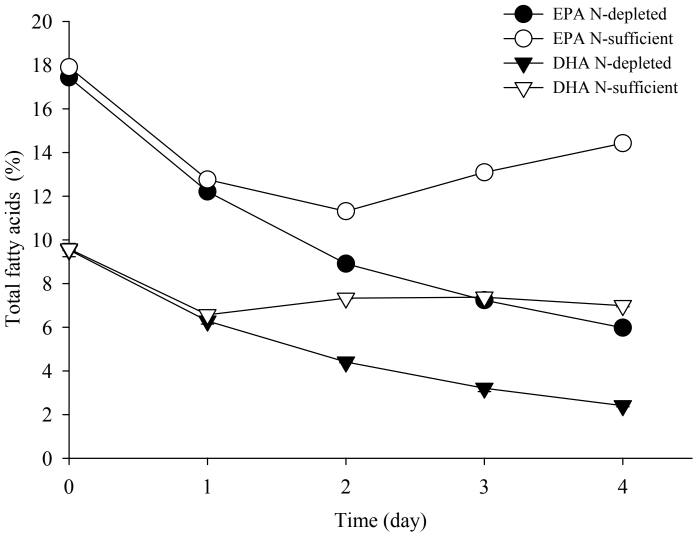


Figure 4. EPA and DHA contents (as % total fatty acid) of *Rhodomonas* sp. over the time during growing in either nitrogen depleted or nitrogen sufficient media; Error bars indicate standard error of the mean, but they are to small to be visible on the graph.

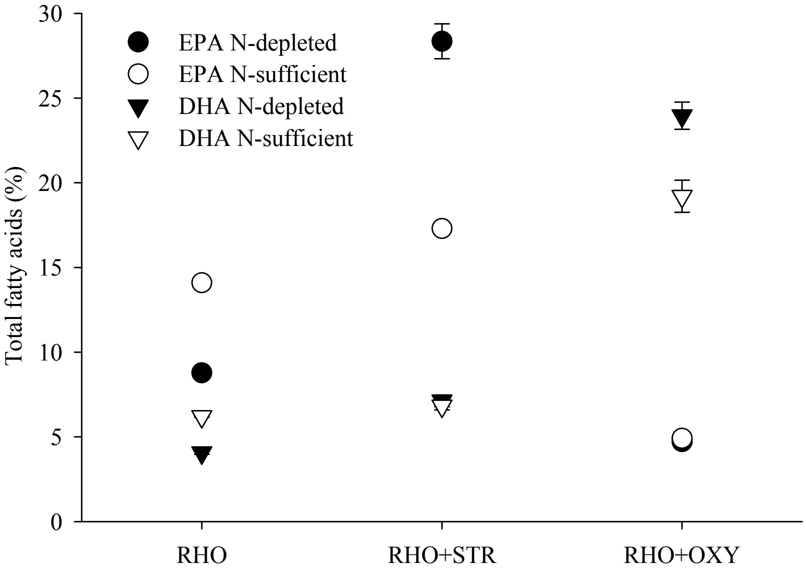


Figure 5. EPA and DHA contents (as % total fatty acid) under nitrogen depleted (filled bars) and nitrogen sufficient (open bars) condition; Error bars indicate standard error of the mean but to small to be visible on the graph.

In the mixture of *S. conicum* and *Rhodomonas* sp. the DHA content remained at 7 % for both nitrogen conditions, while the EPA was significantly higher under depleted condition (28 %

of total fatty acid) than under sufficient conditions (17%). On the other hand in *O. marina* the percentage of DHA was high in nitrogen depleted (24 % of total fatty acid) and low in the sufficient environment (19 %). The EPA was in both treatments low at ca 5 % (Table II).

Table II. Fatty acid content (percentage of the total fatty acid) of the used food for *Acartia longiremis;* (R) means fed *Rhodomonas* sp.

Species	*Rhodomonas* sp.		*Strombidium conicum* (R)		*Oxyrrhis marina* (R)	
N-supply	sufficient	depleted	sufficient	depleted	sufficient	Depleted
Saturated fatty acid						
14:00	6.74	8.66	3.31	3.72	10.5	6.36
16:00	11.19	16.95	9.47	7.83	19.07	21.08
18:00	0.17	1.42	1.98	0.93	0.9	0.64
Monounsaturated fatty acid						
14:1(n-5)	–	–	1.78	1.57	1.23	2.16
16:1(n-7)	0.72	1.2	3.28	2.55	5.66	2.06
18:1(n-7)	4.63	3.99	5.33	3.06	7.63	6.96
18:1(n-9)	2.67	7.21	1.77	1.96	2.7	5.04
Polyunsaturated fatty acid						
16:2(n-4)	0	0	1.26	3.63	0	0
18:2(n-6)	2.73	5.2	1.38	2.38	1.54	2.93
18:3(n-3)	18.45	19.37	10.42	13.8	9.1	10.57
18:4(n-3)	30.36	21.51	30.41	22.02	15.18	9.67
20:5(n-3)	14.09	8.77	17.3	28.35	4.91	4.72
22:6(n-3)	6.2	4.06	6.82	7.12	19.2	23.96
FA < 2%	2.05	1.65	5.5	1.07	2.4	3.86

The molar C:N ratio (Fig. 6) confirmed that the nitrogen depleted *Rhodomonas* sp. treatments were in fact nitrogen limited. Nitrogen sufficient food had a molar C:N ratio of 4 to 5, while the nitrogen depleted phytoplankton reached a higher molar C:N ratio from 7 to 9. The mixture of the nitrogen depleted *Rhodomonas* sp. and heterotrophic protists also showed relatively high C:N ratios (7 to 9).

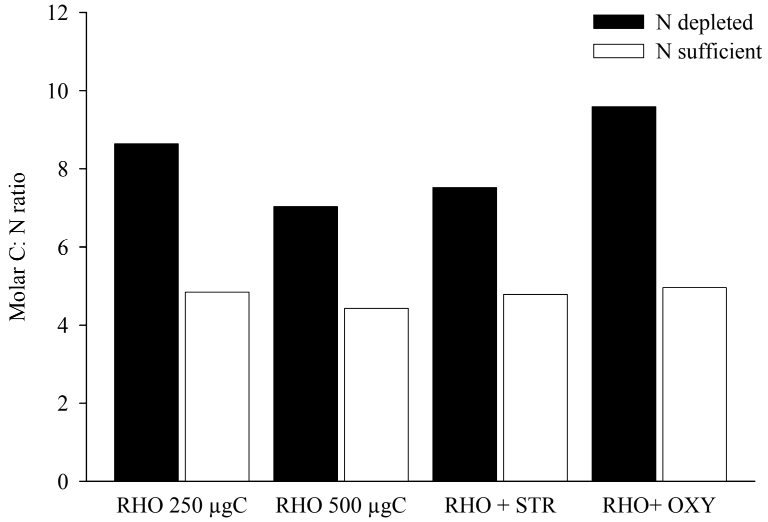


Figure 6. Molar C:N ratios of the different treatments at the beginning of experiment 3; Treatments under nitrogen depleted (filled bars) and nitrogen sufficient (open bars) conditions; Error bars represent standard error of the mean.

The presence of the heterotrophic protists *S. conicum* or *O. marina* resulted in a significantly higher egg production (4 egg female^{-1} day^{-1} $p < 0.01$ ANOVA) (Fig. 7) compared to 1 egg female^{-1} day^{-1} yielded from feeding on monocultures of *Rhodomonas* sp. in different concentrations.

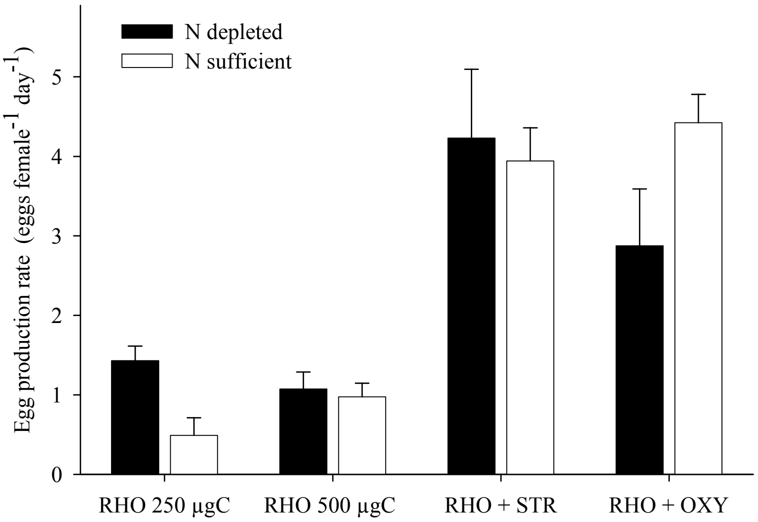


Figure 7. ***A. longiremis*****. Egg production rates after incubation in either nitrogen depleted (filled bars) or nitrogen sufficient food (open bars); Error bars represent standard error of the mean.**

There was no significant difference between the two different microzooplankton types ($p = 0.45$ ANOVA). No significant effect of nitrogen status was found on egg production, but we observed a marginally trend of the interaction between limitation and heterotrophic addition (Table III).

Table III. ***Acartia longiremis;*** **statistical results for comparison for egg production rate (one-way ANOVA);** ***p*** **< 0.05 indicates significant differences**

	Degrees of Freedom	Mean square	F ratio	p
Intercept	1	133.22	234.64	**0.000**
Treatment	3	16.41	28.90	**0.000**
Nitrogen effect	1	0.02	0.03	0.872
Treatment vrs nitrogen effect	3	1.59	2.80	0.076
Error	15	0.57		

3.4. Discussion

Our results showed that the presence of heterotrophic protists could support higher egg production rates in *A. longiremis* compared to saturated concentrations of *Rhodomonas* sp. alone. The highest egg production rate (5 eggs female^{-1} day^{-1}) that was reached during these laboratory experiments were also found in nature (Peterson et al. 2002). We observed no difference in hatching success between the different treatments, and the hatching success was similar to what is reported in other studies (Tang & Taal 2005). Differences in hatching success have been attributed to the fatty acid content as a food quality factor (Broglio et al. 2003, Arendt et al. 2005), but this cannot be collaborated by our results.

When phytoplankton becomes nitrogen depleted several aspects of algal cells, such as carbon content and fatty acid composition, change (Koski et al. 1998, Ahlgren & Hyenstrand 2003, Klein Breteler et al. 2005). This change can be so strong that it affects copepod egg production (Kuijper et al. 2004, Augustin & Boersma 2006). It is well known that overall food concentration may heavily influence copepod egg production (Kiørboe et al. 1985, Calbet & Alcaraz 1996, Maps et al. 2005). Further, larger prey size (such as for the heterotrophic protists used here) compared to *Rhodomonas* sp. may cause higher feeding rates in *Acartia* sp. (Berggreen et al. 1988, Tang & Taal 2005), or a higher feeding efficiency.

Alternatively, heterotrophic protists, like those used here, may also act as trophic upgraders of the food quality for copepods (Klein Breteler et al 1999), but it is still unclear what specific factor(s) of the ingested prey are most important for the copepod reproduction.

In our study, the egg production rate of copepods fed *Rhodomonas* food mixtures including *O. marina* or *S. conicum* were not significantly different from each other but higher than for the single *Rhodomonas* diets. In concert with these results, it has been shown that the presence of heterotrophic protists affects the fatty composition, especially the content of EPA and DHA. Studies with *O. marina* have shown that it is able to trophically transfer or modify biochemical compounds such as DMS (Wolfe et al. 1997), toxins (John et al. 2002) or fatty acids (Kleppel & Burkart 1995, Klein Breteler et al. 1999, Stevens et al. 2004). This dinoflagellate also seems to have the ability to enhance the food quality by changing the fatty acid composition of their prey (Kleppel & Burkart 1995, Klein Breteler et al. 1999, Tang & Taal 2005, Veloza et al. 2006). In contrast, a recent study by (Veloza et al. 2006) reported lower EPA contents in *O. marina* even when fed *Rhodomonas* sp. compared to the EPA content of *Rhodomonas* sp. itself. But in the same study *O. marina* contained the highest lipid content. However, when *O. marina* was fed with bacteria no upgrading was observed (Ederington et al. 1995). Several studies, using *Strombidium sulcatum* as microzooplankton link also fail to show trophic upgrading of the food quality for copepods (Broglio et al. 2003, Klein Breteler et al. 2004).

Based on the assertion of (Stoecker & Capuzzo 1990) that heterotrophic protists can be a rich source of nitrogen, we expected that the C:N ratio of the samples of *Rhodomonas* sp. and heterotrophic protists would be lower than the C:N ratios of nitrogen limited *Rhodomonas* cultures. This was not the case. From this we can conclude that nitrogen as such is not limiting egg production in animals fed on nitrogen limited algae. Further, during nitrogen depletion the content of PUFAs did not change compared to the increasing content of SFAs and MUFAs, but certain PUFAs such as EPA and DHA varied in an opposite manner compared to that of the total fatty acid content. But also in the heterotrophic protists no clear picture of increased amounts of highly unsaturated fatty acids was observed. Hence, neither the nitrogen content of the heterotrophic protists nor their fatty acid profile can explain the higher egg production when fed mixtures of autotrophs and heterotrophs.

Nevertheless, even if we do not know the mechanisms it is clear that copepods may increase their reproductive output by feeding on heterotrophic protists. In the Baltic Sea ciliates like *Strombidium* sp. are found in higher numbers than flagellates like *O. marina* (Setaelae & Kivi 2003, Höglander 2005). Copepods further show high feeding rates on ciliates, and the mesozooplankton could potentially obtain up to 70% of their carbon demand by consuming ciliates in the Baltic Sea (Johansson et al. 2004). The ciliates are considered to be important nutrient regenerators (Johansson et al. 2004). But possibly, demand for carbon, rather than nitrogen, may drive the copepods to increase the feeding efficiency by feeding on heterotrophic protists when they are present. *Acartia tonsa* showed a slightly higher ingestion rate for *O. marina* compared to feeding on *Rhodomonas* sp. (Tang & Taal 2005). Thus, it seems that different heterotrophic protists may compensate and therefore upgrade the nutritional value of the phytoplankton food, at least in some cases, but further experiments have to be done to determine whether different heterotrophic protists in general act as trophic upgraders for mesozooplankton in the Baltic Sea and elsewhere under nutritional depleted conditions.

IV. SALINITY AND TEMPERATURE EFFECTS ON REPRODUCTION, GRAZING AND SURVIVAL OF *TEMORA LONGICORNIS* IN THE BALTIC SEA

4.1. Introduction

The central part of the Baltic Sea, the Baltic Proper, is divided into the Arkona Basin, Bornholm Sea and Gotland Sea and characterized by a permanent saline stratification by intermittent inflow water from the western Baltic seas and by fresh water surplus from the eastern adjacent seas and draining rivers (Nausch 1996). In these brackish environments, salinity is a driving force for the distribution and life cycles of marine organisms (Remane & Schlieper 1958). Salinity and temperature are two of the most important abiotic factors affecting growth and survival of aquatic organisms (Kinne 1964). In addition, decreasing salinity also alters other environmental conditions such as food supply.

Especially the salinity-temperature interaction can have great impacts on the distribution of copepods in coastal and estuarine situations (Mauchline 1998). A shift in temperature can modify the effects of salinity by enlarging, narrowing or shifting the salinity range that an individual can tolerate. On the other hand salinity can modify the effects of temperature accordingly (Kinne 1964). In the Baltic Proper the temperature ranges from 2 to 19 °C. The variability of the temperature varies over water column. Recent studies even have observed higher temperature than in the past in the intermediate water layers (Elken et al. 1996, Nausch et al. 2003).

In general, temperature is known to influence copepod reproduction directly (Corkett & Zillioux 1975, McLaren & Corkett 1981, Halsband-Lenk et al. 2002, Hirst & Kiørboe 2002) or indirectly by temperature dependent body size and growth (Vidal 1980b, McLaren & Corkett 1981, Crawford & Daborn 1986, Klein Breteler & Gonzalez 1988, Ban 1994, Koski & Kuosa 1999, Köster 2003).

Only a few calanoid copepod species seem to be flexible enough to cope with conditions such as those in the Baltic Sea. *Temora longicornis* (Müller 1792) is widely distributed and common in marine (e.g., North Atlantic, North Sea) as well as in brackish areas (e.g., estuaries, Baltic Sea). In the Baltic Sea *T. longicornis* occurs up to the eastern Gotland Sea with a decrease in the salinity to 7 (Wasmund et al. 1996). This calanoid copepod species is generally known to be euryhaline and mesotherm (Ackefors, 1969; Hernroth and Ackefors 1979) with an omnivorous feeding behaviour. Some combined studies on hydrographical and population dynamic data like abundance of *T. longicornis* in the Baltic Sea have shown that this species is mainly found near the surface, with relatively high temperature, low salinity and higher food quantity, but potentially earlier nutrient limitation that in deeper layers (Dippner et al. 2000, Möllmann & Köster 2002, Hänninen et al. 2003, Vuorinen et al. 2003). All of these factors influence growth and reproduction, and it has been shown that *T. longicornis* can be influenced by either temperature (Dippner et al. 2000, Halsband-Lenk et al. 2002, Devreker et al. 2005), or by food quality and quantity (Peterson & Kimmerer 1994, Koski 1999, Koski & Klein Breteler 2003, Maps et al. 2005). Most studies, however, did not consider these factors simultaneously, and only a few studies investigated the effect of salinity, temperature, food and its combined effects on copepods. Hence, to understand the population dynamics of *T. longicornis* in the brackish water conditions of the Baltic Sea Proper, we conducted combined studies on mortality, grazing and egg production in the field and the laboratory. At the same time, we carried out an experiment to investigate the extent of the local adaptation with respect to salinity in *T. longicornis*, by selecting animals from different habitats with different salinities, and exposing them to other salinities.

4.2. Material and methods

Field Data and experiments

During three cruises carried out between May 2002 and May 2003 by the GLOBEC-Germany project (Fig. 1, Table I), profiles of depth, temperature and salinity were obtained by CTD at station BB0023 (BB23 55°16.6'N 15°45.39'E) located in the deepest and central part of this area. At the same cruises the vertical distribution of female *Temora longicornis* was examined in the Bornholm Basin. Plankton samples were taken with a Multinet (50µm mesh size, 0.25 m² opening). The sampling was performed in stacked 10 meter intervals from the bottom to the surface regardless of day time. The samples were rinsed carefully into vials and preserved in 4 % borax buffered formaldehyde sea water solution. The abundance was interpolated from individuals found in a subsample and water flow through the net.

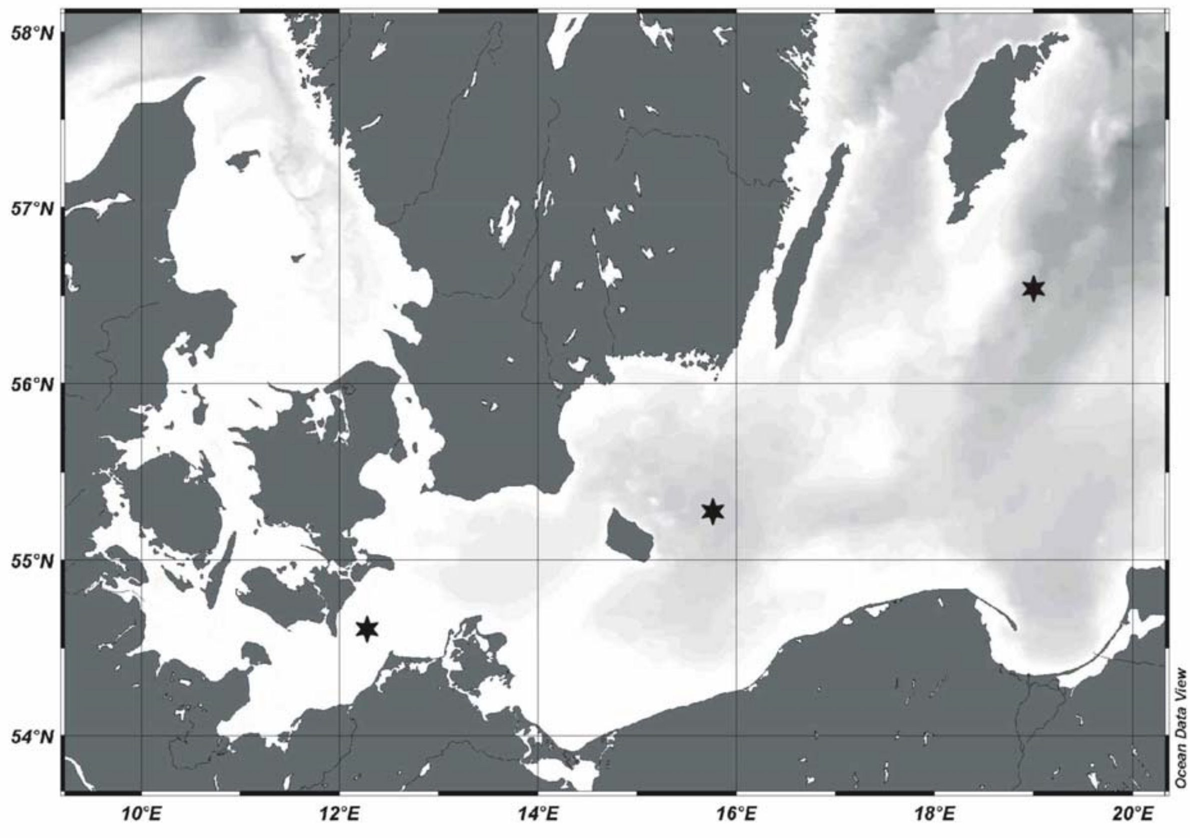


Figure 1. Sampling station and regions in the central Baltic Sea; Arkona Sea (Panel A), Bornholm Sea (Panel B) and Gotland Sea (Panel C)

Field experiments

The experiments with copepods from the field were conducted during GLOBEC cruises (Table I). WP2 plankton net samples and sea water were collected at different stations in the Baltic Sea, selected to have different salinities but similar temperatures (Table II).

The sea water samples were stored in darkness at *in situ* temperatures. *T. longicornis* females were sorted, using a dissecting microscope, and incubated in 1 l glass bottles. In the first experiment *T. longicornis* was incubated with natural sea water from the depth of the chlorophyll maximum and natural sea water enriched with *Thalassiosira weissflogii.* Every 24 h the water was renewed with 0.2 µm filtered seawater. At the same time fresh *T. weissflogii* from batch cultures were added in a food concentration of 500 µg C l^{-1}, which is known to saturate feeding and thus prevent food limitation in this species (Maps et al. 2005). At second experimental set up 10-15 copepods from each station were adapted in 1 l glass bottles rotating on a plankton wheel with 1 rpm. Data was collected for four days. Eggs and dead females were counted and removed every day to calculate mortality and *EPR*.

Laboratory Experiments

Copepods used in these studies were the progeny of adults collected with a WP2 net at the Kiel Bight (54°N 10°E) in October 2004. *T. longicornis* females were isolated and adapted to the laboratory condition of a salinity of 12, 12:12 hours of dark: light rhythm, at 15 °C. Prior to every experiment copepods were acclimated to the experimental temperatures by 2 °C steps per day. These copepod cultures were maintained with *Rhodomonas* sp. at saturated food concentrations. For the incubations 0.2 µm filtered seawater was adjusted to the respective salinities.

Experiment: Temperature effect on egg production

The temperature experiments were accomplished using a temperature gradient table with 10 different temperatures and maximal 6 replicates (Thomas et al. 1963). In each replicate 5 females were incubated in a glass beaker with 250 ml of prey suspension. The experimental temperatures ranged from 7-24 °C. The salinity was kept constant at 14. Mortality, ingestion and egg production were measured for 24 hours. This set up has been conducted two times (Experiment 1 and 2).

Experiment: Salinity and food quality interactions effects on egg production:

Adult females were sorted in 620 ml glass bottles and rotated with 1 rpm on a plankton wheel. The copepods were fed with *Rhodomonas* sp. grown in batch cultures with nitrogen depleted and nutrient sufficient f /2 media (Guillard 1975a, Augustin & Boersma 2006). The food concentration was maintained at saturated conditions. The temperature was kept constant at 15 °C (±0.4) and the salinity was adjusted to 14 or 7. All other conditions were similar to the other laboratory experiments. Mortality and egg production were estimated over three 24-hour periods.

4.3. Results

Field data

In the central station of the Bornholm Sea, the salinity was uniformly around 7 in the upper layer (Fig. 2A, B, C), and the halocline was situated at ca 40 m depth during all three cruises (Table I). Below that depth the salinity increased up to 15-19. In November 2002 the temperature in the upper 40 m was 9 °C, while in May 2002 and 2003 the temperature in the upper 40 m ranged from 10-12 °C in the surface to ca 4 °C at 40 m depth (Table I).

Table I. Overview of the cruises for distribution of *Temora longicornis* females and the hydrographical condition in the whole water column at this time.

Cruise number	Date	Salinity range	Temperature range (°C)	Depth of the halocline (m)	Abundance N_{min}- N_{max} (ind. m^{-3})
HE 168	05.05. - 24.05.2002	7 -17	9 - 12	42	5 - 160
HE 181	11.11. - 29.11.2002	7 - 15	4 - 10	35	60 - 1650
AL 220	15.05. - 03.06.2003	7 - 18	3 - 12	44	5 - 60

Table II. Overview of the cruises and the hydrographical conditions during the sampling for the field experiments.

Station	Cruise number	Position	Date	Salinity range	Temperature range (°C)
Bornholm Sea	AL 219	55°16.6'N 15°45.39'E	18.04.2003	7.2 - 19.3	2.6 -3.4
Bornholm Sea	AL 226	55°16.6'N 15°45.39'E	10.08.2003	7.0 - 14.8	3.2 -18.8
Arkona Sea	AL 238	54°36,7'N 12°16.4'E	28.05.2004	10.3 - 22.4	9.0 - 11.4
Bornholm Sea	AL 238	55°16.6'N 15°45.39'E	30.05.2004	7.3 - 17.7	3.2 - 10.2
Gotland Sea	AL 238	56°32.49'N 18°59.79'E	08.06.2004	7.1 - 12.2	2.9 - 12.3

The vast majority of *T. longicornis* females were always found above the halocline. Although there were a few individuals below the halocline in November they were virtually absent under the halocline in May (Fig. 2).

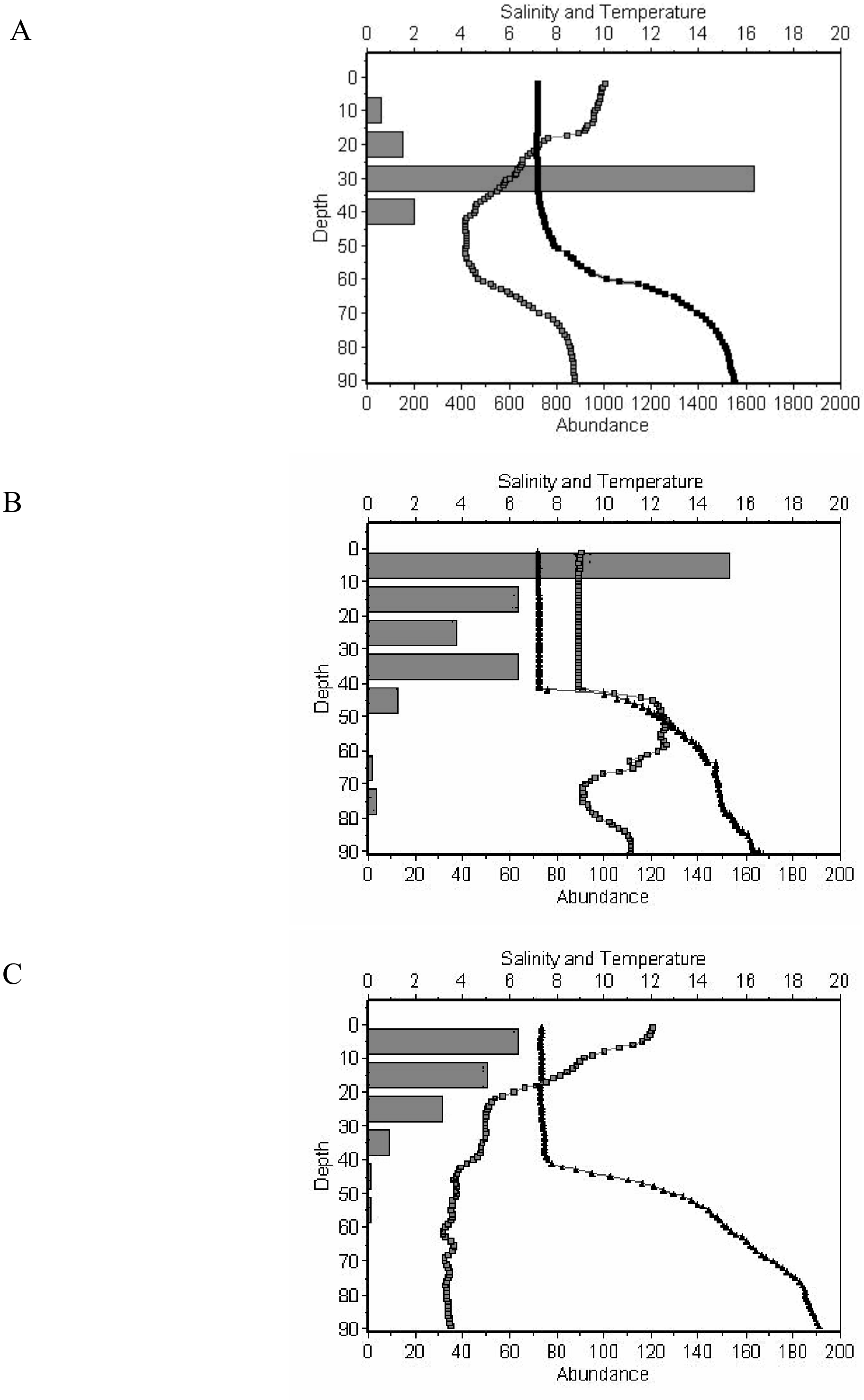


Figure 2. Central Bornholm Sea station: vertical distribution of salinity (black dotted line), temperature (grey dotted line) and abundances of *Temora longicornis* females (horizontal bars) at different times of the year: Panel A Nov 2002, Panel B May 2002 and Panel C May 2003.

The abundance of copepods varied from 60 to 1600 females m^{-3}. The highest abundance was found at salinity around 7 and at temperatures between 7-12 °C. Salinities in the different areas ranged from 7 in the Bornholm Sea to 20 near Kiel, whereas the temperature of the surface layer was fairly constant.

Field experiments

In the first experiment *T. longicornis* from the Bornholm Sea was fed with natural phytoplankton assemblage (10 °C, salinity 7.6) and the mortality rate was less then 5 %, but females produced less then 1 egg female^{-1} day^{-1} (Fig. 3). In contrast females produced up to 4.9 eggs female^{-1} day^{-1} after incubation with saturated food concentrations of *T. weissflogii* (Fig. 3).

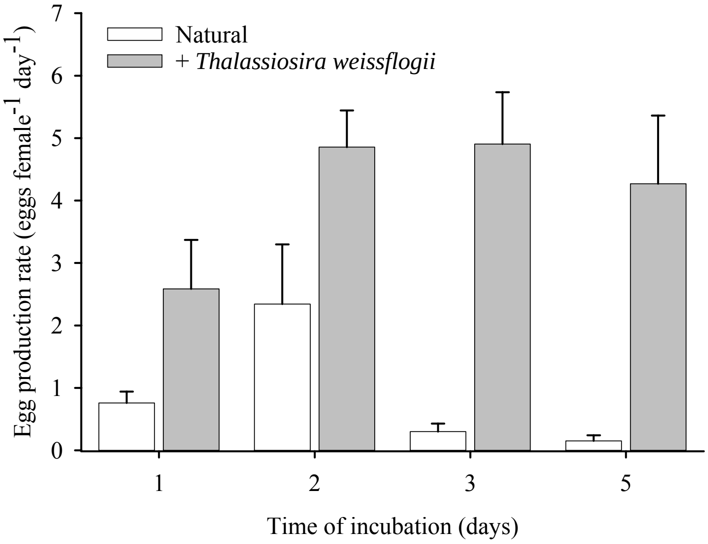


Figure 3. ***Temora longicornis*** **from the Bornholm Sea: egg production rate over the time feeding on natural food (open bars) and on** ***Thalassiosira weissflogii*** **(filled bars). Error bars indicate standard error of the mean.**

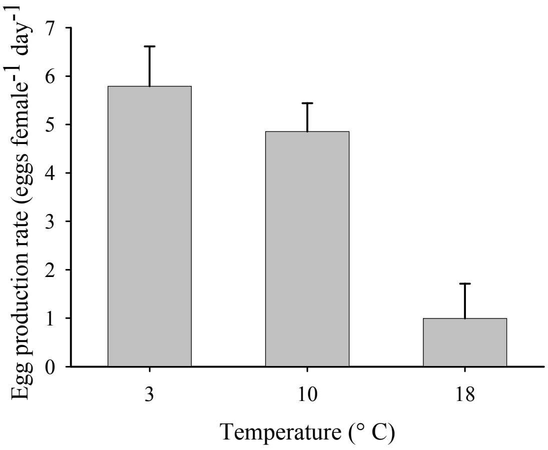


Figure 4. ***Temora longicornis*** **from the Bornholm Sea: egg production rate at different field temperatures feeding on surplus concentration of** ***Thalassiosira weissflogii*****. Error bars indicate standard error of the mean**.

The *EPR* measured at different cruises with different temperature (Table II) showed no direct relation to temperature when they were fed with saturated food conditions (Fig. 4).

Comparing *T. longicornis* females from the Arkona Sea (salinity 10) incubated in water with a higher salinity (25) than the original sea water (10 to 25) and sea water with a lower salinity (10 to 7.5) the mortality was less then 20 % in all replicates (Fig. 5A). However, females from Bornholm and Gotland Seas (7-8 *in situ*) showed a significantly higher (up to 90%) mortality at a higher salinity (18) (Fig. 5B, C), while the incubation in 7.5 salinity sea water resulted in mortality rates less than 10 % (Fig. 5B, C).

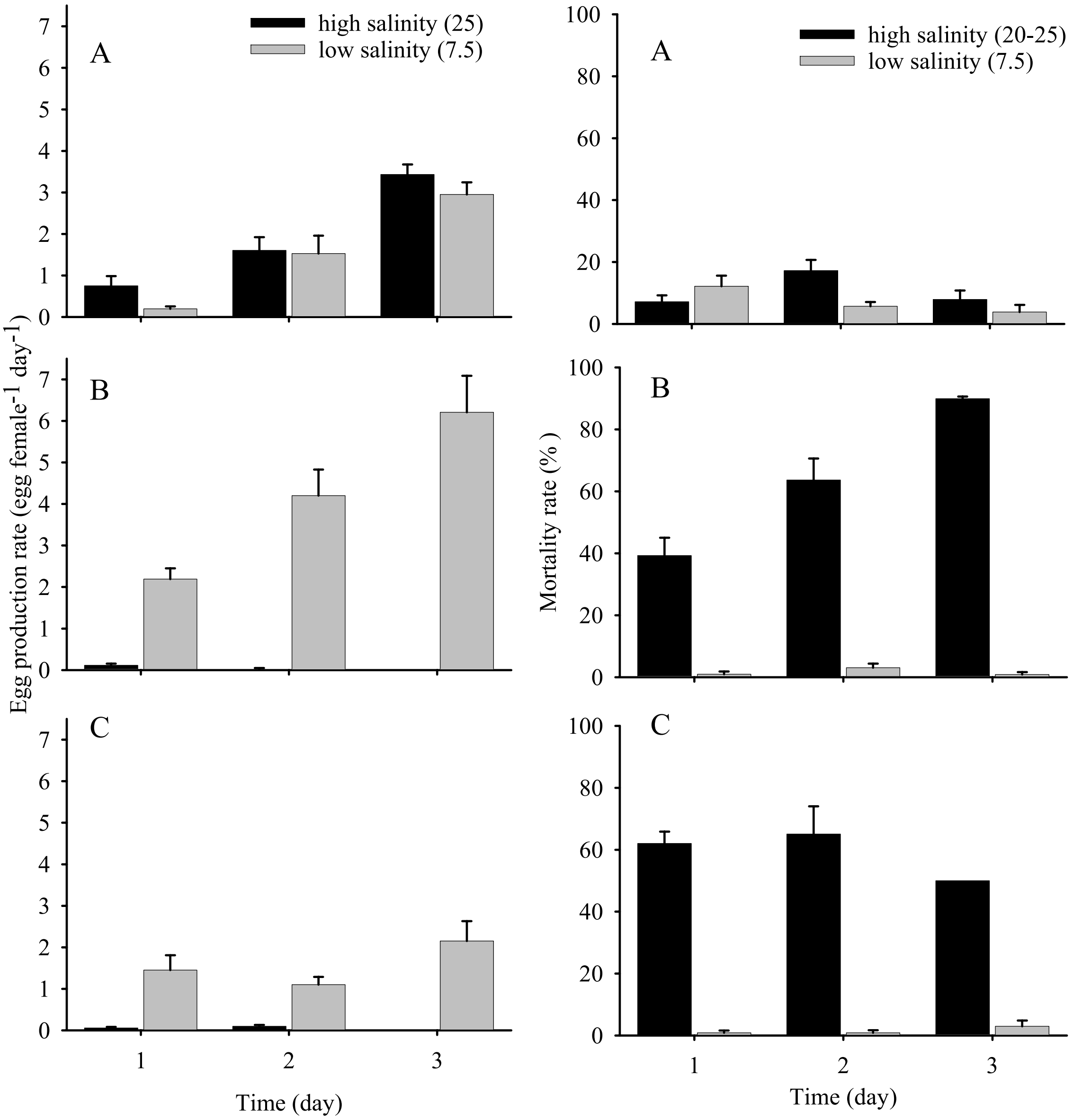


Figure 5 and 6. ***Temora longicornis:*** **mortality rate (Fig. 5, left) and egg production rate (Fig. 6, right) incubated over three days at different salinities feeding on** ***Thalassiosira weissflogii*****: Panel A Arkona Sea, Panel B Bornholm Sea and Panel C Gotland Sea dark bars represent high salinity and grey bars indicate low salinity. Error bars represent standard error of the mean.**

EPR of *T. longicornis* from Arkona Sea increased with a higher salinity to 3.4 eggs female^{-1} day^{-1}, when the salinity increased from 10 to 25, whereas the *EPR*s of females from Bornholm and Gotland decreased to zero at salinity above 18. *T. longicornis* from Bornholm Sea showed the highest *EPR* (6.2 eggs female^{-1} day^{-1}) at a salinity of 7.5 (Fig. 6A). At the same salinity *T. longicornis* from Arkona Sea produced 3.0 eggs female^{-1} day^{-1}and from Gotland Sea 2.2 eggs female^{-1} day^{-1} (Fig 6B, C). The *EPR* with *T. longicornis* from Gotland Sea was not increasing at a salinity of 7.5.

Laboratory experiments

The first laboratory investigation showed that *T. longicornis* can live and reproduce in a wide temperature range (Fig. 7A, B, C). The mortality rate between 7 and 18 °C was low except for one 12 °C replicate. Above 18 °C the mortality rate was higher than 20 % and increased to 75 % at 22 °C (Fig. 7A). However, the upper temperature limit was probably not reached within the tested temperatures. With the temperature and food conditions offered here no temperature dependence on the ingestion rates were observed. *T. longicornis* ingested between 60000 and 250000 cells female^{-1} day^{-1} (Fig. 7 B). The *EPR* of *T. longicornis* was related to temperature, and the highest *EPR* (3.6 eggs female^{-1} day^{-1}) was recorded at 12 °C. Mean *EPR* with 3 and 4 eggs female^{-1} day^{-1} occurred between 10 and 15 °C. Below 8 °C and above 18 °C *EPR* was reduced to less then 1.2 eggs female^{-1} day^{-1} (Fig. 7C).

The experiments with females of *T. longicornis* in different salinities and constant temperature showed an increasing mortality after 3 days. At the fourth day the mortality was 60 % day^{-1} at salinity 7, while it was between 20 and 40 % day^{-1} at salinity 14 (Fig. 8A). The mortality rate between the different food treatments was not significantly different. *T. longicornis EPR* was higher at high salinities (14) up to 3 eggs female^{-1} day^{-1}, while at salinity 7 the *EPR* remained low, ca 1 egg female^{-1} day^{-1} (Fig. 8B). The *EPR* by females fed nitrogen depleted and sufficient food, respectively, was not significantly different (p = 0.15, ANOVA), although there is a tendency that slightly higher *EPR*s occur with depleted food (Fig. 8B).

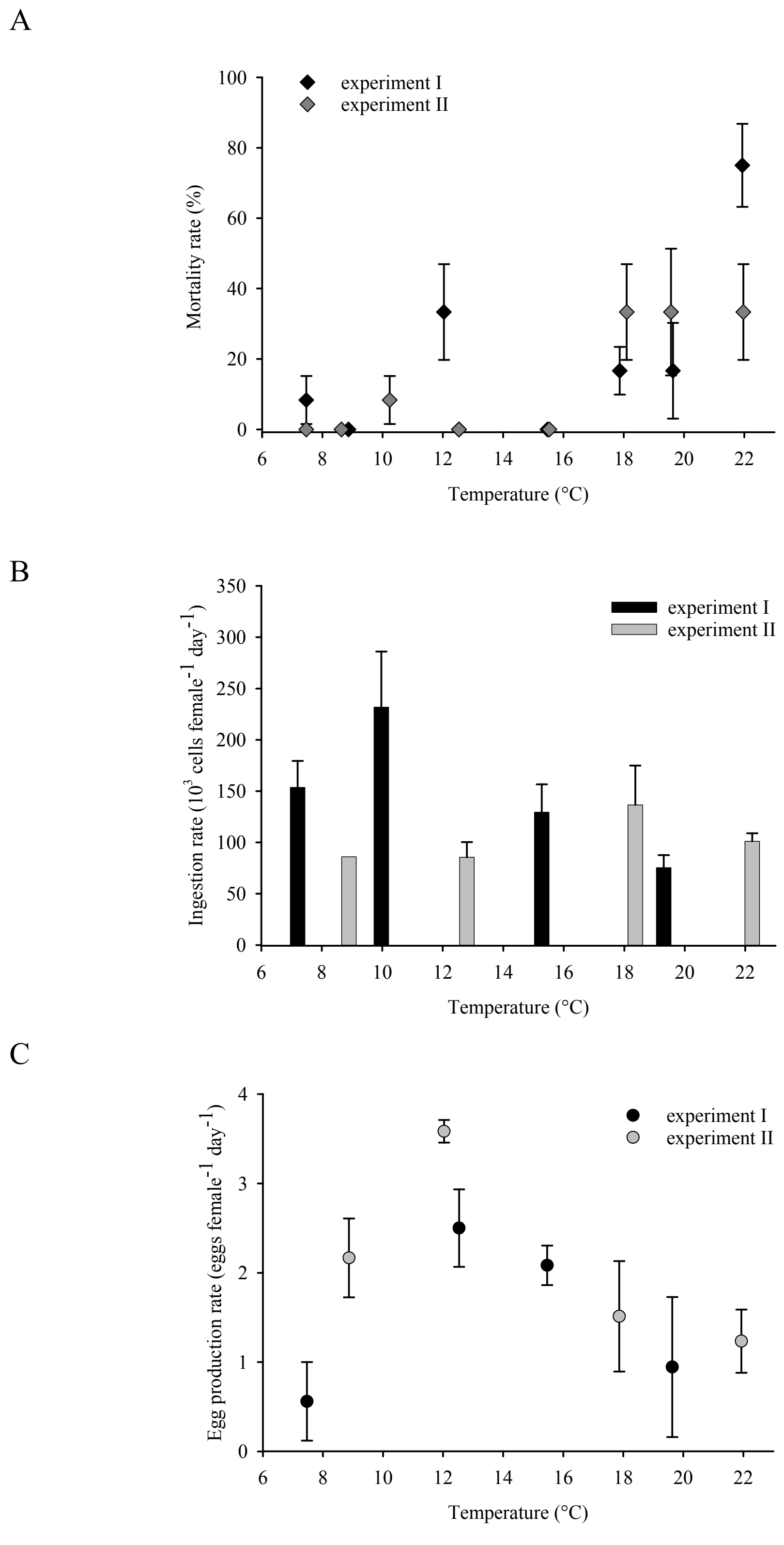
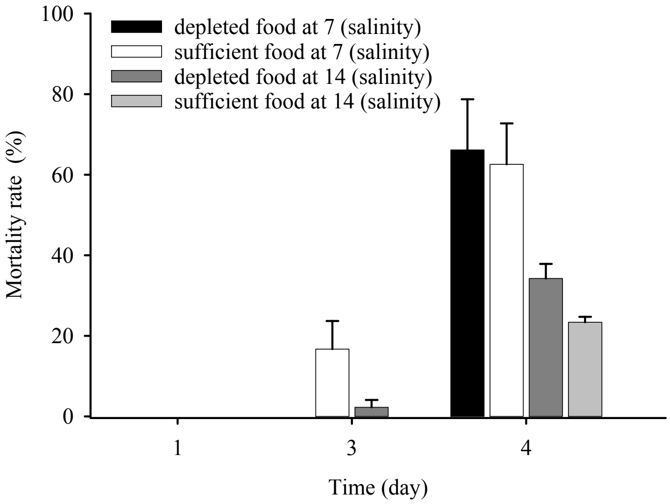


Figure 7. Laboratory reared *Temora longicornis*: incubated at different temperatures feeding on *Rhodomonas* sp.; Panel A mortality rate, Panel B ingestion rate and Panel C egg production rate different filled symbols and bars represent different experiments. Error bars indicate standard error of the mean.

A



B

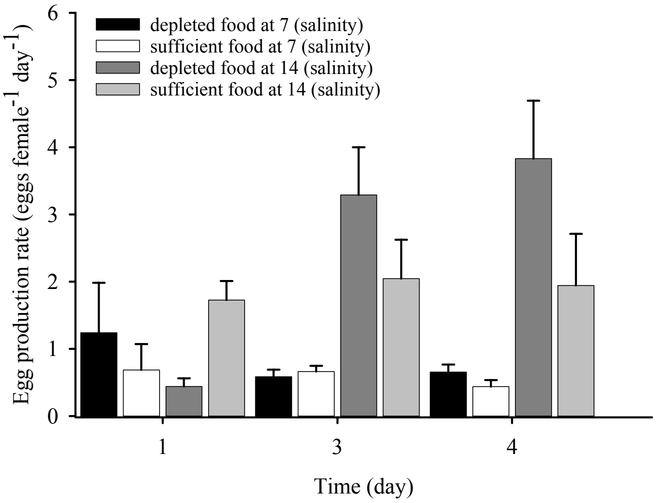


Figure 8. Laboratory reared *Temora longicornis:* incubated with nitrogen deplete and sufficient *Rhodomonas* sp. at salinities of 7 (dark coloured bars) and 14 (light coloured bars); Panel A mortality rate, Panel B egg production rate

4.4. Discussion

The Baltic Sea is characterized by relatively large fluctuations in salinity and temperature related to season and large scale weather systems such as the Northern Atlantic Oscillation (Hänninen et al. 2000, Gustafsson & Westman 2002, Möllmann et al. 2005, Omstedt & Hansson 2006). Thus, marine organisms must cope with both extreme and variable abiotic factors to survive and reproduce in such a brackish water system (Kinne 1964).

The copepod *T. longicornis* is common above the halocline of the Baltic Sea (Fig. 2, and Hansen et al. 2006), as well as in marine systems (Dam & Peterson 1993, Titelman & Tiselius 1998, Halvorsen & Tande 1999, Hansen et al. 2006). *T. longicornis* thus appears to be able to adapt to such brackish habitats above the halocline where the salinity is more stable, but temperature less stable, than below the halocline (Fig. 2). However, the distribution above the halocline could also be due to the higher concentration of algae (Höglander et al. 2004) and other food in this layer, although some other studies found no correlation between the distribution of these copepods and food quantity (Dam & Peterson 1993, Titelman & Tiselius 1998, Köster 2003). Further, the abundance of *T. longicornis* varied widely between the years (Table I) and former investigations have related the changes in abundance to either the variation in surface salinity (Hänninen et al. 2003) or sea surface temperature (Dippner et al. 2000). It is therefore unclear to what extent salinity, temperature and/or food quality and quantity affect the population size, distribution and growth. Therefore a more detailed investigation was required to investigate which of the environmental factors may control the survival and reproduction in this copepod.

Feeding *T. longicornis* from the Bornholm Sea with surplus food concentrations of *T. weissflogii* in summer 2004 resulted in increased *EPR*, compared to *EPR* in natural water. This suggested that they were food limited at this station and time. In general, low food gives poorer physiological status to cope with stress like abnormal salinity (Rippingale & Hodgkin 1977). However, *T. longicornis* fed *T. weissflogii* yielded high *EPR* at both 3 and 10 °C temperatures, while the rates were much lower at 18 °C (Fig. 4). This shows that egg production does not increase in a simple relation to temperature as suggested for a number of copepods by Huntley and Lopez (1992), but that temperature can be overlaid by other factors (e.g. Kleppel et al. 1996a) such as combined salinity-temperature effects (Hall & Burns 2002), and perhaps seasonal development of the gonads (Norrbin 1994).

The copepods from the Arkona Sea showed low mortality rates and *EPR* of 3 eggs female^{-1} day^{-1} independent of a change in salinity. In contrast, the mortality of copepods from the Bornholm and Gotland Seas was high (above 50 %) in a salinity of greater then 18. This result suggests that *T. longicornis* is adapted to the lower salinity at the north Easterly stations and could not cope with a high increase of salinity, whereas this is not the case for the more easterly population. In the Bornholm Sea, the *EPR* of females incubated with *T. weissflogii* in salinity of 7.5 was high, whereas the *EPR* of copepods at the same salinity from the Gotland Sea was low. The *EPR* in the Gotland Sea did not increase after incubation for 3 days. Therefore we conclude that the food limitation was not the main reason for the low rates in the Gotland Sea. In contrast we suggest that the low *EPR* might be due to osmotic stress caused by the low salinity. A reduced fecundity can be caused by osmotic stress (Kinne 1964). Alternatively, since the history of the females is unknown we can not exclude a general low vital condition because of food limitation or a completed reproductive cycle as have been shown for other copepods (Båmstedt et al. 1999).

The laboratory experiments showed a clear relationship between temperature and *EPR* but not with ingestion rate. Temperature dependence in *EPR* is well known (Halsband-Lenk et al. 2002, Maps et al. 2005), but an optimum temperature has not yet been reported for populations in the Baltic Sea. The optimum (12 °C) found here at a salinity of 14 is a typical summer water temperature in the upper water layer, and is close to the laboratory culture conditions the copepods were kept at (15 °C and salinity 14). With increasing temperature above 18 °C the mortality increased. Indeed, some observations show that *T. longicornis* is absent from the upper layer in summer when the temperature is high (Hall & Burns 2002). This can be also a combined effect of salinity and high temperature which has been observed at other euryhaline species (Hall & Burns 2002).

The egg production at salinities of 7 and 14 indicated that *T. longicornis* from the Kiel Bight was better adapted to the higher salinity conditions. The food quality did not influence the *EPR* at the two salinities (Fig. 8). The mortality rate was low in the beginning and increased during the experiment. The increased mortality could, however, be due to stress of the experiment itself. But as the mortality rate first increased at the lower and later at higher salinities, the experimental stress may have been increased by additional salinity stress. With the salinity of 14 the adapted *T. longicornis* shows a slight reaction to food quality. A higher *EPR* at nitrogen depleted food condition has been also shown for other calanoid copepod species (Augustin & Boersma 2006).

We conclude that *T. longicornis* are locally adapted with respect to salinity. Animals from the regions of lower salinity did not survive and reproduce well when exposed to higher salinities. It remains to be seen whether this is a phenotypical adaptation, *i.e.* adapting animals more slowly to other salinities would result in better survival and reproduction, or whether the animals are genetically adapted to the different conditions in the different areas. Further, it is necessary to investigate whether the direction of a salinity change (up or down) affects the response. It could well be that it is more difficult to adapt to an increase in salinity than an decrease (Lee & Petersen 2003). The role of the food quality at low and higher salinity seems to be overlaid effects by other factors. Based on our results, we conclude that *T. longicornis* in the Baltic Sea should select areas and times of the year with a water temperature of 12 °C, that the nutrient content of the food does not play an important role and that especially in the more easterly regions, higher salinities are less optimal. This translates to a life above the halocline where temperatures are around 12-14 °C during large parts of the year, nutrients may become limiting for algal growth, but salinities are lower. This is exactly where we do find *T. longicornis* in the Baltic Sea. Whether this means that other factors, such as predation risk (which is typically higher, at shallower depths), do not play a role shaping the seasonal and spatial distribution of *T. longicornis* in the Baltic Seas remains to be seen. Hence, the results help to understand the distribution of the Baltic *T. longicornis* in marine and brackish waters, and show that further research is needed to clarify the nature of the adaptation of zooplankton to the strongly variable environment in the Baltic Sea.

V. SEASONAL EFFECTS OF TEMPERATURE, FOOD QUALITY AND QUANTITY ON REPRODUCTION OF *TEMORA LONGICORNIS* IN THE NORTH SEA

5.1. Introduction

In marine pelagic food webs mesozooplankton, and in particular copepods often make up the dominating part of the zooplankton biomass, and have a strong influence both as grazers on phytoplankton and as a prey for fish larvae, young fish and jellyfish (Cushing 1990, Kiørboe 1998, Stenseth et al. 2002). The main parameter influencing population dynamics of calanoid copepods apart from mortality is the birth rate. Even though the factors that influence egg production are well established, the relative influences of such factors as food quantity, food quality and temperature are still under much discussion (Ianora 1998, Paffenhöfer et al. 2005). Some investigations on the effect of temperature conclude that temperature is the main driver and is more important than the effects of food (Uye & Shibuno 1992, White & Roman 1992, Campbell et al. 2001, Halsband & Hirche 2001, Shreeve et al. 2002, Lee et al. 2003). However, other studies have shown that egg production was not always related to, or even showed negative correlations to temperature (Bautista et al. 1994, Hay 1995b, Gomez-Gutierrez et al. 1999, Koski & Kuosa 1999, Burdloff et al. 2002, Gorokhova 2003, Devreker et al. 2005). A number of experimental studies have shown that copepod egg production is affected by both food concentration and food quality (e.g. Ambler 1986, Støttrup & Jensen 1990, Kleppel 1993, Sterner et al. 1993, Jónasdóttir 1994, Klein Breteler et al. 1999, Urabe & Sterner 2001, Jónasdóttir et al. 2002, Maps et al. 2005, Poulet et al. 2006). Two main schools exist with contrasting views on the factors that determine the quality of the food. It is still under much discussion whether (and when) essential elemental or biochemical components are the main determining factors of food quality. As a result, some authors use C:N contents and ratios of the food while others use fatty acid composition to relate to copepod egg production (Pond et al. 1996, Sterner & Schulz 1998, Boersma 2000, Müller-Navarra et al. 2004, Hessen & Elser 2005).

In the North Sea, *Temora longicornis* (Müller 1785) is one of the most abundant calanoid copepod species and present in the zooplankton during the whole year (Halsband-Lenk et al. 2004). *T. longicornis* is an omnivore that can feed selectively (Cotonnec et al. 2001, Guisande et al. 2002, Koski et al. 2005). There are several laboratory studies investigating the effect of food quality of *T. longicornis,* using different mono-algal diets (Debs 1984, Dam & Lopes 2003, Arendt et al. 2005). Moreover, in several field studies reproduction has been correlated with C:N ratio or fatty acid composition of the seston (Bautista et al. 1994, Hay 1995a, Jónasdóttir et al. 1995). The main problem with these correlative studies is that they do not account for co-linearity between different factors. For example, changes in nutrient conditions for the algae often induce changes both in the biochemical composition of the algae as well as changes in total food concentration. Therefore, experimental approaches are needed to assess whether and when food quantity or quality is the most important factor in the field. Hence, in this study we investigated the effects of seasonal changes in temperature, food quality and quantity on *EPR* of *T. longicornis* in a combination of using natural food and in addition of single phytoplankton species containing different food quality properties.

5.2. Material and methods

The experiments took place at the Biologische Anstalt Helgoland. Between April 2004 and April 2005 monthly samples were taken with the research vessel FK "Aade" on the Helgoland Roads (Fig. 1).

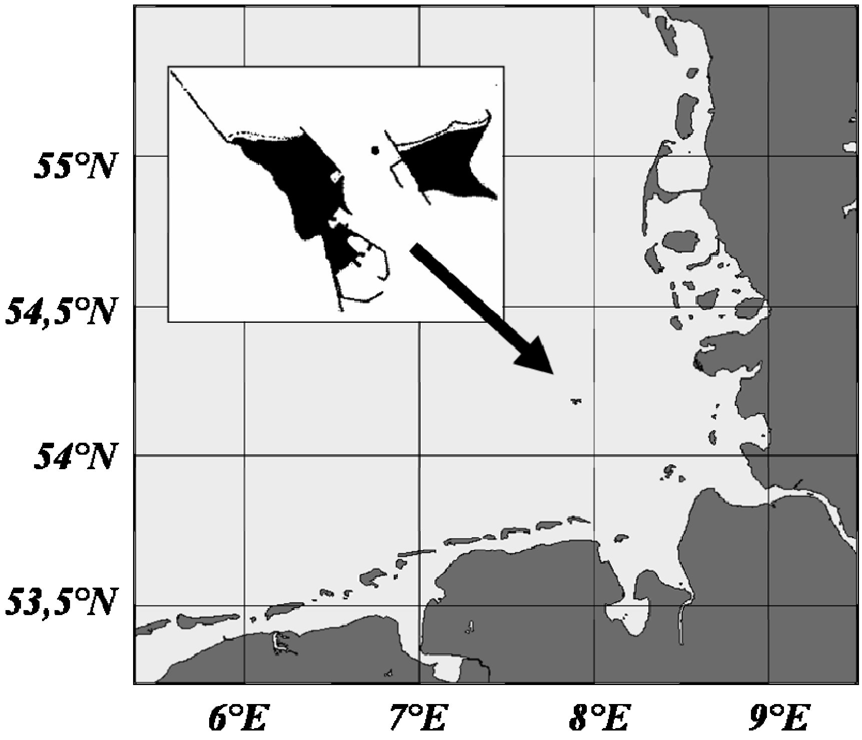


Figure 1. Position of the sampling station at Helgoland Roads in the German Bight is denoted by the black point between the two islands.

Phytoplankton samples were taken, well mixed and preserved with Lugol's solution. An aliquot of 25 ml was counted under an inverted microscope using the Utermöhl method Water samples for fatty acids and C:N contents of the seston were taken in buckets. For estimation of the C:N content and the fatty acid content of the seston, water was filtered on pre-combusted GF/C filters (Whatman) at low pressure and stored at -20°C and respectively -80 °C for further analysis.

Additionally, 200 l natural sea water was collected for the experiments. The sampled sea water was immediately transported to a temperature-controlled room and filtered gently through a 100 µm net. Dark:light rhythm and temperature of the room was similar to the ambient field conditions. The seawater was stored in a tank, and used in the consecutive days of the experiments. Cultures of *Rhodomonas* sp. and *Dunaliella* sp. were grown in f/2 media without silicate (Guillard 1975b) and kept at 12:12h light : dark rhythm with constant 16°C. Shortly after sampling *T. longicornis* females and males were sorted under a microscope in a temperature controlled room, and were incubated in 1 l bottles at a plankton wheel with 1 rpm. Four different treatments were investigated simultaneously (Table I).

Table I. Overview of the 4 different food treatments and its properties.

Treatments	Additions to the natural food	Quantity	Quality
1	No addition	natural	only natural
2	Enriched by doubling natural seston > 10µm	enriched	only natural
3	*Rhodomonas* sp.	enriched	high
4	*Dunaliella* sp.	enriched	low

The food suspension with "double" concentrations of natural seston were prepared by gently filter away half of the volume of water trough a 10 µm net Using this method we obtained double the concentration of the natural plankton composition in the prey field of *T. longicornis* (Dutz unpublished).

Two treatments consisted of natural sea water and an addition of 500 µg C l^{-1} cultured algae, which is a saturated food concentration (Koski & Breteler 2003, Maps et al. 2005). In one series the natural seawater was enriched with cultures of the chlorophyte *Dunaliella* sp., while the other treatment consisted of sea water enriched with *Rhodomonas* sp. In comparison *Dunaliella* sp. contains less essential fatty acids than *Rhodomonas* sp. (Koski & Breteler

2003). For the egg production experiment, we incubated 10-15 females and 3-5 males in each of 5 replicates. The experiments were done under similar condition as the natural conditions at the day of sampling. Copepods were adapted for three days, previous to the experiment. Every day food was renewed and females were transferred gently. Dead females were removed. For egg production measurements females were sorted in 100 µm sieves kept in 1 l beakers. After 24 h eggs were removed and counted to calculate the egg production rate. Hatching success was calculated by counting the eggs after 24 h. After every experiment 10-30 females were photographed under a microscope with a digital camera system (Olympus). Afterwards the mean body length of the copepod was estimated by measuring the length of the cephalothorax with analySIS an image analyzing pc program (® SIS GmbH).

The carbon concentration and C:N ratio were measured with a Fisons EA 1108 CHN analyser. Lipid extraction was performed with minor modifications as described in von Elert (2002) using ultrasonic disruption in dichloromethane:methanol (v/v:2/1), silicate and a washing procedure with aqueous KCl solution (0.88 %). For quantification of fatty acids, 13:0 and 23:0 fatty acids were added as internal standards prior to extraction. The water phase was removed and the organic remainder was evaporated using nitrogen gas. The esterification was done using methanolic sulphuric acid at 70 °C for 30 min (von Elert 2002). The FAMEs were washed from the methanolic sulphuric acid using iso-hexane. Excess hexane was evaporated using nitrogen gas. All chemicals used were suprasolv or GC grade. FAMEs were analysed by gas chromatography using a Varian CP 8400 gas chromatograph equipped with a DB-225 column (J&W Scientific, 30 m length, 0.25 mm ID, 0.25 µm film). The FAMEs were detected by flame ionization and identified by comparing retention times with those derived from standards of known composition.

Statistical analysis

Initially, to examine the effect of temperature, prosoma length, and food treatment on egg production, the following general linear model (glm) was employed:

$$y_{tlf} = \mu_0 + k_1 T_t + k_2 L_l + k_3 (T_t L_l) + F_f + e_{tlf} \qquad \text{Eq. 1.}$$

y_{tlf} denotes egg production at the tth temperature (T), of an individual of lth length (L), receiving the fth food treatment (F). μ_0 is the overall intercept, k denotes constants and e_{tlf} is the unexplained error. T_tL_l is the interaction term between prosoma length and temperature. The model assumes a linear relationship between egg production, prosoma length and temperature modified by the food treatment received. The NLME library of Splus was used for this test (Pinoheiro & Bates 2000). Subsequently, to i) examine the effect of the actual nutrients (e.g. C and N) in the food treatments on egg production and ii) identify the most important factors affecting egg production, we performed two separate stepwise backwards regressions; the first including temperature, length, carbon and nitrogen food concentration as independent variables and the second using temperature, length and C:N ratio as independent variables. Egg production was used as the dependent variable in both analyses. The first analysis allowed us to compare the effect of C and N, while the second allowed us to estimate the effect of C:N, a common measure of food quality (Hessen & Elser 2005). These analyses were done by the use of STATISTICA 7.0 (Statsoft inc.) To linearize the effects, all data were ln-transformed before applying the different models.

After having established the overall significances of explanatory variables, we concentrated on different seasons. Especially, the post bloom warm summer situation contrasted with the pre-bloom colder winter. Hence, we analysed whether there was a significant difference between the treatments in these periods. A different response between natural seston and enriched seston would indicate that the quantity of the food determines reproduction, as more of the same invokes a reaction. Non-significant differences between these two treatments, but at the same time a higher egg production with added algae, means that the quality of the food is limiting egg production.

5.3. Results

Environmental conditions

The Helgoland Roads sampling station (54°11.3'N, 7°54.0'E) is characterised by a shallow water depth and strong currents that provide a well-mixed water column. From March 2004 until April 2005 the temperature varied from 2.6 to 19.3 °C (Fig. 3). The maximum temperature occurred in August, and the coldest in March. This range is within previous reported long term temperature data (Wiltshire & Manly 2004). The carbon concentration of the natural seston ranged from 231 to 728 $\mu g\ C\ l^{-1}$ and showed three peaks during the investigated period (Fig. 4). The first small peak in May 2004 was concurrent with a small

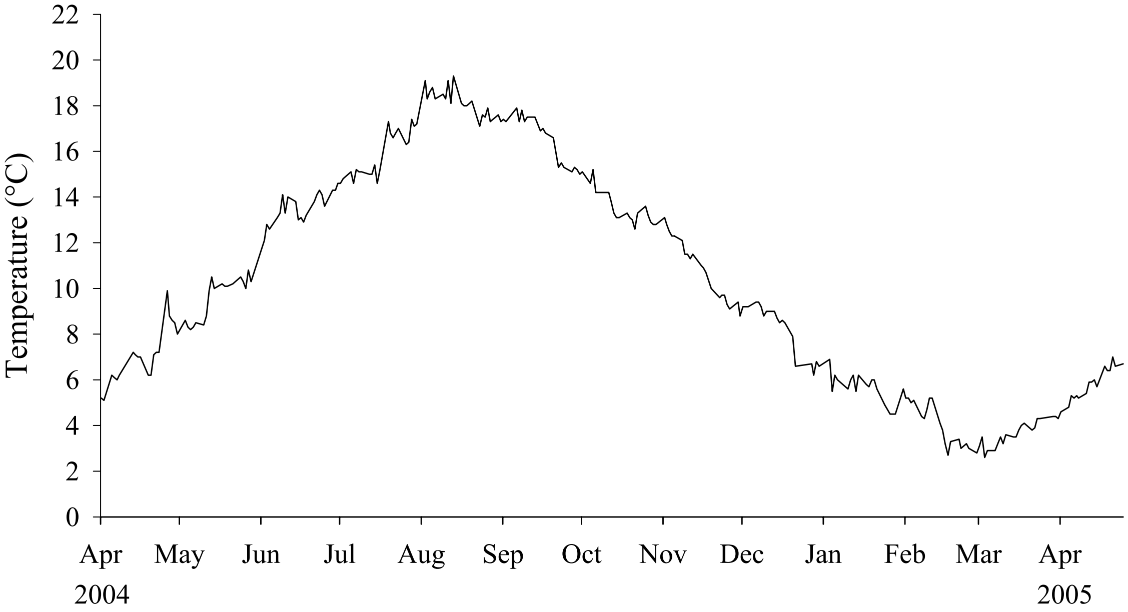


Figure 2. Water temperature during the sampling period at the Helgoland Roads.

increase of diatom carbon, the second in August 2004 coincided with an increase in both diatom carbon and particulate nitrogen concentration, while the third peak in January 2005 declined before the spring bloom diatom carbon reached the highest levels at the termination of the investigation in April 2005 (Fig. 3).

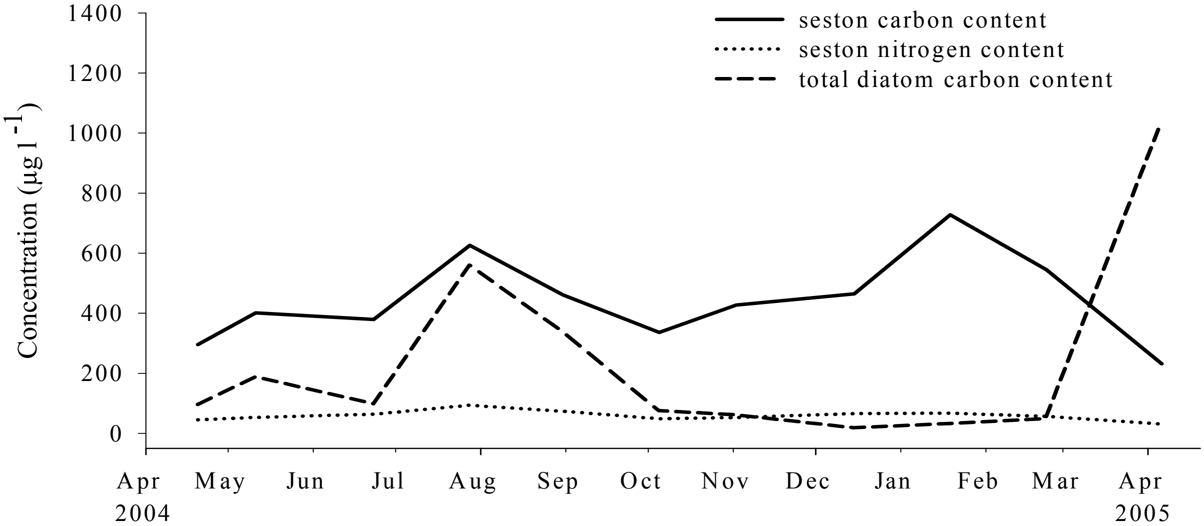


Figure 3. Concentration of seston carbon, seston nitrogen and total diatom carbon during the sampling period at the Helgoland Roads.

The saturated fatty acids (SFA) in the water column increased in May 2004 and were still high in August and decreased to a minimum between October 2004 and January 2005 (Fig. 4).

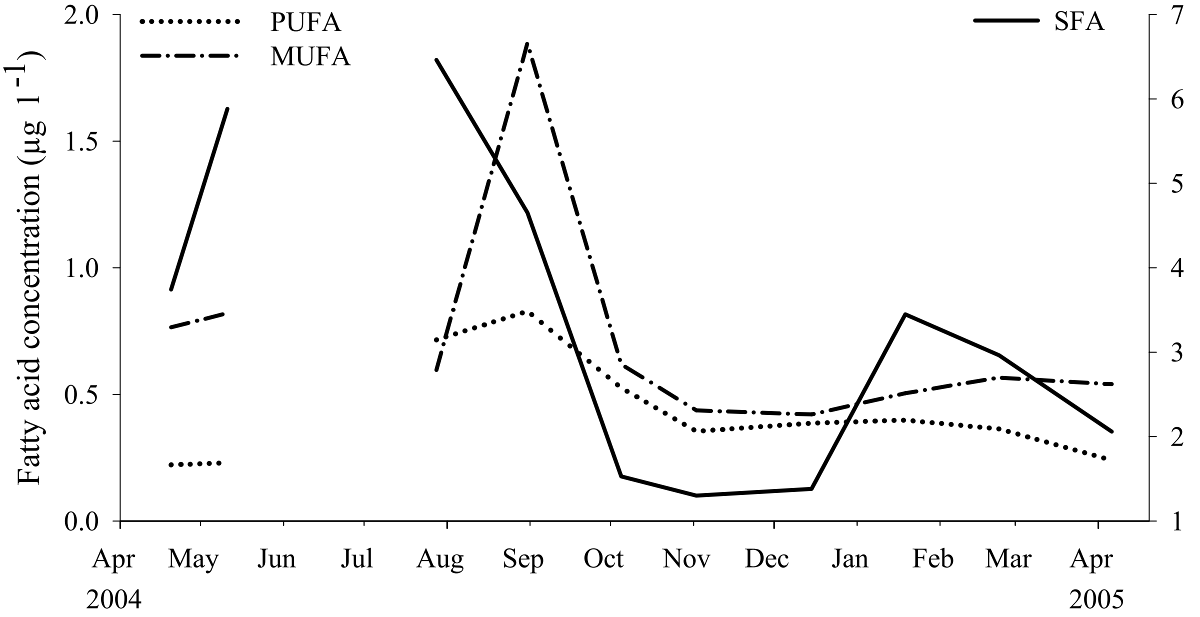


Figure 4. Concentration of saturated fatty acids (SFA), monounsaturated fatty acid (MUFA) and polyunsaturated fatty acids (PUFA) during the sampling period at the Helgoland Roads.

The polyunsaturated fatty acids (PUFA) showed only one peak in September 2004 during the end of the autumn bloom of diatoms. This peak was dominated by the content of EPA and DHA, which showed the highest concentration of 4.9 and 3.1µg FA l^{-1} respectively at this time (Fig. 5).

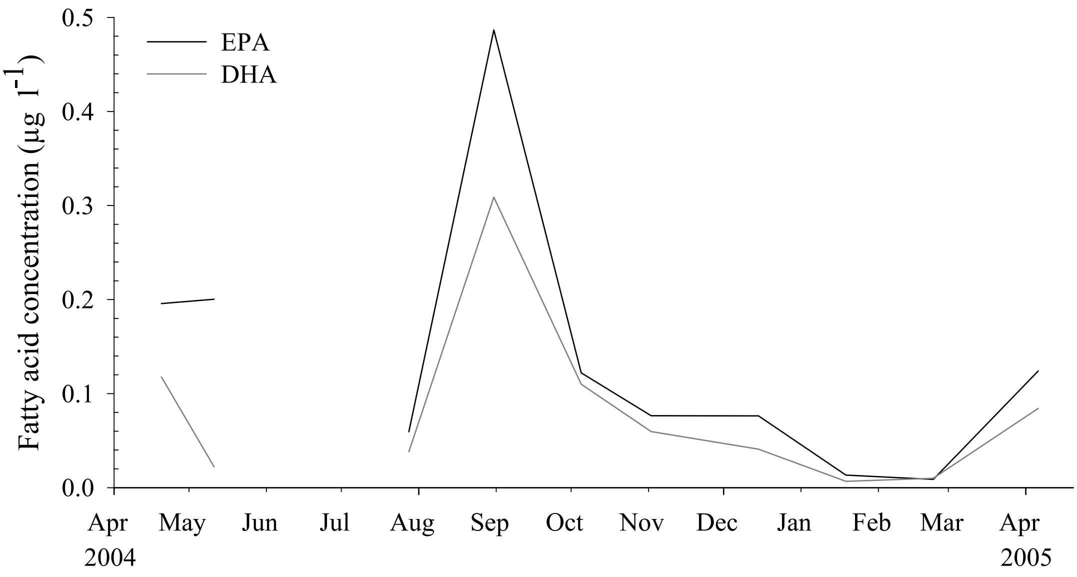


Figure 5. Content of EPA and DHA in the natural seston during the sampling period at the Helgoland Roads.

The food quantity measured as carbon concentration was higher in all treatments with added phytoplankton cultures, whereas the enrichment with > 10 µm natural seawater resulted in increased concentrations except in August and April 2005.

The lowest and least variable molar C:N ratios (4.5 – 6.1) were found in the food enriched with *Rhodomonas* sp. (Fig. 5), The three others varied more and the natural plankton assemblage ranged from 5.1 to 9.3 and showed the highest C:N ratio.

Copepod size and egg production

T. longicornis females were present in all samples except in early August, when the concentration was too low for experiments. The average copepod body length varied between 890 and 1174 µm. The largest were found in April 2004 and the smallest in October (Fig. 6).

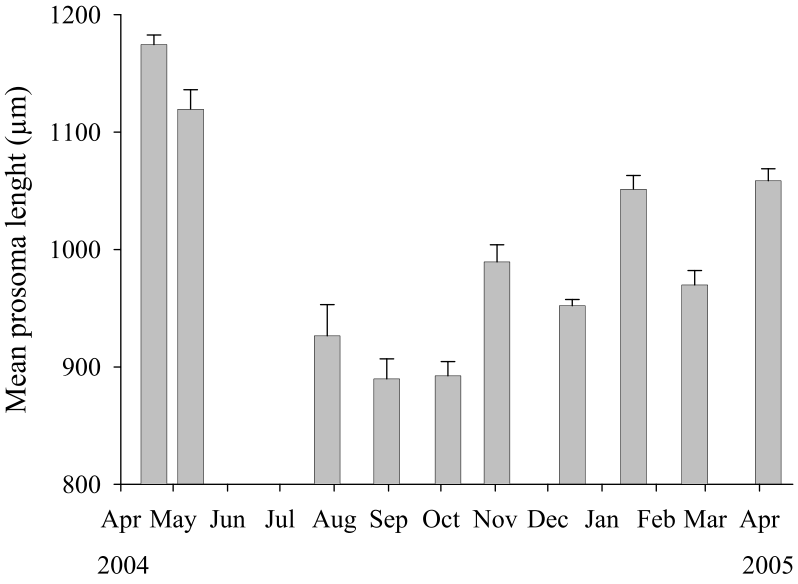


Figure 6. Prosoma length of *T. longicornis* during the sampling period at the Helgoland Roads.

The females of *T. longicornis* produced eggs throughout the investigated period. The highest *EPR* recorded was 12, 10, 14 and 15 eggs female^{-1} d^{-1} in natural seston, double seston, seston with *Dunaliella* sp., and seston with *Rhodomonas* sp., respectively (Fig. 3). The overall lowest *EPR* was recorded in late (31) August 2004 (1.2-4.2 eggs female^{-1} day^{-1}) and late January 2005 (0.5-2.5 eggs female^{-1} day^{-1}).

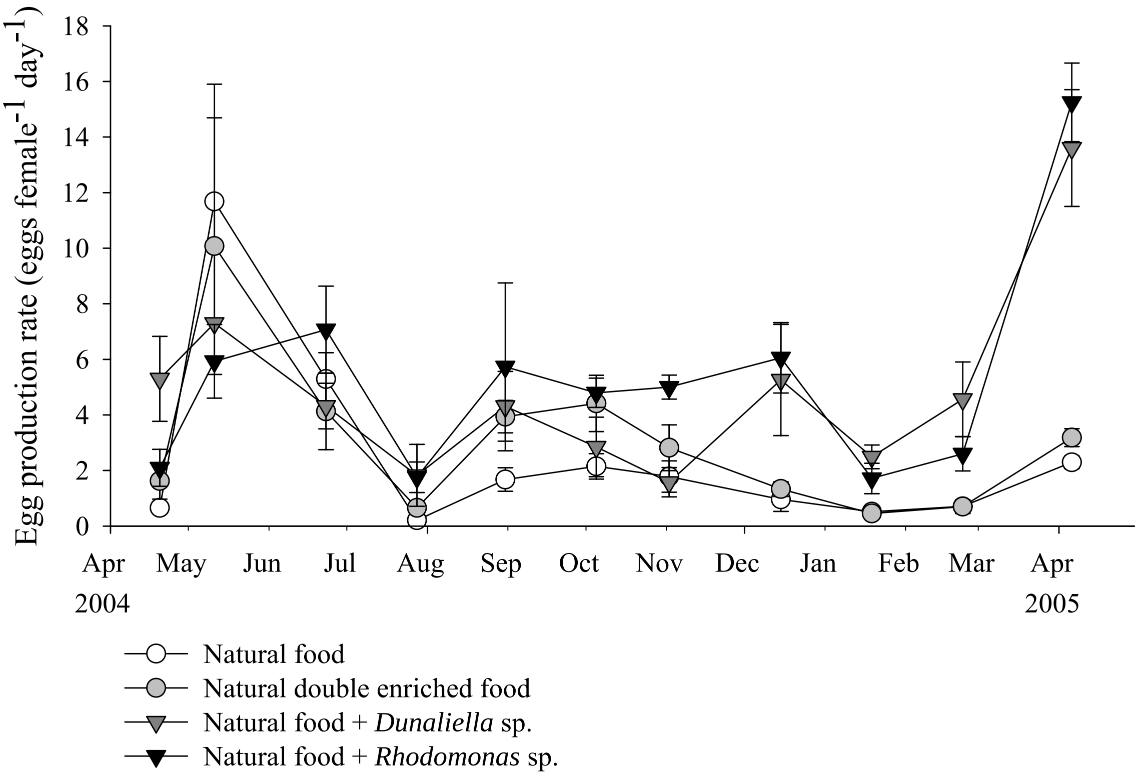


Figure 7. Egg production rate of *T. longicornis;* different colours represent the treatments, different symbols represent natural food (circle) and with addition of cultured algae (triangles). Error bars represent the Standard error of the mean.

The general linear model (Eq. 1) found temperature to be non-significantly (p = 0.09), positively correlated to *EPR*, while prosoma length and food treatment had a significant ($p < 0.05$) positive effect on *EPR*. No significant interaction effect of length and temperature was found (p = 0.10), which also was visible when comparing the egg production versus temperature (Fig. 8). Tukey post-hoc tests showed that both the food treatments with added algae significantly increased *EPR* ($p < 0.05$) compared to natural seston, while no significant overall effect on *EPR* was found between any other treatments.

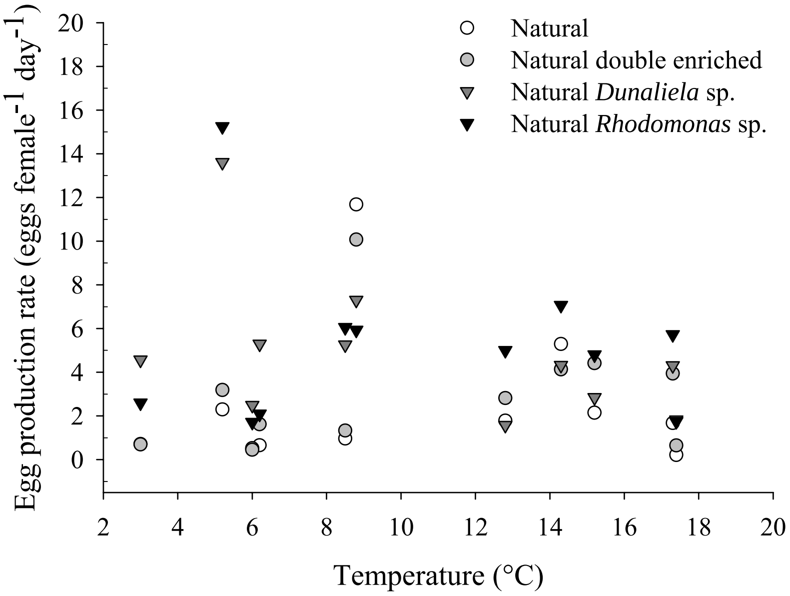


Figure 8. Egg production versus temperature of *T. longicornis;* different colours represent the treatments, different symbols represent natural food (circle) and with addition of cultured algae (triangles).

Having established that food treatment was important for the *EPR*, we tested the combined effects of temperature, length, and food carbon and nitrogen for the reproductive output, using stepwise backwards regression. This analysis left only length and food nitrogen content as significantly (p = 0.02 for both), positively correlated to *EPR* (p = 0.04). Together, these two variables explained ca 16% of the variation in the data (r^2 = 0.163). The analysis including length, temperature and C:N ratio as independent variables again left length as positively correlated to *EPR*, while C:N ratio was significantly, negatively correlated to *EPR* (p = 0.015). These two variables explained approximately 17 % of the variation in *EPR* (r^2 = 0. 174).

This suggested that temperature was not a strong factor regulating the egg production by the omnivorous *T. longicornis* at the sampled station (Fig. 8). However, *in situ* food concentrations (in terms of N) was in general limiting for the *EPR*, there was a general increase in *EPR* with increasing food quality (in terms of decreasing C:N ratio), and larger individuals produced more eggs than smaller in comparable food environments.

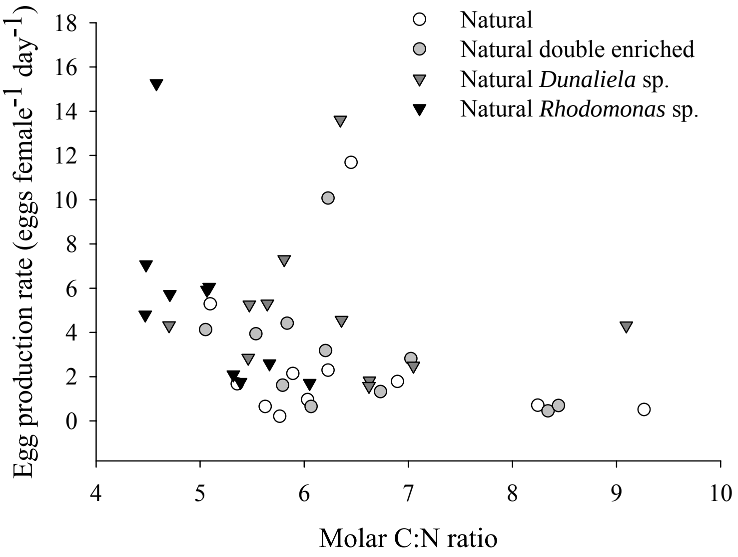


Figure 9. Egg production versus C:N ratio of *T. longicornis;* different colours represent the treatments, different symbols represent natural food (circle) and with addition of cultured algae (triangles).

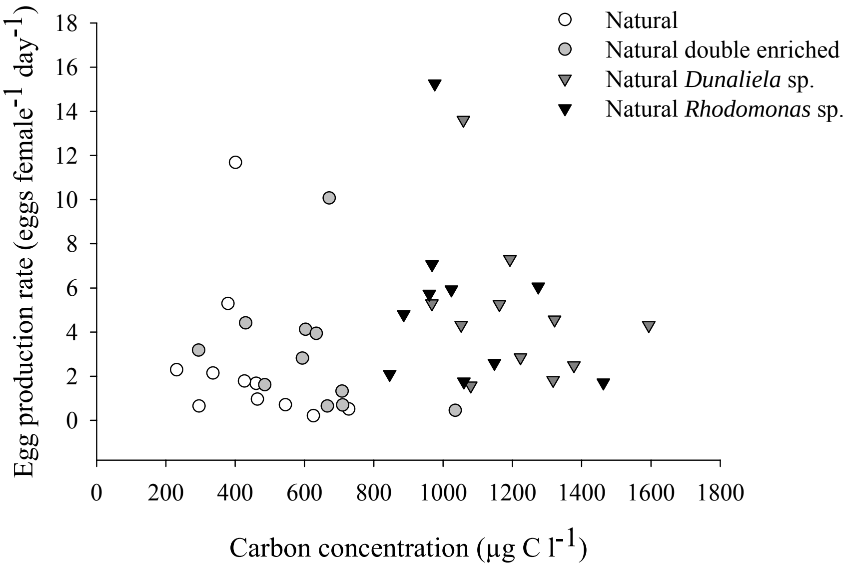


Figure 10. Egg production versus carbon concentration of *T. longicornis;* different colours represent the treatments, different symbols represent natural food (circle) and with addition of cultured algae (triangles).

Effects of food quality versus food quantity in different seasons.

The periods of spring and summer diatom blooms May-July 2004 showed a very variable pattern in *EPR*, with opposite response in *EPR* to the two diatom maxima in May and July, respectively. In contrast, the warm (14-18 °C) post-diatom period (Aug-Oct 2004) showed a significantly lower *EPR* in natural seston than in all other food treatments (2-way ANOVA, $p < 0.02$, and Fishers PLSD, $p < 0.04$), and there were no significant difference between treatments with added algae, compared to the double seston treatments (Fishers PLSD, $p > 0.35$). This indicates that the *EPR* was mainly limited by low overall food concentrations *in situ* during the fall post-diatom period (Fig. 10).

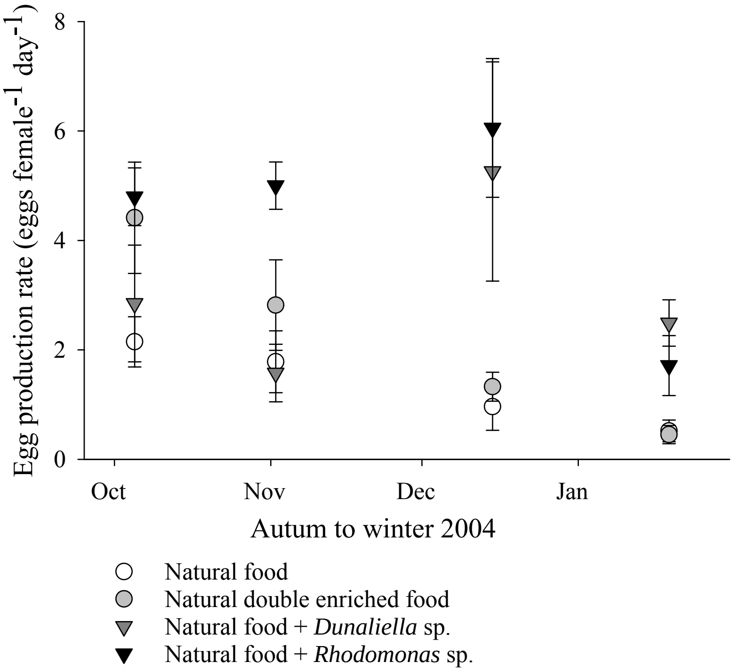


Figure 11. Egg production in the autumn and winter 2004 of *T. longicornis;* different colours represent the treatments, different symbols represent natural food (circle) and with addition of cultured algae (triangles).

In contrast, during the cold (4-8 °C) winter pre-diatom period (Dec 2004-Feb 2005) *EPR* appeared to be limited by food quality, rather than quantity; both the treatments with added algae showed significantly higher *EPR*, compared to natural seston (2-way ANOVA, $p < 0.0001$, and Fishers PLSD, $p < 0.0008$), but there were no significant difference between the natural seston and doubled natural seston (Fishers PLSD, $p > 0.85$)(Fig. 11).

5.4. Discussion

The aim of this study was to investigate the combined effects of temperature, food quality and quantity of *T. longicornis* over one annual cycle. Our results did not support previous observations that temperature has a strong impact on *EPR* in the field and in laboratory studies of copepod reproduction (Huntley & Lopez 1992, Calbet & Agusti 1999, Halsband-Lenk 2001, Castro-Longoria 2003). Instead, our results support the conclusion that copepod reproduction in the sea is more strongly controlled by a number of factors including food quantity and quality (Lawrence & Sastry 1985, Bautista et al. 1994, Maps et al. 2005, Castellani & Altunbas 2006). Although the temperature did not appear to influence the *EPR* significantly in this investigation, it is known that temperature does influence a number of metabolic processes not measured here, and may therefore have impacted the copepod *EPR* indirectly partly decoupled over time. Such effects would not be disclosed in the simple linear models used here. A commonly reported effect is the influence of temperature on the growth and prosoma length over a time (Runge 1984, Devreker et al. 2005).

The copepod body length varied between 890 and 1174 µm, with the largest animals found in April 2004 and the smallest in October (Fig. 4), which was also observed earlier (Halsband-Lenk 2001). There was a strong positive correlation between body size and *EPR*. This is in concert with previous literature showing that the maximum *EPR* is limited by the length of the prosoma (Lin & Li 1988, Hopcroft & Roff 1998, Devreker et al. 2005). The highest *EPR* recorded in natural seston was 12 eggs female^{-1} d^{-1}. The *EPR* was below 1 egg female^{-1} day^{-1} was measured in June, August and in winter from December to February (Fig. 3). These results are slightly lower than previously reported (Halsband-Lenk 2001, Laakmann 2004).

General effects of food quality and quantity throughout the seasons

Our data indicate that both total food concentration (in terms of particulate nitrogen) and food quality measured as C:N ratio had positive effects on *EPR*. However, as these measurements are partly correlated, these results should be interpreted with some caution. Indeed, in stoichiometric based investigations of food quality the effects of food quantity and quality are not always easily distinguished from each other (Sterner & Schulz 1998).

In a previous study with *A. tonsa* and *A. clausii* fed on controlled cultures of *Rhodomonas* sp. grown in full f/2 medium and nitrogen deficient f/2 medium, respectively (Augustin & Boersma 2006) showed that the N-deficient cultures (molar C:N ratio = 9) supported higher *EPR* than algae from the full medium (C:N = 4.5) at similar food concentrations. These initially surprising results are supported by the recent dynamic energy budget model Kuijper et al. (2004) that shows a dome-shaped reaction to prey C:N ratio with a gross growth efficiency for N increasing from prey with a C:N ratio at 5, peaking between 10 and 15 and decreasing again at higher ratios. These results were further supported by results of (Urabe & Watanabe 1992) and (Boersma & Elser 2006) suggesting a higher egg production at a prey C:N ratio around 10 compared to at < 5, due to a combination of different C and N requirements for maintenance and reproduction.

How do these data relate to the field data found here and elsewhere? One possible explanation could be that in situations with high C:N ratios most of the seston is of low quality (high C:N ratio) due to a combination of generally limiting nutrient conditions for all plankton leading to a high grazing pressure on the particles with lowest C:N ratio, again resulting in a uniform high C:N ratio (assuming also low trophic upgrading due to a general lack of the basic elements in the system). While in the opposite case with a low overall C:N ratio there would still be detritus and particles with relatively high C:N ratio around, but also potential prey with low C:N ratio, and abundant elements in the ecosystem supporting recombination through e.g. trophic upgrading etc. However, such interactions would need to be carefully investigated in future studies, preferably utilising specific methods where individual of prey could be directly investigated.

Effects of food quality versus food quantity in different seasons.

The periods of spring and summer diatom blooms in May-July 2004 showed a very variable pattern in *EPR*, with completely different responses during the two diatom maxima. Interestingly the highest abundance of diatoms in 2004 coincided with an overall minima in *EPR* in July, while during the smaller May diatom maxima the *EPR* was the highest registered that year, and the food treatments gave an effect opposite to all other dates in the investigation: the highest *EPR* with natural seston, followed by doubled seston, added *Dunaliella* sp. and added *Rhodomonas* sp. showing the lowest *EPR*. This could indicate a food inhibition effect by other biochemical components than aldehydes (Poulet et al. 2006). However, this needs to be further investigated in future studies.

In contrast, comparing the different periods with lower food abundance, the warmer autumn post-diatom period (Aug-Oct 2004) with the winter pre-diatom period (Dec-Feb 2005) showed more clear trends. In autumn all additions of food, including the doubled natural seston, resulted in similarly increased *EPR* in all increased food treatments. This suggests that food quantity was a limiting factor during late summer-early fall, and is in concert with previous studies (Calliari et al. 2004). In contrast, during winter there was no increase in *EPR* in doubled seston, but a significantly higher *EPR* in both treatments with added phytoplankton. This suggests that food quality was limiting during the winter period. In fact, other authors reported similar effects of food quality in spring and autumn (Park & Lee 1995). However, despite the fact that species of *Rhodomonas* and *Dunaliella* often have been reported to be a high and low quality food, respectively (Støttrup 1990, Irigoien et al. 2002), I observed no differences between the species in any of the seasons. The most likely explanation for this finding is that either alga substituted with natural seston are a very good resource, and the cultured algae and the seston act as complementary resources.

Hence, we conclude that overall, temperature is not significantly correlated with reproduction in *T. longicornis*. We have also shown that there are distinct seasonal changes in the importance of the different factors influencing reproduction. Further combined studies on reproduction of copepods in the field and with laboratory experiments using multi-species diets are necessary to understand the complex relation between temperature and different aspects of the food for the population dynamics of *T. longicornis*.

VI. GENERAL DISCUSSION

6.1. Factors controlling the population dynamic of zooplankton

Trophic relationships in pelagic ecosystems are influenced by a range of environmental factors. The most important factors influencing the zooplankton populations and their distribution are generally considered to be temperature, salinity, food and predation (e.g. Mangel & Clark 1986, Huntley & Lopez 1992, Hall & Burns 2002), whereof aspects of the first three factors are investigated this thesis.

Copepods dominate the zooplankton biomass in pelagic food webs and are main consumers of phytoplankton and protozooplankton (Stoecker & Capuzzo 1990, Sommer & Stibor 2002), while they are also important as a prey for fish larvae, young fish and jellyfish (Cushing 1990, Kiørboe 1998, Stenseth et al. 2002). Understanding the characteristics and drivers of environmental introduced fluctuations in copepod populations provide opportunities for adaptive management of the resources in our aquatic systems (Armitage et al. 1973). Population dynamic is mainly determined by rates of reproduction, growth and mortality (Ohman & Wood 1995, Ohman & Hirche 2001, Edvardsen et al. 2002).

This thesis mainly focuses on the reproductive response in some copepods, and some observations on mortality in relation to environmental factors are presented. Reproductive rates in copepods also relate to growth, because the adult copepods do not grow but use most of their excess energy from food intake for reproduction. This is often seen as an approximation of copepod growth. However, it has been shown that copepod growth rates estimated through egg production rates of adults may not always be equivalent to juvenile growth (Calbet et al. 2000). Thus caution should be exercised when estimating growth from reproduction rates.

6.2. Abiotic factors

Copepods may migrate vertically up to hundreds of meter daily (Mauchline 1998) and must thus be adapted to the variable physical and chemical environment in the sea. This is especially true in coastal areas, where variability in these factors is much wider than in the open sea. Recent investigations suggests that the most important factors controlling the reproduction and growth in marine systems is temperature, while in brackish systems the salinity is assumed to be a stronger factor (Huntley & Lopez 1992, Hall & Burns 2002). However, the results presented here did not support the conclusion that temperature had a strong impact on copepod reproduction, which is in accordance with other literature (e.g. Kiørboe & Nielsen 1994, Hay 1995b, Kleppel et al. 1996b, Gomez-Gutierrez & Peterson 1999, Devreker et al. 2005).

Salinity

Especially in the brackish areas like the Baltic Sea, salinity is an important factor that limits the distribution of different organisms (Remane & Schlieper 1958). For crustaceans, as most other organisms, salinity is known to cause osmotic stress by influencing several metabolic processes and interacting with other environmental factors (Anger 2003). In the Baltic Sea, recent correlations have shown that the abundance of calanoid copepods can be related to temperature and salinity (Möllmann et al. 2003). The salinity may also affect the population indirectly, by limiting the growth or hatching success of calanoid copepods (Holste & Peck 2006). Experimental results in this thesis suggest that *T. longicornis* may be locally adapted with respect to salinity. Animals from the regions of lower salinity did not survive and reproduce well when exposed to higher salinities. Comparing females from the Arkona, Bornholm and Gotland Seas, copepods from the Bornholm Sea treated with a lower salinity (7.5) than *in situ* (8) showed the highest *EPR* (6.2 eggs female $^{-1}$ day^{-1}). While lowest *EPR* of 2.2 eggs female^{-1} day^{-1} were found with individuals from the Gotland Sea exposed to higher salinities of 20. *T. longicornis* from the Kiel Bight reared at salinity of 12 also showed significantly highest *EPR* at salinities close to that of the environment it was caught and cultured in.

This gives a first suggestion of local adaptation to salinity of *T. longicornis* in this environment. However, it remains to be seen whether this is a phenotypical adaptation, e.*g.* adapting animals more slowly to other salinities would result in better survival and reproduction, or whether the animals are genetically adapted to the different conditions in the different areas. Further, it is necessary to investigate whether the direction of a salinity change (up or down) affects the response. It could well be that it is more difficult to adapt to a decrease in salinity than an increase. Further, the role of the food quality at low and higher salinity seems to be overlaid by salinity effects like osmotic stress. However, e.g. common garden experiments specifically testing adaptation are necessary to determine whether these species are genetically adapted, or not. In addition to the direct effects of single factors such as those investigated here, synergetic effects due to combination of low food or temperature is possible and should be accounted for.

Temperature

In the North Sea *EPR* of *T. longicornis* were measured at *in situ* temperatures that varied between 2.6 to 19.3 °C. In the Baltic Sea the temperature varies within a similarly wide seasonal range (from 0 up to around 20 °C) in the surface layer (Wasmund & Uhlig 2003). Thus, considering the relatively large seasonal variations in temperature they could have a large potential effect on the copepod populations. On the other hand copepods like *Acartia* spp. and *Temora* spp. with the capability to migrate vertically might be able to avoid unfavourable water layers (Hay et al. 1991, Hansen et al. 2006).

Comparing data from the whole season, temperature only showed a weak (non significant) positive correlation to *EPR* in Helgoland Roads (Chapter V). Similarly, the results from the Baltic Sea (Chapter IV) did not support previous observations that temperature may have a strong impact on copepod *EPR* in laboratory studies, in these (Fransz et al. 1989, Halsband-Lenk 2001) and other areas (Huntley & Lopez 1992, Calbet & Agusti 1999, Halsband-Lenk 2001, Castro-Longoria 2003). Instead, our results support the conclusions that copepod reproduction in the sea may be strongly controlled by a number of factors including food quantity and quality (Lawrence & Sastry 1985, Bautista et al. 1994, Maps et al. 2005, Castellani & Altunbas 2006). Although, there was no simple correlation between temperature and *EPR* in the copepods from the sea in this thesis, there was a clear dome shaped relationship between temperature and *EPR* in reared *T. longicornis* from the Kiel Bight that indicates a more complex relationship to temperature. It is known that temperature influence a number of metabolic processes not measured here, that may have impacted the copepod *EPR* indirectly partly decoupled over time. One example of such commonly reported indirect effect is the influence of temperature on the growth and prosoma length over a time (Runge 1984, Devreker et al. 2005). The size of the body, mostly measured as prosoma length, is known to be strongly influenced by temperature dependent growth (Vidal 1980a, Warren et al. 1986, Klein Breteler & Gonzalez 1988, Lee et al. 2003). While some investigations have found that body size is influenced by both food quality and quantity (Twombly & Tisch 2000), the effect on body size of food and temperature were reported to be small and significant mainly in the oldest stages of copepods (Vidal 1980a, Ban 1994, Twombly & Tisch 2000).

On the other hand, there were strong correlations between body size and *EPR* in the present data. Thus, it is possible that there were a significant indirect effect of temperature on body size affecting the *EPR* during the season. As discussed below the variation in body size may also be due to different degree of food limitation during the season. This illustrates that the impact of temperature on the biology of calanoid copepods may be very complex. The effect of changing temperatures on plankton dynamics is important to understand, especially because of the present global change in temperature. Indeed, a significant increase in water temperature was also shown in the North Sea in recent years (Wiltshire & Manly 2004). The ecosystems of the North and Baltic Seas are also closely linked to changes in the climate evidenced through the coupling to the NAO index (Beaugrand & Reid 2003). The climate is the main force of ecosystems and affects trophic levels including phytoplankton, zooplankton, and benthos to fish (Reid et al. 2003). The recent climate shift has modified the plankton ecosystem in a way that the phytoplankton composition (Wiltshire & Manly 2004) and the survival of fish like cod was reduced (Beaugrand et al. 2003).

Based on the results from the Baltic Sea, one may conclude that *T. longicornis* may prefer water temperatures around 12 °C, and that the nutritional content of the food may play a smaller role, especially in the more easterly regions where higher salinities are less optimal. This translates to a life above the halocline where temperatures are around 12-14 °C during large parts of the year, salinities are lower but nutrients may become limiting for algal growth. This is exactly where we do find *T. longicornis* in the Baltic Sea. Whether, this means that other factors, such as predation risk (which is typically higher, at shallower depths), do not play a dominant role in shaping the seasonal and spatial distribution of *T. longicornis* in the Baltic Seas. It remains to be seen, and is unlikely considered in general population models such as the unified Foraging Theory (Mangel & Clark 1986). Hence, these results help to understand the distribution of the Baltic *T. longicornis* in marine and brackish waters, and show that further research is needed to clarify the nature of the adaptation of zooplankton to the strongly variable environment in the Baltic Sea.

6.3. Biotic controlling factors

There are several biotic factors controlling the reproduction and growth in copepods; including mate availability, prey-predator interactions, competition and different aspects of the food. In this study the focus was on the impact of food on copepod egg production. There are further many different aspects of importance when it comes to food. Food availability (including prey size, prey behaviour and other non-predational defence mechanisms such as toxins), quantity, quality and digestibility are all important. Since copepod females do not grow significantly, and the relatively small copepods used here do not store large amounts of energy (Norrbin 2001), the assimilated food is mostly used for respiration and reproduction. Although there is a large number of studies on different aspects of copepod feeding and reproduction it is still difficult to assess feeding by copepods in their natural environment (Nejstgaard et al. 2003) and the effect of the different natural food regimes on copepod reproduction in the complex food webs still remains to be understood and quantified.

Food quantity

In the field, food limitation often occurs during the year (e.g. Checkley 1980b, Durbin et al. 1983, Kiørboe & Nielsen 1994, Richardson & Verheye 1998, Campbell et al. 2001, Kimmerer et al. 2005). Effects of food limitation for *T. longicornis* were observed in this study during summer both in the Baltic Sea and in the North Sea. Additions of cultured algae in high concentrations in addition to the natural prey field resulted in increased egg production, regardless if the diatom *Thalassiosira weissflogii* or the cryptophyte *Rhodomonas* sp. were used. On the Helgoland Roads *T. longicornis* appeared to be food (quantity) limited for most of the year, except possibly during the coldest period from Dec 2004-Feb 2005, when the *EPR* may have been more limited by food quality. This conclusion is supported by the recent work of Knotz (THESIS), and the unpublished results of A. Wesche, but is in direct contrast to the conclusions of Halsband and co-workers (Halsband & Hirche 2001, Halsband-Lenk et al. 2004), who argued that food is never limiting for copepod growth and reproduction in the German Bight around Helgoland. It remains to be seen whether these different results for the same research area are a result of changes that have occurred in the time between the two studies, or whether the different approaches in these studies are responsible for the contrasting conclusions. However, in accordance with Halsband-Lenk (2001) there was no significant correlation between *EPR* and food concentration in terms of total particulate carbon in the data of this study, but there was a significant correlation with particulate nitrogen. Furthermore a significant negative correlation between C:N ratio and *EPR* was also found, again indicating the N as a quality indicator. This is in agreement with Anderson and Pond (2000), which suggests that the copepods may have been N-limited rather than C-limited, which may explain the differences between the investigations. Hence, from the results presented in this thesis it can be concluded that the food (quantity) limitation in terms of nitrogen was important during most of the year, which again implies food quality effects, discussed below.

Food quality

The composition of the food, in terms of essential compounds necessary to support survival, growth and reproduction of copepods, is one of the main food-quality determining factors (Paffenhöfer et al. 2005). A number of different elemental and biochemical compounds of the diet such as carbon, nitrogen, protein, amino acidy and fatty acid content have been found to be correlated to copepod fecundity (Jónasdóttir 1994, Pond et al. 1996, Kleppel et al. 1998, Koski et al. 1998, Klein Breteler et al. 1999).

In this study the food quality was assessed using the C:N ratio and fatty acid composition in relation to *EPR*. Nitrogen often becomes strongly limited in oceanic and other marine areas, which influences the elemental and biochemical composition of the diet of copepods (Elser et al. 2000). This thesis has shown that in cultures, nitrogen depleted phytoplankton compared to those grown in nitrogen sufficient media had a positive impact on the *EPR* in two *Acartia* species. This was initially a surprising result, because both the field data from Helgoland Roads, and published data have shown that a high C:N ratio can have a negative effect on the growth and reproduction of copepods (Checkley 1980a, Jones et al. 2002, Van Nieuwerburgh et al. 2004). However, the laboratory results support the recent idea that a moderately high prey C:N ratio (10-15), close to the Threshold Elemental Ratio, should sustain a higher *EPR* than a C:N ratio substantially less than 10. Mineral limitation can be related to the biochemical composition (in terms of fatty acids or amino acids) of the phytoplankton species and cause a biochemical limitation for the consumer like the copepods (Anderson & Pond 2000, Kuijper et al. 2004). However, the model by Kuijper et al. (2004) emphasizes the need to consider direct C and N requirements for maintenance in order to understand dietary constraints to mesozooplankton production. They point out that zooplankton is unable to utilize dietary N efficiently for egg production, even if it is scarce in the diet, because of the N demands for maintenance by the adult. Thus, marine copepods may be adapted to a relatively high C:N ratio between 10-15. This is regularly occurring in the plankton after the spring bloom, when the nitrogen is limited for phytoplankton. Other laboratory studies have shown that this N-limitation can cascade trough a food web and influence fish larvae feeding on copepods reared on nitrogen depleted food (Malzahn et al. *in prep.*).

The response to nitrogen depletion was tested in the laboratory under constant condition on in simplified food chains. But in the field many environmental factor are varying in different time spans and the food relationships are a complex food web. In the field copepods can feed selectively and use different sources of food (Cotonnec et al. 2001). Several investigations reported that the trophic interaction between phytoplankton and zooplankton can be interrupted by a link of heterotrophic protists that are efficient predators of smaller phytoplankters, and themselves more easily available to the copepods because of a significantly larger size, which is closer to the optimal prey size for many copepods (Hansen et al. 1997). However, besides the upgrading in prey size from nano sized to larger microzooplankton, it is debated whether the heterotrophic protists upgrade the quality of the diet for copepods by concentrating nitrogen or certain fatty acids, compared to the algae diet (Klein Breteler et al. 1999, Tang & Taal 2005). The role of heterotrophic protists as potential trophic upgraders of suboptimal algal food for marine copepods is still not completely understood. However, it has also been shown that a trophic link through heterotrophic protists may upgrade the nutritional quality of phytoplankton as food for copepods (Tang & Taal 2005). In this thesis possible trophic upgrading was tested on the common Baltic Sea copepod *Acartia longiremis* feeding on *Rhodomonas* sp. grown under nitrogen sufficient and depleted conditions, in the presence and absence of two heterotrophic protists, *Oxyrrhis marina* (dinoflagellate) and *Strombidium conicum* (ciliate). When the heterotrophic protists were present in the food, the egg production of *A. longiremis* was significantly higher than when feeding on *Rhodomonas* sp. alone. There was no significant difference in egg production between diets containing either the heterotrophic dinoflagellate or the ciliate. *Rhodomonas* sp. cultured in nitrogen depleted media showed an increase in saturated and mono-unsaturated fatty acids compared to a nitrogen sufficient environment. In general, the content of polyunsaturated fatty acids remained equal but single fatty acids like EPA and DHA decreased under nitrogen limitation. The high *EPR* of *A. longiremis* fed on the mixture of *Rhodomonas* sp. and *Oxyrrhis marina* or with *Strombidium conicum*, could be not correlated to a single fatty acid or nitrogen condition of the food. Hence the role of the trophic upgrading by heterotrophic protists for copepods appears to be complex and in need of more detailed investigations.

Further, the doubling of the natural food concentration in winter did not increase the egg production, while adding any of the cultured algae did, to a similar extent for both the algae. It was counter intuitive that no significant difference in *EPR* was registered between the two treatments where the assumed good food algae *Rhodomonas* sp. for copepod egg production (Støttrup 1990), and the less good *Dunaliella* sp. where mixed into natural seston of supposed low food quality. Still, this indicates that 1) the copepods were limited by some food quality factor in the natural plankton so that increase in the food quantity did not boost *EPR* (0.5-1.3 eggs fem^{-1} d^{-1}), but the difference between the two added algae did not cascade significantly through the system. The lack of nutrient cascading effects could be due to e.g. trophic food web upgrading of the *Dunaliella* and/or that the copepods were able to compensate for the potential nutritional lack in *Dunaliella* by ingesting alternative food. This is further supported by the laboratory studies (Chapter III), where there was no clear difference in egg production when heterotrophic protists were fed to copepods with algae from N-deplete or sufficient cultures, respectively. On the other hand, the field results from winter could not be explained by low total natural seston nitrogen content (56-66 µg N l^{-1} between Dec 2004 and Feb 2005), C:N ratio (6.0 in Dec 2004) or low temperature (8.3 °C in Dec 2004), because the natural seston nitrogen content was lower, (45 µg N l^{-1}), the C:N ratio similar (5.6) and the temperature was lower (7.0 °C) in April 2004 when the highest *EPR* (12 eggs fem^{-1} d^{-1}) was recorded. Thus there are likely other factors governing the interaction between food quantity, quality and *EPR*, than those measured here. One such factor could be possible inhibiting agents as suggested by Poulet (2006). However, this is a complex field that needs more detailed studies of both selective feeding *in situ,* and detailed biochemical composition of the prey, including chemical signalling. Furthermore, this is a new field where still very little is known, especially from aquatic environments (Pohnert 2004, Long & Hay 2006)

Conclusion and future perspectives

Temperature was found to have only a limited direct effect on the reproduction. However more complex indirect effects on the reproduction cannot be excluded. In contrast the work in this thesis clearly showed that the variation in food nitrogen content affected egg production in copepods, both in the simple food webs in the laboratory experiments and in complex natural plankton during different seasons. The dome shaped relationship between C:N ratio and egg production reported in the published literature and supported by the laboratory observations in this thesis could be not found in the more complicated field situations.

However, these results supports the necessity to take the food quality into account as an important factor for the population dynamics of calanoid copepods in temperate seas like the North and Baltic Sea. Further investigations have to evaluate the effects of different nutritional conditions in a range of different phytoplankton species. In this thesis only the cryptophyte *Rhodomonas* sp. was used to manipulate the C:N ratio. Different phytoplankton groups might react differently to nutrient manipulation and cause different reproductive responses in the copepods. In particular, studies combining investigations of different factors like food quality and food quantity in situ (preferably) or using more natural phytoplankton assemblages are needed. This study showed only effects of nitrogen depletion. Other essential mineral elements like phosphorous are also known to influence the reproduction, especially in brackish and fresh water systems (Boersma 2000, Malzahn et al. *in prep.*). However, they may also have a significant but little known impact on the secondary production of zooplankton like copepods as e.g. recently shown for ultra oligotrophic P-limited systems in the Mediterranean (Thingstad et al. 2005). Much more work has to be done to understand the driving forces controlling the reproduction in copepods in the sea.

VII. SUMMARY

This thesis reports on the reproduction, survival and distribution of calanoid copepods in response to food quantity and quality and environmental factors such as temperature and salinity in laboratory and field studies from the Baltic and the North Sea. The organisms investigated here are the common calanoid copepods *Acartia clausii*, *A. longiremis* and *Temora longicornis*, and as prey the cryptophyte algae *Rhodomonas* sp., the diatom *Thalassiosira weissflogii*, heterotrophic dinoflagellates *Oxyrrhis marina* and oligotrich ciliates *Strombidium conicum*.

The first study investigated the reproductive response by *Acartia clausii and A. tonsa* to monoalgal food with different C:N ratios. The cryptophyte *Rhodomonas* sp. was cultured under nitrogen depleted and sufficient conditions, resulting in molar C:N ratios of 9.1 and 4.5, respectively. Adult females were fed the cryptophyte at saturating concentrations. Ingestion rates and egg hatching differed between species, but were not significantly affected by the quality (C:N ratio) of the food. Both species produced more eggs when the diet consisted of nitrogen-limited *Rhodomonas*. Although these results were initially surprising, they agree with the recent suggestion that a moderately high prey C:N ratio (10-15) supports a higher egg production rate (*EPR*) than a C:N ratio substantially lower than 10.

The second study focused on the hypothesis that phytoplankton of lower food quality may be nutritionally upgraded when fed via a trophic link of heterotrophic protists to copepods. To investigate this, the common Baltic Sea copepod *A. longiremis* was fed *Rhodomonas* sp. grown under nitrogen sufficient or depleted conditions, in the presence or absence of either the dinoflagellate *O. marina* or the ciliate *S. conicum*, respectively. When heterotrophic protists were present in the food the egg production of *A. longiremis* was significantly higher than when feeding on *Rhodomonas* sp. alone, but the egg production did not vary significantly between diets containing either of the heterotrophic protists. *Rhodomonas* sp. cultured in nitrogen depleted media showed an increase in saturated and monounsaturated fatty acids compared to a nitrogen sufficient media. In general, the content of polyunsaturated fatty acids remained equal but single fatty acids like EPA and DHA decreased under nitrogen limitation. However, the high egg production rate of *A. longiremis* fed on the mixture of *Rhodomonas* sp. and *Oxyrrhis marina* or with *Strombidium conicum*, could not be correlated to any single fatty acid or stoichiometric condition of the food. Instead, these results showed that both types of microzooplankton appeared to improve the nutritional value of the food in terms of fatty acid

composition. Hence the role of the trophic upgrading by heterotrophic protists for copepods appears to be complex and in need of more investigation.

The third study focused on effects of environmental factors on reproduction, survival and distribution of copepods in brackish water environments. In the Baltic Sea, the temperature and salinity vary over wide ranges during the seasons and over vertical and horizontal distances. This is assumed to strongly influence zooplankton distribution and reproduction. In the highly stratified central Baltic Sea *T. longicornis* is common only in the upper brackish water layer. To investigate what factors may control the distribution, mortality, grazing and reproductive response of adult *T. longicornis* females were investigated in a range of temperatures (8-24 °C) and salinities (8-25), in the field and laboratory. In the Bornholm Sea the *EPR* of wild caught *T. longicornis* appeared to be limited by *in situ* food concentrations but not by low temperature. The copepods showed lower *EPR* in water from the *in situ* environment (1-2 eggs female^{-1} day^{-1}), compared to when incubated in non-limiting food concentrations of *Thalassiosira weissflogii* (yielding ca 5 eggs female^{-1} day^{-1}, in both 3 and 10 °C). Comparing females from the Arkona, Bornholm and Gotland Seas, copepods from the Bornholm Sea treated with a slightly lower salinity (7.5) than *in situ* (8) showed the highest *EPR* (6.2 eggs female $^{-1}$ day^{-1}). While the lowest *EPR* of 2.2 eggs female^{-1} day^{-1} was found with individuals from the Gotland Sea exposed to substantially higher salinity (20) compared to what was found in its habitat (7-8). *T. longicornis* from the Kiel Bight reared at 15 °C and salinity of 12 showed a dome shaped relationship between temperature and *EPR* with highest rates close to the culture temperature, at 12 °C (3.6 eggs female^{-1} day^{-1}). The effect of salinity on *EPR* was significant with higher rates at 14 (3.8 eggs female^{-1} day^{-1}) compared to at 7 (0.7 eggs female^{-1} day^{-1}), when tested under different food qualities. That leads to the conclusion that salinity, temperature and food concentration have strong influence on the population dynamic of this species, apparently depending on the area of origin. *T. longicornis* found in the Bornholm and Gotland Seas appears well adapted to the relatively low salinity (7-8) found there, and they were not able to reproduce at salinity higher than found in their natural habitat (7-12), while the reverse was true for copepods from the from the more westerly Arkona Sea, and copepods from Kiel Bight reared in higher salinities. These results suggest that there may be local adaptation to different environmental conditions in the same species explaining the distribution of the Baltic Sea *T. longicornis* population, but further studies are needed to test this hypothesis and investigate to what degree phenotypic or genotypic adaptation may be involved.

The fourth study focused on the influence of environmental factors on the egg production by *T. longicornis* in the North Sea, where it is very abundant and shows high seasonally variability in egg production. Between April 2004 and April 2005 the influence of temperature, food quantity and food quality on reproduction by *T. longicornis* was investigated, using natural plankton from Helgoland Roads (North Sea). In addition to the natural seston as food, food quantity and quality was varied by either doubling the *in situ* concentration of particles larger than 10 µm, or by adding cultured phytoplankton, either *Rhodomonas* sp. or *Dunaliella* sp. to the natural seston. The *EPR* were measured at *in situ* temperatures that varied between 2.6 to 19.3 °C. By comparing data from the whole season, temperature only showed a weak (non significant) positive correlation to *EPR*. Instead, prosoma length was significantly positively correlated to *EPR*, and both treatments with added algae resulted in significantly increased *EPR*, while also doubled natural food showed a (non-significant) increase in *EPR* in all seasons except winter (Dec 2004 – Feb 2005). There was also a strong significant negative correlation between C:N ratio and *EPR*, and positive correlation to nitrogen concentration, while carbon concentration was not significantly correlated to *EPR*. Comparing data from different periods with low natural food concentrations indicated that food quantity may limit *EPR* during the warm (14 – 18 °C) post diatom bloom period (Sep – Oct 2004), while food quality may limit *EPR* during the cold (4 – 8 °C) pre diatom bloom period (Dec 2004 – Feb 2005). Although, *Rhodomonas* sp. is reported to be of higher food quality for copepod egg production, compared to *Dunaliella* sp. when fed as monocultures, no such difference was evident when mixed into a complex natural seston. These results do not support the idea in the current literature that temperature is a major controlling factor of copepod reproduction in the sea. Instead we conclude that in the Helgoland Roads, food quantity, in terms of total particulate N, may generally be a limiting factor for the reproduction by *T. longicornis*, while food quality, in terms of decreasing C:N ratio and increasing body size also significantly increase the *EPR* in this omnivorous copepod in natural plankton.

VIII. ZUSAMMENFASSUNG

Die Arbeit beschäftigt sich mit der Reaktion von Nahrungsquantität und –qualität sowie Umweltfaktoren wie Temperatur und Salzgehalt auf die Reproduktion, das Überleben und die Verbreitung von calanoiden Copepoden. Diese Experimente wurden mit Organismen aus der Nord- und Ostsee sowie unter Labor- also auch unter Freilandbedingungen durchgeführt. Hierbei waren die calanoiden Copepoden *Acartia clausii*, *A. tonsa*, *A. longiremis* und *Temora longicornis* in Kombination mit *Rhodomonas* sp.(Chrypthophycea), *Thalassiosira weissflogii* (Bacillariophycea), dem heterotrophen Dinoflagellaten *Oxyrrhis marina*, sowie einem oligotrichen Ciliaten *Strombidium conicum* untersucht worden.

Im ersten Teil der Arbeit wurde eine Algenart mit verschiedenen C:N Verhältnissen verfüttert und die Reaktion auf die Reproduktion von *Acartia clausii* und *A. tonsa* beobachtet. Die Cryptophytenart *Rhodomonas* sp. wurde unter Stickstoffmangel und – überschuss kultiviert und erreichte dabei ein molares C:N Verhältnis von 9.1 bzw. 4.5. Ausgewachsene Weibchen wurden mit der Cryptophytenart in einer nichtlimitierten Konzentration gefüttert. Die resultierenden Fraß- und Schlupferfolgsraten waren zwischen den Arten zwar unterschiedlich, aber waren nicht von der Qualität der Nahrung beeinflusst. Der Fraß von Stickstoff limitierten Algen führte bei *A. tonsa* zu einer Zunahme der Dauereierproduktion, während *A. clausii* bei keinem Versuchsansatz Dauereier produzierte. Wie auch immer, beide Arten produzierten mehr Eier wenn das Futter aus Stickstoff limitierten *Rhodomonas* sp. bestand. Obwohl diese Ergebnisse auf den ersten Blick sehr überraschend waren, stimmen sie mit aktuellen Ideen überein, bei der eine relativ hohes C:N Verhältnis (10-15) in der Nahrung eine höhere *EPR* unterstützt als eine niedrigeres C:N Verhältnis (<10).

Die zweite Studie bezieht sich auf die Hypothese, das Phytoplankton von geringerer Nahrungsqualität aufgewertet werden kann, wenn der Fraß über die trophische Verbindung von heterotrophen Protisten zu den Copepoden geht. Daher wurde, die in der Ostsee verbreitete Copepodenart, *A. longiremis* mit *Rhodomonas* sp, gefüttert, die unter Stickstoffmangel bzw. angereicherten Bedingungen gewachsen war. Zusätzlich wurde mit den heterotrophe Organismen *O. marina* (Dinoflagellat) bzw. *S. conicum* (Ciliat) gefüttert. Wenn heterotrophe Protisten in der Nahrung vorhanden waren, dann war die *EPR* signifikant höher als wenn sie nur *Rhodomonas* sp. alleine gefressen hatten. Aber zwischen den beiden Versuchsansätzen mit den heterotrophen Protisten gab es keinen Unterschied. Wurde *Rhodomonas* sp. mit Stickstoffmangel kultiviert, konnte ein Anstieg der gesättigten und einfach gesättigten Fettsäuren im Vergleich zu *Rhodomonas* sp. mit angereicherten Stickstoff

im Nährmedium gemessen werden. Generell blieb der Gehalt von mehrfach ungesättigten Fettsäuren gleich, obwohl der Gehalt von einzelnen Fettsäuren wie EPA and DHA bei Stickstoffangel unterschiedlich schwankte. Die hohe *EPR*, die bei der Fütterung aus einer Mischung von *Rhodomonas* sp. und *Oxyrrhis marina* bzw. mit *Strombidium conicum* gemessen wurde, konnte mit keiner einzigen Fettsäure korreliert werden oder auf die stoichiometrischen Verhältnisse der Nahrung zurückgeführt werden. Stattdessen haben diese Ergebnisse gezeigt, dass beide Typen von heterotrophen Protisten den Nährwert der Nahrung bezüglich der Fettsäurezusammensetzung scheinbar erhöhen. Folglich scheint die Rolle der trophischen Aufwertung von heterotrophen Protisten für Copepoden komplizierter zu sein und benötigt weiter Untersuchungen.

In einem dritten Versuch wurde der Effekt von Umweltfaktoren auf die Reproduktion, das Überleben und die Verbreitung von Copepoden im Brackwasser untersucht. In der Ostsee schwanken die Temperaturen und der Salzgehalt über einen weiten Bereich über die Zeit und sowohl in vertikaler als auch horizontaler Ausdehnung. Daher lässt sich ein starker Einfluss auf die Verbreitung und Reproduktion des Zooplanktons vermuten. *T. longicornis* ist in der stark geschichteten Zentralen Ostsee nur in den oberen Wasserschichten verbreitet. Um zu untersuchen, welche Faktoren diese Verbreitung steuern, wurde die Sterberate und die Reproduktion von ausgewachsenen *T. longicornis* Weibchen, in einem Temperaturbereich von 8-24 °C und bei einem Salzgehalt von 8-25 in Labor- und Feldexperimenten bestimmt. In der Bornholmsee schien die *EPR* von wild gefangenen *T. longicornis* unter *in situ* Nahrungsbedingungen limitiert zu sein, was aber nicht bei niedrigeren Temperaturen beobachtet wurde. Die Copepoden zeigten eine geringere *EPR* im ursprünglichen *in situ* Wasser (1-2 Eier Weibchen^{-1} Tag^{-1}) im Vergleich zu den Tieren, die mit einer gesättigten Nahrungskonzentration von *Thalassiosira weissflogii* gehältert wurden (ca. 5 Eier Weibchen^{-1} Tag^{-1}, bei 3 und 10 °C). Vergleicht man die Weibchen aus der Arkona-, Bornholm- und Gotlandsee, so zeigten die Copepoden von der Bornholmsee, die in geringerem Salzgehalt (7.5) als *in situ* (8) gehältert wurden, die höchste *EPR* (6.2 Eier Weibchen^{-1} Tag^{-1}), während die geringste *EPR* von 2.2 Eier Weibchen^{-1} Tag^{-1} bei Individuen von der Gotlandsee, die einem höheren Salzgehalt von 20 im Vergleich zum Habitat (7-8) ausgesetzt wurden, gefunden wurde. *T. longicornsis* aus der Kieler Bucht, die bei 15° C und einem Salzgehalt von 12 gehältert wurden, zeigten eine glockenkurvenartige Beziehung zwischen Temperatur und *EPR* mit einen Maximum bei einer Hälterungstemperatur von 12 °C (3.6 Eier Weibchen^{-1} Tag^{-1}). Der Effekt des Salzgehaltes bei verschiedenen Nahrungsqualitäten war signifikant mit höheren *EPR* bei einem Salzgehalt von 14 (3.8 Eier Weibchen^{-1} Tag^{-1}) im Vergleich zu 7 (0.7

Eier Weibchen^{-1} Tag^{-1}). Das läßt schlussfolgern, das das der Salzgehalt, die Temperatur und die Nahrungskonzentration einen großen Einfluss auf die Populationsdynamik dieser Art haben, unabhängig davon, ob *T. longicornis* in der Bornholm- und Gotlandsee gefunden wurde, und dass sie dort gut an relativ geringe Salzgehalte (7-8) angepasst ist. Außerdem waren sie nicht in der Lage sich bei höheren Salzgehalten in ihrem natürlichen Habitat (7-12) zu vermehren, während das Gegenteil für die Copepoden aus dem Gebiet westlich von der Arkonasee und die Copepoden aus der Kieler Bucht zutraf. Diese Ergebnisse deuten darauf hin, dass eine lokale Anpassung an verschiedene Umweltbedingungen bei der gleichen Art, die Verbreitung von *T. longicornis* in der Ostsee erklären könnte. Allerdings sind weitere Studien erforderlich, um diese Hypothese zu testen und zu untersuchen, welche Form der phänotypischen oder genotypischen Anpassung damit verbunden ist.

In dem letzten Teil der Arbeit wurde der Einfluss von Umweltfaktoren auf die Reproduktion von *T. longicornis* in der Nordsee betrachtet, wo diese Art sehr abundant ist und hohe saisonale Schwankungen in der Eiproduktion aufweist. Von April 2004 bis April 2005 konnte der saisonale Einfluss von Temperatur, Nahrungsquantität und -qualität auf die Reproduktion von *T. longicornis*, bei Fütterung mit natürlichem Plankton von der Helgoland Reede (Nordsee) untersucht werden. Zusätzlich zum natürlichen Seston als Nahrung, wurde die Nahrungsquantität und -qualität durch Verdopplung der *in situ* Konzentration der Partikel (>10µm) oder durch Zugabe von Kulturalgen (*Rhodomonas* sp. bzw. *Dunaliella* sp.) zu dem natürlichen Seston variiert. Die *EPR* wurde bei *in situ* Temperaturen mit einem Schwankungsbereich von 2.6 to 19.3 °C gemessen. Im Vergleich der Daten von einem ganzen Jahr zeigte die Temperatur nur eine schwache (nicht signifikante) positive Korrelation zur *EPR*. Stattdessen korrelierte die Prosoma-Länge mit der *EPR* signifikant positiv. In beiden Versuchsansätzen mit Zugabe von Kulturalgen war der Anstieg der *EPR,* während bei der Anreicherung mit doppelter natürlicher Nahrung die *EPR* (nicht signifikant) anstieg, mit Ausnahme des Winters (Dez 2004 – Feb 2005). Dort gab sich eine signifikant negative Korrelation zwischen C:N Verhältnis und *EPR* sowie eine positive Korrelation zur Stickstoffkonzentration, während die Kohlenstoffkonzentration nicht signifikant korreliert war. Bei dem Vergleich von verschiedenen Zeiten mit geringer Nahrungskonzentration scheint die die *EPR* während der warmen (14 – 18 °C) Phase nach der Blüte der Diatomeen (Sep – Okt 2004) nahrungslimitiert waren, während in der kälteren Phase (4 – 8 °C) vor der Blüte (Dez 2004 – Feb 2005) die natürliche *EPR* durch die Nahrungsqualität eingeschränkt war. Obwohl *Rhodomonas* sp. als qualitativ gute Nahrung für Copepoden gilt, war bei der Zugabe von der eher minderwertigen geltenden *Dunaliella* sp. als Mischung mit natürlicher

Nahrung kein entsprechender Unterschied ersichtlich. Diese Ergebnisse sprechen gegen die bisherige Annahme, dass die Temperatur der Hauptkontrollfaktor bei der Reproduktion von marinen Copepoden ist. Stattdessen lässt sich schlussfolgern, dass die Quantität der Nahrung im Sinne von totalem partikulärem Stickstoff ein limitierender Faktor für die Reproduktion von *T. longicornis* sein kann, während Nahrungsqualität im Sinne von C:N Verhältnissen und eine zunehmende Körpergröße signifikant die *EPR* dieser omnivoren Copepoden im natürlichen Plankton beeinflusst.

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X. DANKSAGUNG

Zuerst möchte ich mich bei PD Dr. Maarten Boersma für die Betreuung dieser Arbeit, seiner Unterstützung, anregenden Diskussionen und niederländischen Heiterkeiten bedanken.

Herrn Prof. Dr. U. Sommer gilt mein Dank für die Betreuung dieser Arbeit.

Dem BMBF, der HGF and GLOBEC Germany danke ich für die finazielle Ermöglichung dieser Arbeit. Gedankt sei hierbei Jürgen Alheit und Justus von Beuskom.

Ich danke allen meinen Kolleginnen und Kollegen insbesondere die Foodwebbers: Anne, Antje, Arne, Britta, Gunnar, Karen, Melanie, Susanna, Silke, Reinhard und Ulf und den GLOBECers: Anne, Britta, Jens- Peter, H3, Janna, Mario, Diak, Miriam, Hannes, Myron, Jan Linda, und alle anderen mit denen ich Seereisen und interessante Diskussionen geteilt habe.

Ich möchte mich für die Unterstützung bei der Durchführung der Arbeiten bei den Mitarbeitertn des AWI, insbesondere bei allen BAHlern und im Speziellen bei Karin, Anne-Katrin, Annette, Meike, Gudrun, Gerrit, Andreas, Stefan, Eva, Donata, Magnus, Andrea, Lars bedanken.

Vielen Dank gilt auch den Seemännern der RV “Humboldt”, RV “Heincke” und RV “Alkor” sowie der „Aade“ mit besonderem Dank an Dieter, Johann und Temu für Unterstützung bei jedem Wetter, den netten Gutenmorgencafé hin und wieder und den vielen netten Gesprächen aus der Seemannskiste.

Alexandra, Andrea, Ansgar, Andreas, Anja & Jens, Anne & Jörg, Calle, Christof, Jens-Peter, Karina, Caro, Kerstin, Lars, Ralf, Regine, Romy, Jeff, Micha, Wolfram, Daniel, Martin, Mathias,Gerd, Nica, Marcel, Norman, Lars, Regine, Steffen, Linde, Gerhard, Robert, Ina, Frank, Gladys danke ich von ganzem Herzen, das ihr für mich da wart, mich unterstützt und vor allem mit mir gelacht, gelebt, genossen, geliebt, getanzt, gefeiert, geschlemmt habt und mir ein das Leben neben der Forschung nicht vergessen lassen habt.

Ein ganz großes unvergessliches Dankeschön gilt Jörg, der mir viele kleine, praktische Dingen mir die Copepodenforschung gezeigt hat und immer wieder zu Diskussionen bereit war.

Einen Dank gilt den Forschungstauchern Carsten,Udo, Saskia, Gerd, Björn, Jochen, Peter, Eddie, Dirk, Max und meinen Freizeittauchern Günter, Alex und Frank, die mir schöne Ausflüge in das Reich meiner kleinen Biester ermöglicht haben.

Ich danke Tanja, Ute, Reinhold, Jessica und PO, die mich immer geduldig im Büro ertragen und den Abeitsalltag geteilt haben.

Tausend Dank gelten meinem Lieblingsmitbewohner Lars und besonders Mela, die sich um alle Kasernenbelange gekümmert und das Leben so dort für mich angenehmer gemacht hat.

Meiner Familie besonders meiner Mutter und meiner Schwester danke ich, dass ihr immer da wart, wenn ich Euch gebraucht habe. Hierbei sei auch Tante Tina, Walter, Axel, Heidi gedankt. Ich bin froh, dass mich Helga, Babsy und Big Mama immer wieder erheitert haben.

Ein riesiges Dankeschön geht an die Unterstützug in den letzten Tagen der Fertigstellung der Arbeit, d.h. an Christian und die Firma Wiehler und Lars Kruse, Frank und Reinhold.

Am Ende möchte ich mich bei meinem Freund Jens bedanke, das er mich so intensiv unterstützt hat und mir soviel Liebe und Kraft gegeben hat, das alles in dieser Zeit zu schaffen.

DESCRIPTIONS OF THE SCIENTIFIC CONTRIBUTION TO MULTIPLE-AUTHOR MANUSCRIPTS

Chapter II.: Effects of nitrogen stressed algae on different Acartia species

Christina B. Augustin & Maarten Boersma

All analyses, text writing and the graphical design were constituted by Christina Augustin. PD Dr. Maarten Boersma supervised this work.

This study was published in April 2006 in the Journal of Plankton Research.

Chapter III.: Effects of food quality under nitrogen depleted conditions on *Acartia longicornis*

Christina B. Augustin, Mario J. Schilling, Janna Peters & Maarten Boersma

All analyses, the text writing and graphical presentation were done by Christina Augustin under the supervision of PD Dr. Maarten Boersma. Mario Schilling and Janna Peters assisted during parts of the experiment. Fatty acid measurements were provided by Janna Peters.

Chapter IV.: Salinity and temperature effects on reproduction, grazing and survival *Temora longicornis* in the Baltic Sea

Christina B. Augustin & Linda Holste, Jan Schulz, Maarten Boersma

All analyses and the text writing were done by Christina Augustin under the supervision of PD Dr. Maarten Boersma. Linda Holste assisted at one part of the experiments and supported with fruitful discussions. Jan Schulz only did the graphical presentation of the metafile data about the vertical distribution of *Temora longicornis* in the Baltic Sea.

Chapter V.: Seasonal changes in food quality, quantity and reproduction in *Temora longicornis* in the North Sea

Christina B. Augustin, Arne Malzahn, Karen Wiltshire & Maarten Boersma

All analyses, the text writing and the graphic presentation were done by Christina Augustin. The work was supervised by PD Dr. Maarten Boersma. Fatty acid data were provided by Dr. Arne Malzahn. Prof. Dr. Karen Wiltshire provided phytoplankton data.

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EDUCATIONAL INORMATION

2002- July 2006	PhD Thesis financed by GLOBEC - Germany Project „Food and climate effects on copepod reproduction in the North and Baltic Sea“ at the Alfred-Wegener-Institute for Polar and Marine Research Bremerhaven, Biological Station Helgoland
2001-2002	Diplomarbeit „Untersuchungen zur Salzgehaltstoleranz von *Pseudocalanus* spp. in der Ostsee“ (Investigations on salinity tolerance of Pseudocalanus spp. in the Baltic Sea) Main subject: Marine Biology Minor subject: Ecology, Oceanography, Microbiology
1996-2002	Matriculation at the University of Rostock, Faculty of Biology
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1989 – 1991	22. Oberschule Rostock – Toitenwinkel (High school)
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SKILLS

1996	Driver licence
1998-2000	4 semester of biology-related English
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2003	Sportbootführerschein–See (Sport boat Driving licence for Sea)
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OCCUPATION EXPERIENCES

1994	School internship at the University of Rostock, Department of fish biology
1996	Participance at the Germany competition „JUGEND FORSCHT“ (youth research)
1996	Work internship as laboratory assistant at the Laboratory of domestic landfill “Hausmülldeponie Parkentin“
1994 – 1999	Temporary employee a pet shop „Vogels Zoohandlung“

SCIENTIFIC EMPLOYMENT

1996	Student assistant at the University of Rostock, Department of Marine Biology, Dr. N. Jönsson: investigations of fish stomachs
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2000	Student assistant at the Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven, Dr. K. Schmidt: phytoplankton counts
2000	Student assistant Plume & Bloom Cruise on RV “Pelagia” (Royal Netherlands Institute for Sea Research, Texel) in the North Sea, Dr. J.Dutz: zooplankton experiments

2002	Student assistant at the Globec Germany Cruise on the RV “Alexander von Humboldt” (Baltic Sea Research Institute, Rostock) in the Baltic Sea, Dr. J. Alheit: zooplankton sampling
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PUBLICATIONS IN INTERNATIONAL PEER-REVIEWED JOURNALS

Augustin, C., Boersma, M.(2006). Effects of nutritional stress on different *Acartia* species, Journal of Plankton Research 28: 429-436

IN REVISION, SUBMITTED & IN PREP FOR INTERNATIONAL PEER-REVIEWED JOURNALS

Boersma, M., Augustin, C. B., Knotz, S., Schütte, T., Malzahn, A. M., Laakmann, S., Beuskom, van J. E. E. (2006) Effects of nutritional quality on copepod reproduction, GLOBEC International Newsletter, Vol.12, No.1: 67-69.

MEETINGS WITH CONTRIBUTED TALKS

2005, 17-20 February, Augustin, C.B., Boersma, M.: Effects of nutritional stress on different *Acartia* species, 12. Crustaceologen-Tagung, DZMB Wilhelmshaven, Germany

2005, 19-24 June, Augustin, C.B., Boersma, M., Beusekom, J. E. E. van, Wiltshire, K. H.: Seasonal patterns in the effects of food quality and quantity on reproduction of *Temora longicornis* in the North Sea, ASLO Summer Meeting , Santiago de Compostela, Spain

MEETINGS WITH CONTRIBUTED POSTER

2004, 27-28 January, Augustin, C., Beusekom, J. E. E., Boersma, M., Knotz, S.: Influence of nutrient limited algae on copepod reproductive success, Status seminar GLOBEC-Germany, Hamburg, Germany

2004, 20-22 June, Augustin, C., Knotz, S.(2004). Effects of different nutrional status of algae on copepods reproduction, AWI-Doktorandentag, Bremerhaven, Germany

2004, 15-20 February, Jamieson, C. D., Augustin, C. B., Boersma, M.: Differential effects of nutritional stress on closely related copepod species, ASLO/TOS Ocean Reserach Conference Honolulu, Hawaii USA

2003, 20-23 May, Augustin, C. B., Boersma, M., Wiltshire, K. H., Knotz, S.: Influence of nutrient limited *Thalassiosira rotula* on copepod reproductive success, Third International Zooplankton Production Symposium, Gijòn, Spain.

STUDENT AWARDS

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WORKSHOPS, SPECIAL COURSES & MEETINGS

2000, practical course for systematic of marine organisms (Calanoid Copepoda, Gammarid Amphipoda and Chaetognatha) Dr. H.G. Andres, Dr. H. Kapp, Dr. K. Schulz, Sylt, Germany

2003, 4th Phytoplankton workshop “Estimation and taxonomy of marine dinoflagellates”, Dr. M Elbrächter, Sylt, Germany

TIME ABROAD & INTERNATIONAL COOPERATION

2001, NIOZ, Netherlands experimental work for the master thesis advised by Dr. W. Klein Breteler, Dr. M. Koski

2006, University of Bergen, Department of Biology experimental work with Prof. T. F. Thingstad, T. Tanaka, J.C. Nejstgaard, P. Simonelli

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