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LIFE-CYCLE STRATEGIES AND IMPACT OF CANNIBALISM IN CALANOID NORTH SEA COPEPODS

DISSERTATION

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CONTENT

SUMMARY

The present study investigated the annual life-cycle strategies of four free-spawning dominant calanoid copepod species and presents a theoretical approach of the seasonal impact of cannibalism on the copepod community in the German Bight (southern North Sea). In a two-year field study, stage-specific abundances, egg production rates, proportion of spawning females and hatching success of *Acartia clausi*, *Temora longicornis*, *Centropages hamatus* and *C. typicus* were estimated at the sampling station Helgoland Roads. The results were related to environmental conditions (temperature, salinity, phytoplankton biomass and taxa) and used to calculate seasonal birth and stage-specific mortality rates.

In laboratory experiments, intra- and inter-specific predatory feeding rates of females on young offspring (eggs and nauplii) were determined. The experiments were conducted with single prey types, mixed animal prey and in the presence of different concentrations of the diatom *Thalassiosira weissflogii*. In a further step, field data and laboratory feeding rates were combined to evaluate the potential seasonal impact of cannibalism in the field.

The four copepod species showed similar patterns with highest reproductive activity and abundance during spring and summer, whereas in autumn and winter the life-cycle strategies differed between species. *A. clausi* hibernated as late copepodite stages and females, which did not produce eggs until February. Within the entire annual cycle, egg production rate and proportion of spawning females were not correlated to temperature. Thus, especially with respect to the ceased reproduction during winter, an intrinsic control of reproduction can be assumed. In contrast, *T. longicornis* reproduced throughout the year, but with lower rates during autumn and winter. Reproductive activity was strongly linked to temperature and phytoplankton biomass. It was the only species, which responded to an unusual autumn phytoplankton bloom with higher egg production rates. A reduced hatching success from late summer to autumn and a strong increase in nauplii density before reproductive activity peaked, indicated the existence of resting eggs. The two congener species *C. hamatus* and *C. typicus* were temporally absent and occurred in low numbers in the waters around Helgoland Island. Both species showed a strong dependence of reproduction on temperature, whereas egg production rate of *C. hamatus* was negatively and of *C. typicus* was positively correlated to temperature. Timing of resting egg production in *C. hamatus*, which is known to produce resting eggs, could not be clearly identified by seasonal differences in hatching success. In *C. typicus*, where the existence of resting eggs is still controversial, a clear pattern of reduced hatching success in late summer was detected.

With respect to birth rates, *T. longicornis* and *Centropages* spp. were capable to renew their populations within one to two days in summer, whereas this process took longer in *A. clausi*. Mortality was the determining factor for population size in all species, but the species differed in the extent of stage-specific mortality. The highest stage-specific mortality rate of *A. clausi* was estimated in the copepodite stage CI-CII (1.1 d^{-1}). *T. longicornis* showed highest mortality in the copepodite stage CIII (0.7 d^{-1}), whereas mortality for *Centropages* spp. accounted highest during the egg-nauplii, and copepodite stage CIII (0.6 d^{-1}). Abundance of fish larvae and chaetognaths as well as temperature were the dominant factors influencing mortality rates of several developmental stages.

The laboratory feeding experiments have shown the capability of females to ingest eggs and young nauplii. There was a dependence of feeding rates on prey density, predator and prey species, prey morphology and behaviour of both. When eggs and nauplii were offered at the same time and in equal density, ambush predators such as *A. clausi* and *Centropages* spp. were more efficient in catching motile nauplii, whereas *T. longicornis*, as a cruising predator, was more successful in feeding on non-motile eggs. It was shown, that concentrations of algae food of about 200 µg C L^{-1} may reduce predatory feeding in *A. clausi* and *T. longicornis*, whereas in *C. typicus* predatory feeding was enhanced. The theoretical approach of determining cannibalism in the field provided a potential maximum daily loss of about 100 and 150 % of eggs and young nauplii during summer. The differences between the years were due to differences in female abundance.

ZUSAMMENFASSUNG

Die vorliegende Arbeit untersuchte die saisonalen Lebenszyklus-Strategien von vier dominanten calanoiden Copepodenarten der Deutschen Bucht (südliche Nordsee). In einem theoretischen Ansatz wurde zusätzlich der potentielle Einfluss von Kannibalismus auf die Copepodengemeinschaft untersucht. Die untersuchten Arten *Acartia clausi*, *Temora longicornis*, *Centropages hamatus* und *C. typic*us gehören zu den Copepoden, die ihre Eier frei in die Wassersäule abgeben. Während einer zweijährigen Feldstudie an der Station Helgoländer Reede (südliche Nordsee) wurden stadienspezifische Individuenzahlen, Eiproduktionsraten, Anzahl der Eier legenden Weibchen und Schlupferfolge der einzelnen Arten gemessen. Die Ergebnisse wurden mit Umweltbedingungen (Temperatur, Salzgehalt, Phytoplanktonbiomasse und -taxa) korreliert und für die Berechnung von saisonalen Geburts- und stadien-spezifischen Sterberaten verwendet. In Laborexperimenten wurden intra- und interspezifische Fraßraten von Weibchen an jungen Nachkommen (Eiern und Nauplien) bestimmt. Die Experimente wurden mit einem Beutetyp, Kombinationen von tierischen Beutetypen und unter Zugabe der Diatomee *Thalassiosira weissflogii* durchgeführt.

Die vier Copepoden-Arten zeigten einen ähnlichen saisonalen Verlauf ihrer Reproduktionsaktivitäten und Individuenzahlen. Die höchsten Eiproduktionsraten und Populationsdichten traten zwischen Frühjahr und Sommer auf. Es gab große art-spezifische Unterschiede in den Strategien, weniger günstige Umweltbedingungen während der Herbst- und Wintermonate zu überdauern. *A. clausi* überwinterte mit älteren Copepodit-Stadien und Weibchen, die ihre Reproduktion komplett eingestellt hatten und erst im Februar wieder anfingen, Eier zu legen. Die Eiproduktionsrate und die Anzahl Eier legender Weibchen zeigten keine Temperaturabhängigkeit, was auf eine innere Steuerung dieser Vorgänge hindeutet. Im Gegensatz dazu legte *T. longicornis* ganzjährig Eier, wies aber eine geringere Rate im Herbst und Winter auf. Die Reproduktion war stark mit der Temperatur und der Phytoplanktonbiomasse korreliert. *T. longicornis* war die einzige der vier Arten, die auf eine ungewöhnliche Herbstblüte mit erhöhter Eiproduktion reagierte. Ein verringerter Schlupferfolg von Spätsommer bis Herbst und ein steiler Anstieg der Naupliendichten vor dem Reproduktionsmaximum deuten auf die Existenz von Dauereiern im Gebiet um Helgoland bei *T. longicornis* hin. *C. hamatus* and *C. typicus* waren zeitweise im Plankton nicht vertreten. Beide Arten zeigten einen starken Einfluss der Temperatur auf die Reproduktion, wobei die Temperaturkorrelation bei *C. hamatus* negativ und bei *C. typicus* positiv war. Anhand des Schlupferfolges konnte die Produktion von Dauereiern für *C. hamatus*, wie sie für diese Art bereits bekannt ist, zeitlich nicht eindeutig eingeordnet werden. Für *C. typicus* wird das Vorkommen von Dauereiern noch kontrovers diskutiert. In dieser Studie deutet aber ein verringerter Schlupferfolg im Sommer und Herbst auf die Produktion hin.

Bezüglich der Geburtenraten waren *T. longicornis* und *Centropages* spp. in der Lage, im Sommer ihre Population innerhalb von ein bis zwei Tagen zu erneuern, während *A. clausi* dazu mehr Zeit benötigte. Für alle Arten war die Sterblichkeit der bestimmende Faktor der Populationsgröße, wobei art-spezifische Unterschiede in den stadienspezifischen Sterblichkeiten auftraten. Bei *A. clausi* war die höchste Sterblichkeit von 1.1 d^{-1} im Copepodit-Stadium CI-CII zu verzeichnen, während für *T. longicornis* die höchste Sterblichkeiten von 0.7 d^{-1} im Stadium CIII gemessen wurde. Ein Verlust von 0.6 d^{-1} trat im Ei-Nauplienstadium, sowie im Stadium CIII von *Centropages* spp. auf. Die Sterblichkeiten der verschiedenen Entwicklungsstadien standen in Zusammenhang mit der Dichte von Fischlarven und Chaetognathen, oder waren abhängig von der Temperatur.

Die Laborexperimente haben gezeigt, dass alle vier Copepodenarten in der Lage sind, Eier und junge Nauplien zu fressen. Dabei wurden die Fraßraten von der Beutedichte, der Räuber- und Beuteart, der Beutemorphologie und dem Verhalten von beiden stark beeinflusst. Wurden Eier und Nauplien zusammen in gleichen Dichten angeboten, waren “Lauerjäger” wie *A. clausi* und *Centropages* spp. effektiver im Fangen der Nauplien, während *T. longicornis* durch permanentes Schwimmen erfolgreicher Eier fraß. Bei Zugabe von Algen in einer Konzentration über 200 µg C L^{-1} zeigten *A. clausi* und *T. longicornis* einen geringeren Fraß an Eiern, während *C. typicus* deutlich mehr Eier fraß. Der theoretische Versuch, den Einfluss von Kannibalismus im Feld zu berechnen, ergab maximal mögliche Verluste von 100 und 150 % der Eier und jungen Nauplien im Sommer. Dabei traten Unterschiede zwischen den Jahren auf, die auf die unterschiedliche Dichte von Weibchen zurück zu führen waren.

1 INTRODUCTION

Copepods constitute the majority of the mesozooplankton in aquatic ecosystems (e.g. Humes 1994, Verity and Smetacek 1996). With adult body sizes of about 0.2 to 2.7 cm they are relatively small organisms. However, they play a key role in energy transfer to higher trophic levels as major food source for fish and their larvae (e.g. Nielsen and Munk 1998, Voss et al. 2003, Möllmann et al. 2004), whales (Gaskin 1982), chaetognaths (Álvarez-Cadena 1993), crustaceans (Hutchings et al. 1991) and jelly fish (e.g. Daan 1986, 1989, Barz and Hirche 2007). They inhabit nearly every aquatic habitat from polar to temperate and tropical zones. Copepods are found in high mountain lakes (Winder et al. 2003), limno-terrestrial habitats like swamps (Comita 1951) or water-collecting bromeliad leaves (Reid and Janetzky 1996), from estuarine to oceanic waters, from surface to deep trenches and from cold polar ice-water interfaces (Mauchline 1998) to hot active hydrothermal vents (Humes 2004).

Due to the important position of copepods in food webs, a deep understanding of their ecology is required to understand the complex interactions in the pelagic. Therefore, detailed knowledge about their distribution, life-strategies and population dynamics as well as feeding mechanisms is essential.

1.1 Distribution and life-cycles

The primarily pelagic calanoid copepods are the most successful group in colonising the marine ecosystem worldwide (e.g. Verity and Smetacek 1996). The environments they live in are highly differentiated and the habitats are influenced by abiotic and biotic factors, such as temperature, salinity, food and predator abundance. These factors as well as their complex interactions vary with time (Remmert 1984). Each single factor influences vital processes and may cause species-specific birth, growth and mortality rates, which in turn, result in species-specific distribution patterns and life-cycles of the species.

1.1.1 Abiotic factors

Temperature and salinity, and their interactions are the most important factors influencing the physico-chemical conditions of the environment, such as viscosity, dissolved gases and osmotic pressure. Theses conditions may cause the exclusion of species from regions with unfavourable conditions, due to species-specific physiological requirements and their adaptive capabilities (Schlieper 1966, Kinne 1970).

Marine calanoid copepods are found from temperatures of -1.9 to 40°C (Lalli and Parsons 1993), and from brackish estuarine waters to high salinity open ocean waters (Mauchline 1998). Species living in more variable environments, such as estuarine or coastal zones, often tolerate wider thermal and salinity gradients than oceanic ones (Kinne 1963). In mid and high latitudes, distribution and life-cycle are influenced by temperature and salinity in a stronger way than in tropical areas, due to the higher variability of these factors, except in tropical estuarine system, where salinity and temperature gradients may also be obviously.

Temperature in conjunction with food affects growth, body size, life span, development and reproduction as well as inter- and intra-specific interactions (Kinne 1970). Growth is an exponential function of temperature, and about 90 % of the variance in copepods` growth rate can be explained by temperature (Huntley and Lopez 1992). Body size, generation time and the longevity increase with increasing latitude, and thus, with decreasing temperature (e.g. Paffenhöfer 1991, Ianora 1998). In high latitudes, individuals are larger in size and their longevity is longer relative to other regions (Conover 1967). Body size may also vary on a seasonal scale, especially in mid and high latitudes, caused by the annual cycle of temperature (Hirche 1992, Riccardi and Mariotto 2000, Halsband and Hirche 2001), whereas in tropical regions, seasonal variation of body size is usually absent (Chisholm and Roff 1990a).

The reproductive activity of copepods varies with temperature, and thus with geographical latitude. Species of tropical and subtropical regions often show a continuous and irregular breeding without any seasonality (Chisholm and Roff 1990b). In mid and high latitudes, seasonal temperature differences result in a marked seasonality in availability of food, which affects reproduction (e.g. Kinne 1970). This in turn, results in a seasonality in abundance. Additionally, species with different reproductive temperature preferences can share the same habitat, exhibiting consecutive temporal spawning periods (Runnström 1927), which depend on the annual temperature cycle.

Temperature shifts are known as trigger for the alternation of dormant and active life phases in copepods of mid latitudes (Dahms 1995, Marcus 1996). Dormancy is a state of suppressed metabolism and/or development (Danks 1987), usually characterised by an increased resistance to adverse conditions (Siewering 1980). It occurs in various ontogenetic stages, from eggs to adults, and it is expressed especially in species from mid to higher latitudes (reviewed in Dahms 1995), i.e. habitats that features strong variations in environmental conditions. The reduction of light intensity and shorter day length are also discussed as triggers for dormancy cycles (Uye 1985, Chinnery and Williams 2003, Engel 2005).

Species-specific requirements and reactions to abiotic factors result in spatial and/or temporal species separation. Copepod species separation is known for many genera, such as *Calanus* (Conover 1988), *Clausocalanus* (Frost 1969), *Euchaeta* (Williams 1985), *Temora* (Halsband-Lenk et al. 2004), and *Acartia* (Krause et al. 1995). The species where restricted to certain geographical regions due to their different thermal requirements or salinity preferences. *Temora longicornis*, for example, is present in cold-temperate seas from northern Norway to the Portuguese coast (Krause et al. 1995), whereas its congener *T. stylifera* is found in warm-temperate regions like the Mediterranean and the tropical Atlantic and Pacific (Rose 1933, Mori 1964). A vertical separation of developmental stages occurs in *Paraeuchaeta* (Auel and Hagen 2005) or *Pseudocalanus* (Renz and Hirche 2006), where different ontogenetic stages inhabit different depth-strata, depending on temperature, salinity and/or food preferences, or also predator avoidance behaviour. On a temporal scale, species are separated by seasonal succession, where `colder` species are followed by `warmer` ones (Fransz and van Arkel 1983). In the North Sea, the cold-adapted *Centropages hamatus* is found from early spring to summer, whereas the congener *C. typicus* is abundant in the warmer and more saline waters in the second half of the year (Fransz et al. 1991).

1.1.2 Biotic factors

Biotic factors are defined by inter- and intraspecific interactions of organisms. For the characterisation of copepods´ life-cycles they have to be considered in conjunction with abiotic factors. The most substantial biotic factor for heterotrophic organisms is food. It has to supply sufficient energy to saturate the nutritional requirements of animals to maintain metabolism, growth and successful reproduction. Copepods feed on a wide variety of prey organisms, from bacteria and detritus to phytoplankton and animal food, such as microzooplankton, other copepods and small fish larvae (Kleppel 1993). In the last decades several studies have shown that food quality rather than quantity may influence reproductive success, and thus affect population dynamics. Nutritionally efficient food for copepods contains highly-unsaturated fatty acids (Jónasdottir et al. 1995), sterols (Klein Breteler et al. 1999, Hassett 2004) and essential amino acids (Arendt et al. 2005). It is demonstrated, that biochemical deficient food, such as aldehyde-producing or nutrient-depleted diatoms could hamper reproduction, embryonic development and hatching success (Ban et al. 1997, Ianora et al. 1996, Ianora et al. 2004, Augustin and Boersma 2006). In turn, dinoflagellates (Miralto et al. 1995, Veloza et al. 2006) and ciliates (Bonnet and Carlotti 2001) are known to have positive effects on fecundity of copepods and viability of eggs due to their high contents of essential fatty acids. However, there are also dinoflagellate species, such as *Alexandrinum* sp., which produce toxins affecting the fecundity of copepods (e.g. Dutz 1998, Teegarden 1999). These results often arise from laboratory experiments with algae-monocultures. Hence, detailed knowledge of what happens in the field is still scarce and further investigations are necessary to evaluate the effect of potential toxic or inadequate food under natural conditions.

For the discussion about the importance of food quality the impact of carnivory has also to be considered. Most copepod species are able to catch and ingest fish eggs and larvae (Turner et al. 1985, Yen 1987), chaetognaths (Davis 1977) or even copepod eggs and nauplii (reviewed in Bonnet et al. 2004). Animal prey serves as an additional energy resource, when other food is scarce (Heinle 1970, Daan et al. 1988, Gaudy and Pagano 1989), but this requires also a flexible digestive system. In general, copepods can adapt their feeding behaviour as well as their digestive system to changes in food quantity and quality (Darchambeau 2005, Knotz 2006), and thus may compensate negative effects of imbalanced food.

Predation is the second biotic factor that influences life and population dynamics markedly. Mass occurrences of predators, such as jellyfish are able to reduce copepod population sizes significantly (e.g. Daan 1986, Greve 1994, Pagès et al. 1996). Copepods tend to feed on their own and other copepod species` offspring, which may also seasonally regulate population sizes (see section 1.2.2). Furthermore, parasitism influences life-cycle and population dynamics of copepods. Numerous parasites, such as dinoflagellates (e.g. Drebes 1988, Kimmerer and McKinnon 1990, Skovgaard 2005) or tapeworms (e.g. Franz and Kurtz 2002) are internally or externally associated with several life-stages of copepods (Théodoridès 1989). An infection often results in reduced survival of developmental stages or reduced reproductive activity of adults (e.g. Albaina and Irigoien 2006, Cornils et al. 2007), and thus influences population density.

1.2 Feeding ecology

The strict separation into herbivorous and carnivorous species (Marshall 1973) is now replaced by the knowledge that most species feed omnivorously (Heinle 1970, Paffenhöfer and Knowles 1980, Kleppel 1993). The diet composition of copepods changes ontogenetically (Kleppel 1993), which is due to an increasing differentiation of the mouthparts, increasing body size and different nutritional requirements. In most species, the first feeding stage is nauplius stage III or IV (NIII or NIV) (Sekiguchi 1974); in *Acartia* spp. and *Temora longicornis*, it is nauplius stage II (NII) (Landry 1983, Klein Breteler et al. 1994). The optimum particle sizes handled by a copepod correspond to a size of 2 to 5 % of the copepod prosome length, independent of its developmental stage. Upper limits for particle capturing increase with increasing developmental stage and range from 15 µm for youngest nauplii to 250 µm for adults, depending on development of the mouthparts (Berggreen et al. 1988). For food detection, copepods use chemo- and mechanoreceptors on their antennae (Poulet et al. 1986). Chemoreceptors detect chemical signals, such as amino acids (Poulet et al. 1986, Tiselius 1992) or exudates and extracts of algae (Huntley et al. 1986). Mechanoreceptors detect hydrodynamic signals and are necessary in detecting motile prey or larger particles (Lenz and Yen 1993).

1.2.1 Feeding behaviour

Copepods generate feeding currents with their antennae and maxillipeds drawing material towards the mouth (Cowles and Strickler 1983). They respond to increased food availability with increased ingestion linearly up to a saturation level (Mayzaud et al. 1992). Furthermore, temperature boosts ingestion rates up to a critical level (White and Roman 1992), beyond that ingestion decreases. Most copepods show a diel feeding periodicity (e.g. Tiselius 1988, Landry et al. 1994), with highest feeding intensities during dusk and dawn. Furthermore, copepods adjust their feeding mode to the particle sizes they encounter: small particles are ingested by regular flapping of the mouthparts, whereas larger ones are handled individually (Price and Paffenhöfer 1986). Copepods may bite off pieces of large algae, remove the long spines from *Chaetoceros* sp. or squeeze out the contents of dinoflagellates (Strickler, pers. comm.), and they may even "nibble" on fish larvae (Knotz, pers. comm., Yen 1987).

There are two main predatory feeding modes – the ambush and cruising type (Jonsson and Tiselius 1990). Ambush predators, such as *A. clausi* or *Centropages* spp., with a slow sinking behaviour interrupted by short jumps, have the advantage of not being detected until they attack. This strategy makes them more successful in capturing motile prey (Paffenhöfer and Knowles 1980, Kiørboe et al. 1999). Cruising predators, such as *T. longicornis*, create a constant, strong and wide-ranging feeding current and feed more or less indiscriminately on whatever prey gets into their reach and is not able to escape (Paffenhöfer and Knowles 1980, Jonsson and Tiselius 1990). Switching behaviour between feeding modes is possible, and already known from *Acartia tonsa* (Jonsson and Tiselius 1990, Kiørboe et al. 1996).

The question whether copepods feed selectively or unselectively is still discussed. It is suggested that copepods select larger particles in relation to their body size (e.g. Hansen et al. 1994, Knotz 2006). Furthermore, copepods are able to discern different food qualities by perception of different amino acids (Poulet and Quellet 1982), and in that way select particles with higher nutritional quality (e.g. Koski and Klein Breteler 2003). It is also suggested that copepods switch between non-selective and selective feeding behaviour, depending on the quantity of food particles. If food particles are scarce, they feed indiscriminately, if food particles are abundant, they select the particles with the best nutritional value for their needs (Donaghay 1988). At the end, selectivity seems to be the result of the combination of cost and benefit with respect to concentration, usability and nutritional adequacy of prey items (e.g. Price and Paffenhöfer 1986) as well as predators and prey behaviour (Jonsson and Tiselius 1990, Titelman and Kiørboe 2003).

1.2.2 Inter- and intra-specific predation (cannibalism)

In a strict sense, the term cannibalism is reserved for intraspecific predation. In this study, it is used for both, intra- and inter-specific feeding within the calanoid copepods. The risk of being eaten by copepods declines with ascending developmental stage, due to larger size and/or higher escape capability (Landry 1978, Lonsdale et al. 1979, Daan et al. 1988). Behaviour of predator and prey, as well as prey morphology is essential factors influencing the feeding success.

Cannibalism is known for many copepod species, both on eggs (e.g. Kang and Poulet 2000, Sell et al. 2001) and nauplii (reviewed in Bonnet et al. 2004). The presence of empty or crumpled egg-shells in experimental containers (e.g. Ianora and Poulet 1993, Ceballos et al. 2006) or differences between egg production rates and abundances of nauplii in the field in the absence of other predators (Peterson and Kimmerer 1994, Liang and Uye 1996, Ohman and Hirche 2001) have often been interpreted as results of cannibalism. It has been shown, that ingesting the own offspring may serves as an additional energy resource and may facilitate population survival, when other food is scarce (Heinle 1970, Daan et al. 1988, Ianora and Buttino 1990, Peterson and Kimmerer 1994, Ohman et al. 2002). Thus, there might be seasonal differences of the impact of cannibalistic feeding within a community, but knowledge about this is still scarce.

2 THESIS OUTLINE

The present work aims at studying the life-cycle strategies and feeding ecology with respect to cannibalism of dominant calanoid copepods in the German Bight (southern North Sea). It is conducted in the framework of the German Global Ocean Ecosystem Dynamics (GLOBEC) project, which investigates the interactions of zooplankton and fish under the influence of physical processes to elucidate the principal mechanisms responsible for the variability of zooplankton and fish production.

The most dominant calanoid copepods in the southern North Sea are *Acartia clausi*, *Temora longicornis*, *Pseudocalanus elongatus*, *Centropages hamatus*, *C. typicus*, *Calanus helgolandicus* and *C. finmarchicus* (Fransz et al. 1991, Krause et al. 1995). Population structure and abundance of these copepods show species-specific seasonal differences and vary strongly with time. The factors controlling life and survival strategies of the populations during the changing living conditions (e.g., temperature, food, predator abundance) are not satisfactorily known, especially at the species level.

The hydrography of the North Sea is changing (Beare et al. 2002), mainly due to a climate-related increased inflow of Atlantic water into the northern North Sea (Reid et al. 2003). In the German Bight, around Helgoland Island, water temperature has been increasing by 1.1 °C since 1962 (Wiltshire and Manly 2004). Changes in hydrographic conditions also affect life-cycles of phyto- and zooplankton and their composition. A delay and shift in spring diatom increase to the end of March was estimated, which was related to warmer sea temperature during autumn and winter (October - December) (Wiltshire and Manly 2004). Higher temperatures during autumn and winter result in a longer persistence of zooplankton grazers and a decrease of the phytoplankton biomass-building potential for spring development. In fact, copepods, which dominated the zooplankton community from the 1950s to the late 1970s, are declining in abundance, while meroplankton with a distinct planktonic life phase has become dominant (Edwards et al. 2005). The numbers of warm-water species, such as *Calanus helgolandicus* or *Centropages typicus* increase, whereas cold-water species, such as *Calanus finmarchicus* or *Centropages hamatus* become less abundant (Beaugrand 2003, 2004). The changes in temperature-cycles may result in changes of phytoplankton development and zooplankton species composition, which in turn, may cause mismatches of species` life-cycles and food resources (Edwards and Richardson 2004).

Small calanoid copepods are known to feed omnivorously, with species-specific predilections (Kleppel 1993). In the context of potential food sources as well as life strategies, the question of cannibalism in these copepods has arisen. In the German Bight, the occurrence and significance of cannibalism has not been studied so far, although cannibalism for the dominant species is known from other regions (e.g. Landry 1978, Conley and Turner 1985, Daan et al. 1988, Sell et al. 2001).

The four free-spawning copepod species *A. clausi*, *T. longicornis*, *C. hamatus* and *C. typicus* dominate the copepod community in the Southern German Bight (Hickel 1975, Greve, unpubl. data). To gain a deeper understanding of their life-cycles and to adjust and improve model predictions, it is essential to determine (1) whether there are changes in composition of copepod species in comparison to earlier studies, (2) how seasonal changes of abiotic and biotic factors influence the copepod life-cycles, (3) whether and which species-specific life strategies may ensure survival during adverse conditions and (4) which impact cannibalism has on the copepod community. Therefore, the *in situ* reproductive activity (egg production, hatching success, proportion of spawning females) and stage-specific abundance of these four species is investigated, natural birth and stage-specific mortality rates are calculated, and inter- and intraspecific predation rates on young offspring (eggs and young nauplii) are determined in laboratory experiments. Differences in life-cycle strategies and feeding ecology are discussed with respect to the impact on copepod community structure in the German Bight. In a theoretical approach the results of field and laboratory experiments are combined to estimate the potential seasonal impact of cannibalism in the field.

3 MATERIAL AND METHODS

3.1 Study area

The North Sea is a continental shelf sea in the northern temperate climate zone with an area of about 575.000 km^2 and a mean depth of 100 m (Banner et al. 1980). It is influenced by waters from the adjacent Atlantic Ocean and the marginal Baltic Sea. Water of high salinity enters the North Sea from the Atlantic via the English Channel in the south and the Fair Isle Current and the Norwegian deep trench in the north. Water with low salinity comes via Kattegat-Skagerrak from the Baltic Sea. The main freshwater and nutrient input into the North Sea derives from the rivers Elbe, Weser and Ems (Krause et al. 1995).

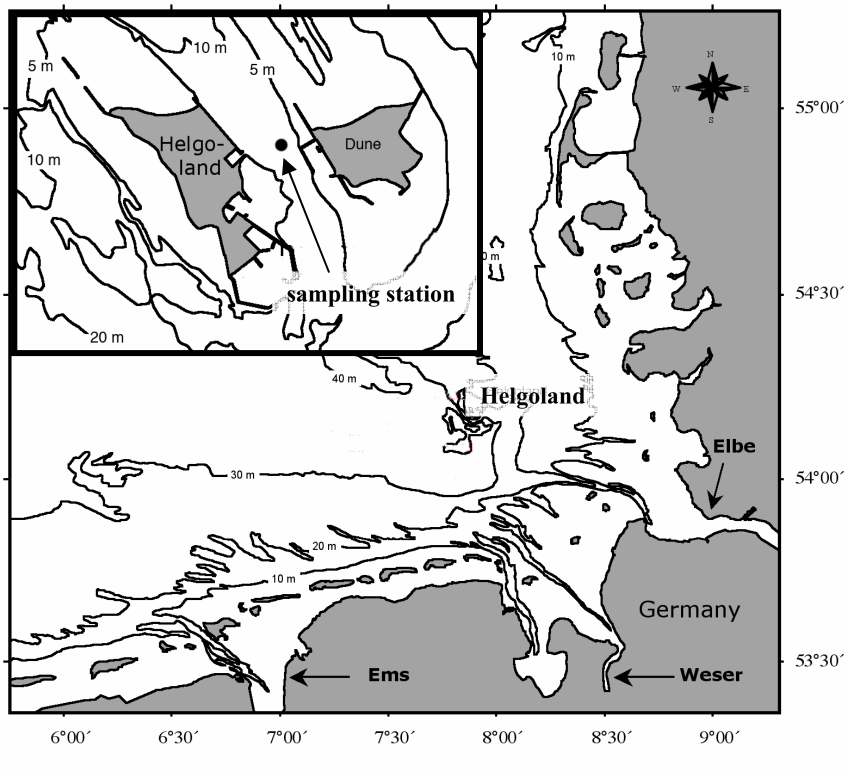

Fig. 1 Map of the German Bight and Helgoland Island with the location of the sampling station Helgoland Roads (54° 11.3`N, 7° 54.0`E). The contour lines show the water depth.

The German Bight comprises the shallow, south-eastern part of the North Sea (Fig. 1). Water depths range from 20 to 40 m (Otto et al. 1990). There are three main water masses influencing the hydrography of the German Bight: Atlantic water, central North

Sea water, and coastal waters (Krause et al. 1995). The formation of frontal zones, due to the coincidence of waters masses of different origins, is common in the German Bight (Otto et al. 1990). Such fronts are characterised by strong horizontal gradients of salinity and/or temperature. In the west of Helgoland Island upwelling fronts are found, caused by upwelling central North Sea bottom water forced by easterly wind stress (Krause et al. 1986).

Helgoland is situated in the central German Bight, about 65 km off the German coast. The long term sampling station Helgoland Roads, where all samples for this study were taken, is located between the main island Helgoland and the sand dune island (54° 11.3` N, 7° 54.0` E). Water depth varies tidally between 5 and 10 m. Due to strong tidal currents and the shallow depth the water column around the island is permanently mixed (Radach et al. 1990). The abiotic factors, water temperature and irradiance show a pronounced seasonality around Helgoland, as typical for temperate regions. In general, salinity is slightly higher during winter, due to a stronger influence of Atlantic water. Nutrient concentrations also show a pronounced annual cycle – high nutrient concentrations during winter, which decrease during spring and reach lowest concentrations mostly in early summer (Radach and Gekeler 1996).

3.2 Sampling

Surface water samples for temperature, salinity, phytoplankton composition and biomass were collected between September 2003 and August 2005 daily at Helgoland Roads by the Biological Oceanography group of the Biologische Anstalt Helgoland. Surface water temperature was measured immediately, salinity was measured in the laboratory by Goodline AutoSal salinometer. The water-sample was gently mixed and sub-sampled into a glass bottle. A phytoplankton sub-sample was preserved with Lugols solution. 25 mL of samples were counted to species level using the Utermöhl method and converted into carbon content with the program `Count` (Tripos Inc., Germany), which is based on the calculations by Hillebrand et al. (1999).

For the determination of zooplankton composition, samples were collected between 8:00 and 10:00 in the morning, in vertical hauls from near the bottom to the surface. A Nansen net (0.35 m^2 opening area, 150 µm mesh size) was used for sampling adult copepods and copepodids. From September 2003 to May 2004, additionally nauplii abundance was sampled with an Apstein net (0.023 m^2 opening area, 55 µm mesh size). The volumes of water that was filtered by the nets were measured using calibrated flow meters fitted in the net openings. The samples were preserved immediately in 4% Borax buffered formalin-seawater solution until analysis under a binocular microscope in the laboratory. Calanoid copepods were identified to species level and life stage (adults, copepodids CI/II, CIII, CIV/V). Nauplii were identified to species level, but not to developmental stage. Living females for experiments were collected as needed by oblique net tows (280 µm Nansen net or 500 µm Calcofi net) at Helgoland Roads and arrived in the laboratory within 2h.

3.3 Reproductive activity

Egg production rate and proportion of spawning females of the four dominant calanoid species *Acartia clausi*, *Centropages hamatus*, *C. typicus* and *Temora longicornis* were determined at least four times per month. In the laboratory, 30 intact adult females were randomly sorted and placed individually in cell wells (Corning) filled with 10 mL of 55 µm prefiltered seawater. The wells were incubated at ambient temperature and light regime in a cold room or an incubator chamber (WTB Binder). After 24 h the wells were inspected, females were removed and all eggs and eggshells were counted. Egg production rates (EPR) were calculated as the number of eggs spawned per female per day. To study hatching success, eggs were incubated in cell wells at *in situ* temperature and hatching was controlled daily for up to 10 days after spawning.

3.4 Stage duration times

Preparatory, for estimation of birth and mortality rates, stage duration times were determined for the monthly mean temperatures. Egg developmental time D was calculated with the equations of McLaren et al. (1969) (*A. clausi*), Corkett and McLaren (1970) (*T. longicornis*) and McLaren et al. (1989) (*Centropages* spp.). Species and stage-specific developmental times were calculated from generation and stage duration times. Generation times were determined using the monthly mean temperatures and the equations of McLaren (1978) for *A. clausi*, of Klein Breteler and Gonzales (1986) for *T. longicornis* and of Liang et al. (1996) for *Centropages* spp.. For the determination of stage-specific duration times we assumed that the relative proportion of stage duration and the generation time is the same, regardless temperature (Corkett and McLaren 1970, Landry 1975). Thus, we divided mean stage-specific duration from the literature (Klein Breteler et al. (1994) for *A. clausi*, and Halsband-Lenk (2001) for *T. longicornis* and *Centropages* spp.) by the given generation times. The stage-specific developmental times were obtained by multiply the calculated proportion of each developmental stage with the generation times we determined for each species and month.

3.5 Birth, population increase and mortality rates

Instantaneous birth rates were calculated with the density of viable eggs (EPR corrected for hatching multiplied by female abundance and egg developmental time) and the individual numbers of the corresponding copepod species by the equation of Edmondson (1968). The population increase was calculated by the equation of Paloheimo (1974). Stage-specific mortality rates were calculated by the vertical life table approach of Aksnes and Ohman (1994) using the field abundances (for detail see MANUSCRIPT).

3.6 Predatory feeding

3.6.1 Collection of predators and rearing of prey

Feeding experiments were conducted between June and August in 2004 and 2005 with adult females from field, that were acclimated for 48h at 10°C without food to avoid spawning during the experiments. Eggs were obtained from females kept at 15°C and fed ad libitum with cultured *Rhodomonas* sp.. The eggs were incubated in Petri dishes at 15°C to obtain nauplii. Nauplii were used as prey at stage II (for detail see PUBLICATION II).

3.6.2 General set-up

The experimental flasks (640 mL) were filled with 0.45 µm prefiltered seawater and different concentrations and combinations of prey and four approximately equally sized females of one species. They were incubated for 6 h on a slowly rotating plankton wheel (1 to 2 rpm) at 10°C and under dimmed light exposure. The experiments were separated into single and mixed animal prey experiments and into experiments with a mixture of animal and algae prey (for detail see Tab. I and PUBLICATION II).

Table I. *Acartia clausi*, *Temora longicornis*, *Centropages hamatus*, and *C. typicus*. Total number of experiments per species conducted with total number of experimental flasks in parentheses

	predator species			
experiment	***A. clausi***	***T. longicornis***	***C. hamatus***	***C. typicus***
I single prey				
eggs (3 species) (up to 7 concentrations 30 to 210 eggs flask^{-1})	5(51)	7(68)	5(45)	6(5)
nauplii (3 species) (up to 5 concentrations 20 to 100 nauplii flask^{-1})	5(43)	5(47)	5(44)	5(44)
II mixed animal prey				
$A_{Egg} + T_{Naup}$ (60 : 60 flask^{-1})	1(4)	1(7)		1(3)
$T_{Naup} + C_{Naup}$ (40 : 40 flask^{-1})	1(3)	1(7)		1(5)
III animal prey and diatom				
T_{Egg} constant + *Th. weissflogii* (60 eggs flask^{-1} + 4 diatom concentrations 0 to 200 µg C L^{-1})	2(12)	2(12)		2(12)
C_{Naup} + *Th. weissflogii* constant (60 nauplii flask^{-1} + 60 µg C L^{-1} diatom)	1(9)	1(9)	1(9)	1(9)

3.6.3 Seasonal impact of cannibalism in field

To determine the potential impact of cannibalism in field, monthly means of all field abundances and the results of single prey experiments were used. Species-specific egg densities were calculated by multiply EPR with female abundance and egg developmental time. The density of young nauplii was assumed to correspond with egg density corrected for hatching success. In the single prey feeding experiments, eggs and nauplii of *A. clausi*, *T. longicornis* and *Centropages* spp. were feed separately to each species. For regression analyses (Statistica 6, StatSoft Inc., Tulsa, OK, USA), the three egg and the three nauplii species were pooled, respectively. The data from the regression analyses were used for a trend analysis (Excel), to deduce feeding rates at field prey density. The laboratory feeding rates f, measured at 10 °C, had to be corrected for temperature due to the dependence of feeding on temperature (White and Roman 1992). I calculated a mean Q_{10} of 3.8 with the values given by Conover and Huntley (1980), Deason (1980), Kiørboe et al. (1982) and Sell et al. (2001). The feeding rates at field temperatures were calculated with the equation:

$$F = f/(3.8\hat{}((10-t)/10))$$

where F is the feeding rate at field temperature, f is the laboratory feeding rate at 10 °C and t is the monthly mean temperature in field. The loss was given as % d^{-1} of the standing stock.

4 RESULTS AND SYNOPTIC DISCUSSION

In this chapter, the factors influencing the life-cycles and the impact of cannibalism within the calanoid copepod species *Acartia clausi*, *Centropages hamatus*, *C. typicus* and *Temora longicornis* in the southern German Bight are summarised and discussed. The publications contain data on special topics of this study, which are discussed in more detail there. Hence, here I present synoptic discussion of the entire seasonal data sets of hydrography and phytoplankton, copepod stage-specific abundances, reproductive activity, and birth and mortality rates. In a following section, the potential seasonal impact of cannibalism was calculated by a theoretical approach. The laboratory feeding rates on young offspring were combined with field abundances of copepods.

4.1 Environmental conditions

Around Helgoland Island, water temperature showed a pronounced seasonal cycle. Maximum temperatures of about 20 °C were reached in summer, lowest temperatures of about 2°C in late winter (Fig. 2a). Salinity varied within and between years, without a clear seasonality. During this study a mean salinity of 32.3 ± 1.1 was measured. The total phytoplankton biomass (PPC in µg C L^{-1}) followed a seasonal cycle with highest values between April and August, and with values mostly below 100 µg C L^{-1} during the rest of the year (Fig. 2b). The occurrence and dimension of phytoplankton biomass maximum varied between years, and reached highest values of 1324, 1469 and 4850 µg C L^{-1} in August 2003 and 2004, and May 2005, respectively. Phytoplankton biomass was usually dominated by diatoms, which contributed between 40 and 90 % of PPC, depending on season (Fig. 2c). In summer, the biomass of dinoflagellates was highest accounting up to 30 % in June and July.

4.2 Distribution

Calanoid copepods occurred all year round with a pronounced seasonal cycle in abundance (Wesche et al. 2007, Fig. 3). In early spring, the proportion of calanoids increased strongly until a proportion of more than 80 % of the total copepod

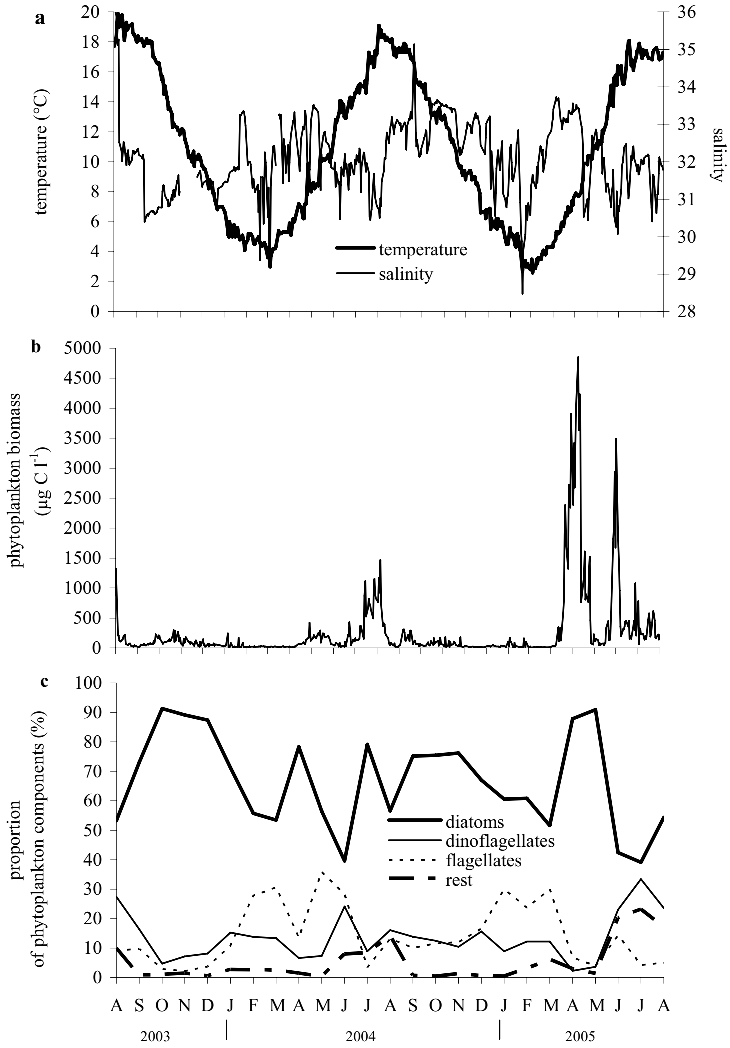

Fig. 2 Annual cycles of temperature and salinity (a), phytoplankton biomass (b), and composition of phytoplankton (c) at Helgoland Roads. The fraction ′rest′ consisted of *Noctiluca scintillans*, coccolithophorids, silicoflagellates, ciliates and green algae.

community in autumn. In autumn, the proportion of cyclopoid and harpacticoid copepods increased, which dominated the community during winter. This seasonal pattern indicates good adaptations of cyclopoid and harpacticoid copepods to autumn and winter conditions.

This study focused on the four calanoid species being dominant during spring and summer in the German Bight (Krause et al. 1995). *A. clausi*, *T. longicornis*, *C. hamatus* and *C. typicus* contributed seasonally more than 70 % of all calanoid copepods (Fig. 3b). *Paracalanus parvus*, *Pseudocalanus* spp. and *Calanus* spp. were combined as `other calanoids` and were dominant during winter (Wesche et al. 2007, Fig. 3b), which also implicated different adaptation to environmental conditions, especially with respect to temperature, salinity and food requirements.

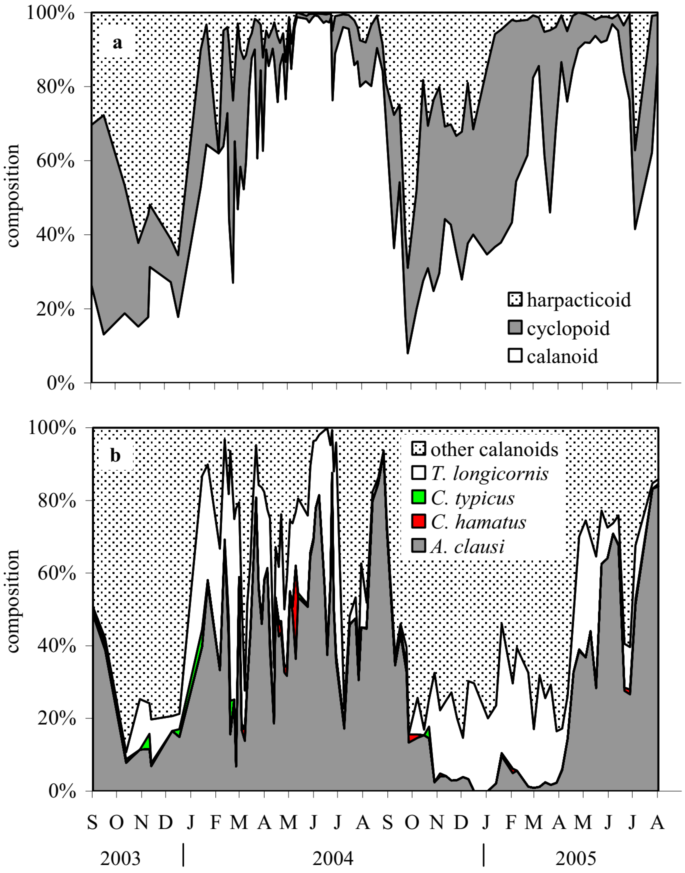

Fig. 3 Annual cycles of composition of total copepod community (a) and calanoid copepod community (b) at Helgoland Roads. Other calanoids: *Paracalanus parvus*, *Pseudocalanus elongatus*, *Calanus* spp..

The copepod species investigated showed distinct characteristics in all developmental stages, from eggs (Fig. 4) to nauplii (Fig. 5) and adults (Fig. 6), except in the congener *Centropages hamatus* and *C. typicus*, where differentiation was not possible in the egg and nauplii stages. All were relatively small species (Fig. 6). They were free-spawners, which broadcast their eggs directly into the water. In comparison to most species of high latitudes (for example *Calanus* spp.) they have relatively low lipid reserves (2.4 to 5.5 % of dry mass, Knotz 2006). Their distribution varies from cold-temperate (*T. longicornis*, *C. hamatus*) to warm-temperate regions (*A. clausi*, *C. typicus*), and except for *C. typicus* all are mostly neritic species (Fransz et al. 1991, Krause et al. 1995).

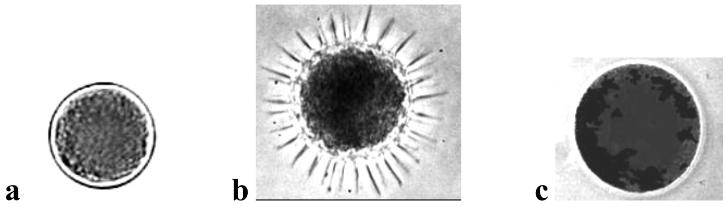

Fig. 4 Eggs of *Acartia clausi* (a), *Centropages* spp. (b), and *Temora longicornis* (c)

Fig. 5 Nauplii developmental stage II of *Acartia clausi* (a), *Centropages spp*. (b), and *Temora longicornis* (c)

PL 869.6 ± 81.3µm

PL 1027.2 ± 111.4µm

PL 1030.9 ± 130.2µm

PL 1241.2 ± 68.1µm

Fig. 6 Adult females of *Acartia clausi* (a), *Temora longicornis* (b), *Centropages hamatus* (c), and *C. typicus* (d). PL: Mean prosome length ± SD of adult females at Helgoland Roads from September 2003 to August 2005.

4.3 Life-cycles

The pattern applicable to all four species was a reproduction peak in spring and an abundance peak in summer. The results confirm the current view of the seasonal cycles of reproduction and population development in temperate regions (e.g. Halsband and Hirche 2001). However, population size, life history and reproductive strategy differed considerably between species, especially with respect to the presence of individuals, the egg production rate, the spawning period and the overwintering strategy. All these variables also differed seasonally, which might have been caused by annual changes in hydrographic conditions, food composition, predator abundance and composition, as well as by the complex interactions of all possible influencing factors.

Acartia clausi

Three *Acartia* species have been reported from the North Sea: *A. clausi*, *A. longiremis* and *A. bifilosa*, with the first being predominant (Krause et al. 1995), and also the most dominant among the calanoid copepods. During the present study, only *A. clausi* was found. It occurred throughout the year with highest numbers in early summer (up to 24 900 ind m^{-3}). In winter, abundance was low and males were virtually absent (Wesche et al. 2007, Fig. 7a). The stage-specific population composition showed a high proportion of adults and late copepodite stages (CIV/CV) during autumn and winter, whereas young copepodids became dominant in spring and summer. Nauplii of *Acartia* spp. outnumbered the other stages most of the time. They were also found during winter, and increased in abundance during spring (Wesche et al. 2007).

In the German Bight, a pattern of discontinued reproduction with a clear disruption during winter and a springtime recovery was typical for *A. clausi*. The results of this study confirm the earlier observations of Halsband and Hirche (2001), with respect to temporal pattern and maximal egg production rates of about 25 eggs fem^{-1} d^{-1} (Fig. 7a). In other regions, such as the Mediterranean, *A. clausi* reproduces year-round, with winter and spring as the main spawning season (Gaudy 1972, Ianora and Buttino 1990). As temperatures there are not too different from autumn temperatures in the North Sea, this abiotic factor is not a likely explanation for the observed seasonal pattern in the German Bight. The complete cessation of reproductive activity at the end of autumn,

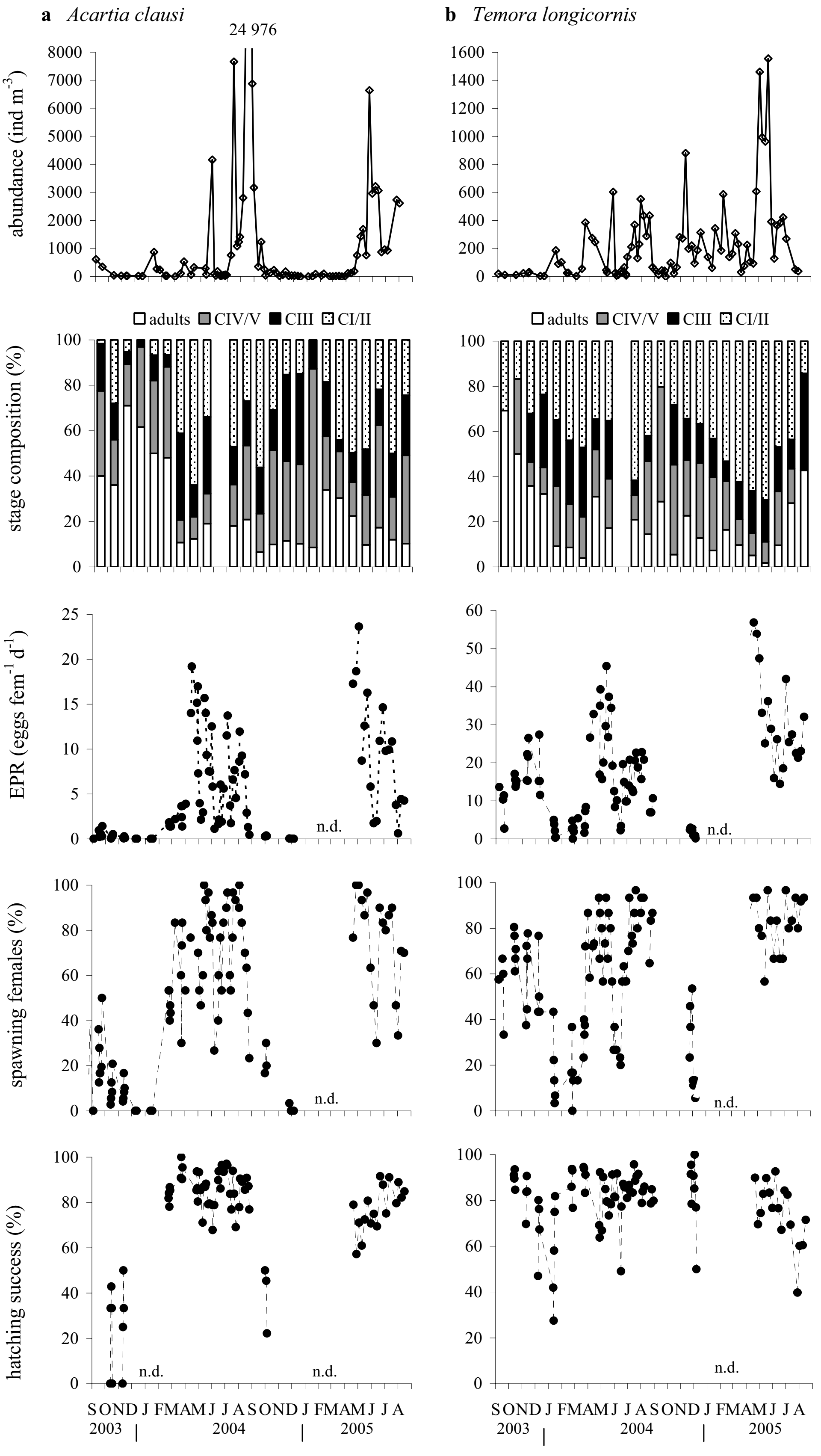

Fig. 7 *Acartia clausi* (a) and *Temora longicornis* (b). Seasonal cycles of total abundance, stage composition, egg production rate (EPR), proportion of spawning females and hatching success at Helgoland Roads.

during a time when food is still available, and the initiation of egg production during a time of low food concentrations indicates intrinsic controls, and an arrested reproductive dormancy (Hirche 1998). Thus, a female diapause is suggested for *A. clausi,* like in the congener *A. longiremis* from North Norwegian fjords (Norrbin 2001). Hence, further examinations are needed to confirm this strategy for *A. clausi*.

Reproductive activity (EPR, proportion of spawning females, hatching success) in *A. clausi* peaked when population size was still low (Wesche et al. 2007, Fig. 7a - April). Thus, high birth rates were found in spring and summer, and *A. clausi* was capable to renew the population within three to four days (Fig. 7a, MANUSCRIPT). Birth rates were correlated to biomass of dinoflagellates, ciliates and flagellates (MANUSCRIPT). Due to the high content of essential fatty acids, microzooplankton, such as dinoflagellates and flagellates, seem to be a more suitable food for reproduction than phytoplankton, and have also positive effects on the viability of eggs (e.g. Kleppel et al. 1998, Veloza et al. 2006).

Compared to the other species, temperature had no influence on the reproduction of *A. clausi* (MANUSCRIPT). The independence of temperature supports the hypothesis of an intrinsic control of reproduction. Otherwise, reproduction could also be affected by seasonal changes in light-intensity, but data to prove this assumption were not available. There was a pattern pointed to lower hatching success in autumn, which might suggest that resting eggs are produced during this season. For this species, resting eggs have been reported from the Pacific (e.g. Kasahara et al. 1974, Marcus 1990), whereas their existence has not yet been reported for the German Bight (Engel 2005). However, resting eggs would also explain the high abundance of *Acartia* nauplii before reproduction has started (Wesche et al. 2007).

Temora longicornis

This species occurred year-round with all developmental stages. In general, its abundance was much lower than that of *A. clausi* (max. 1554 ind m^{-3}). Nauplii were also present during winter and showed a strong increase in early spring (Wesche et al. 2007, Fig. 7b). Most of the time, the proportion of young (CI-CIII) and late copepodite stages (CIV-adult) was relatively balanced, except for spring when young stages contributed up to 80 % of the population, and in autumn 2003 and 2004 when older copepodids were dominant. Within the young copepodite stages, stage CI-CII was predominant (Fig. 7b).

Reproduction of *T. longicornis* is characterised by a response to its nutritional environment (e.g. Fransz et al. 1989, Wesche et al. 2007). Thus, continuous breeding is generally observed (Kiørboe and Nielsen 1994, Halsband and Hirche 2001, Wesche et al. 2007, MANUSCRIPT). In the present study, highest egg production rates of up to 57 eggs fem^{-1} d^{-1} in spring and low egg production during winter were measured (Fig. 7b). In autumn 2003, egg production increased unexpectedly. This could be related to an unusual phytoplankton bloom (Wesche et al. 2007). The controlling factors of birth rate in this species were temperature, salinity, and the biomass of flagellates and diatoms (MANUSCRIPT).

With respect to birth rates, *T. longicornis* is capable to renew its population within less than one day, except for the winter (MANUSCRIPT). The high proportion of young developmental stages on total population (CI-CIII accounted for more than 50 % on population size), could be caused by the high egg production rates. Otherwise, mortality of copepodite stages CIII-CV was most of the time about 60 % (MANUSCRIPT), which may explain the low proportion of late developmental stages in the population of *T. longicornis* (Fig. 7b).

T. longicornis is known to produce resting eggs in addition to subitaneous eggs (Lindley 1990, Engel and Hirche 2004). Castellani and Lucas (2003) suggested spring and late summer as the main period for resting egg production. This study could not clearly identify periods of resting egg production, but times of decreased mean hatching success in late autumn-early winter 2003, and summer 2004 and 2005, suggests to resting egg production during these periods. Nauplii, emerging from resting eggs probably contributed to the still high proportion of young copepodids during winter, when reproduction was low. Furthermore, the strong increase in nauplii abundance at a time before the spring bloom occurred and before the highest reproductive activity was reached may originate from resting eggs (Wesche et al. 2007).

Centropages hamatus and *C. typicus*

Both species occurred in low numbers in the German Bight with maximal abundance of 450 ind m^{-3} during this study (Fig. 8). Unfortunately, copepodite stages of *C. hamatus* and *C. typicus* were determined to species level only until May 2004 (Wesche et al. 2007). Therefore, species-specific data on seasonal differences in stage-specific abundances as well as birth and mortality rates were lacking and could only be presented on genus level. Regarding the fraction of adults, which have been determined to species level, the temporal absence or very low portion of *C. hamatus* in the pelagic was observed during late autumn and early winter (Fig. 8). This species appeared in early spring and stayed throughout the summer (Halsband and Hirche 2001, Wesche et al. 2007). In adjacent regions, such as Kattegat and English Channel, *C. hamatus* is recorded year-round and even reproduction was not disrupted (Kiørboe and Nielsen 1994, Le Ruyet-Person et al. 1975). Thus, the few individuals found during winter might be advected into the waters around Helgoland (Wesche et al. 2007).

C. typicus is deemed to be a species associated with warmer and more saline Atlantic waters. It had formerly been considered as a sporadic immigrant into the German Bight (Fransz et al. 1991), but in recent years it has become more abundant, especially from late summer to winter (Hay 1995, Halsband-Lenk et al. 2004). Nevertheless, the occurrence of *C. typicus* varied strongly and still implied a dependence on advection and prevailing currents. Lindley and Reid (2002) suggested population centres of *C. typicus* in the German and the Southern Bights, persisting throughout the winter. However, during this study, specimens of *C. typicus* were often absent in quantitative vertical tows. On the other hand, large adults (mostly females) of this species were found in very high numbers in longer net tows during summer (personal observation). The proportion of young copepodite stages (CI-II) in *Centropages* spp. was often lower than that in the other species and showed no clear seasonal trend, in the present study. From autumn 2004 to the end of the study in summer 2005 copepodite stage III (CIII) was the predominant developmental stage in *Centropages* spp.. This might be caused by the higher egg production in 2005 compared to 2004.

Maximum egg production rates of 80 eggs fem^{-1} d^{-1} in *C. hamatus* and 106 eggs fem^{-1} d^{-1} in *C. typicus* were the highest of the species investigated during this study (Fig. 8). Species-specific egg production rates and birth rates of the genus were higher in 2005

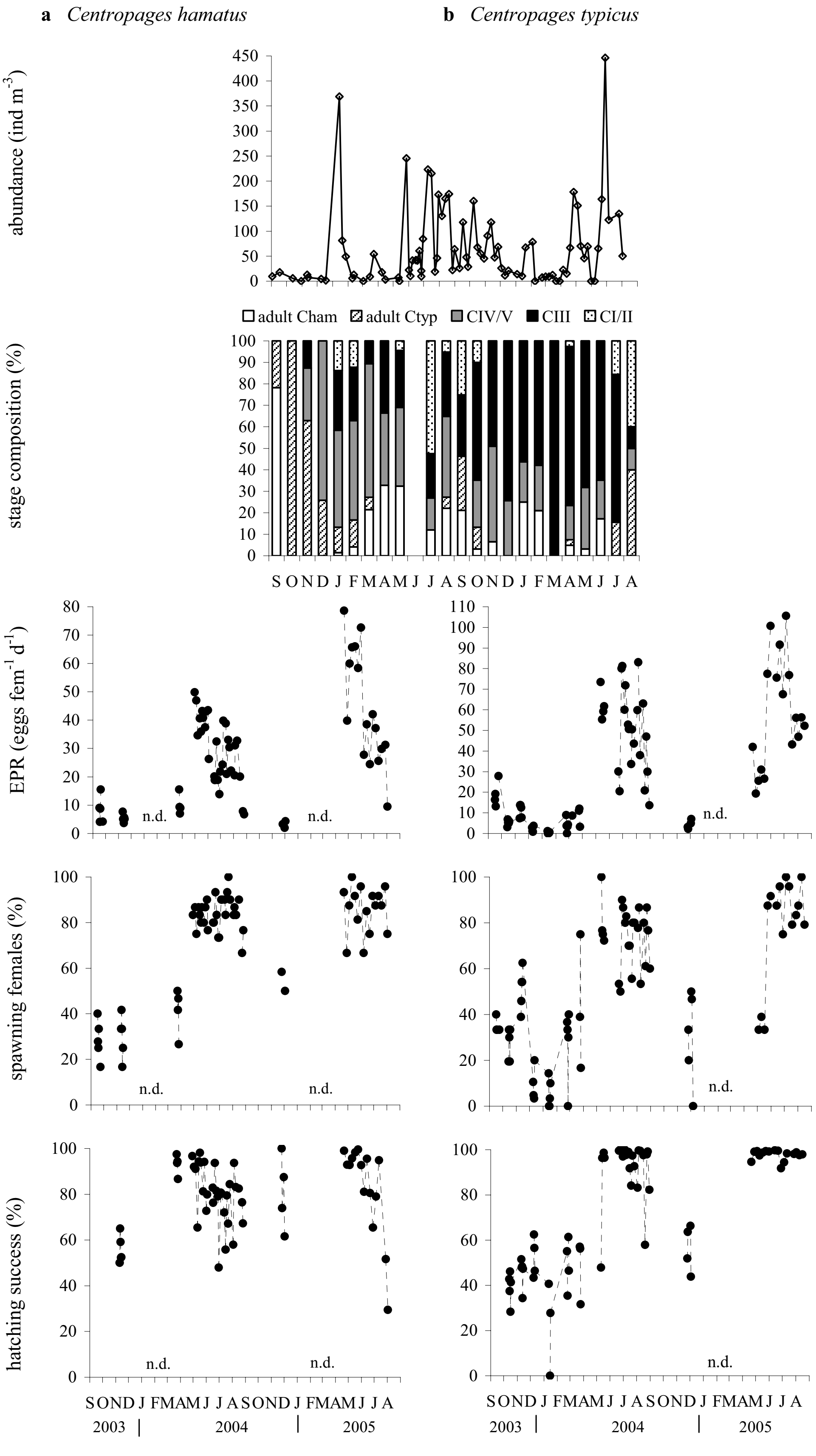

Fig. 8 *Centropages hamatus* (a) and *C. typcius* (b). Seasonal cycles of total abundance, stage composition, egg production rate (EPR), proportion of spawning females and hatching success at Helgoland Roads.

than in 2004, which may have caused the higher proportion of young stages in 2005 with respect to genus level. Birth rates of *Centropages* spp. were positive correlated to temperature and dinoflagellate and ciliate biomass, and negative to salinity and flagellate biomass (MANUSCRIPT). The temperature correlation of the species-specific egg production appeared to be opposite in the two species. Egg production, proportion of spawning females, and hatching success were negatively correlated to temperature in *C. hamatus* and positively in *C. typicus*. This result supports the separation into the `cold-water` species *C. hamatus* and the `warm-water` species *C. typicus* (Grant 1988). They seem to differ in temperature-dependant adaptations of their reproductive strategies.

The existence of resting eggs in *C. hamatus* is generally accepted for the North Sea (Lindley 1990) and also for the German Bight (Engel and Hirche 2004). Due to the absence of hibernating stages in the pelagic, the population has to be built-up by nauplii, that are emerging from resting eggs in spring. In *C. hamatus*, the seasonal course of hatching success suggested late summer and autumn as period of resting egg production, although the trend was not really clear (Fig. 8a). Mean hatching success was about 60 %, compared to spring with a hatching success of more than 90 %. In *C. typicus* a pattern with low hatching (less than 50 % during autumn and winter) was much more pronounced (Fig. 8b). During summer hatching success was always more than 90 %. However, in this species the existence of resting eggs is still disputed (e.g. Ianora and Scotto di Carlo 1988, Lindley 1990, Miralto et al. 1995). Engel and Hirche (2004) found no evidence of resting eggs in the German Bight. In the present study, calculated egg developmental time never exceeded five days (Annex Table I). Thus, viable subitaneous eggs had to hatch within the control interval of ten days.

There is evidence to assume a progressive climate-related change in species composition in *Centropages* spp., in the German Bight: (1) warmer temperatures especially during autumn and winter (Wiltshire and Manly 2004), (2) stronger dominance of the more oceanic species *C. typicus* (Halsband-Lenk et al. 2004, personal observation), (3) extremely low individual numbers and the only sporadic occurrence of *C. hamatus* even in spring (personal observation) and (4) high egg production rates of *C. typicus* already during summer. This has to be considered in further studies and special attention should be given to the species-specific occurrence, abundance and proportion, all on developmental stage level.

4.4 Factors controlling population size

Population size varied as a result of addition or loss of individuals. In the present study, no correlation of population increase with birth rate was found, which implicated a stronger influence of mortality on population size around Helgoland Island (MANUSCRIPT). Halsband-Lenk (2001), who investigated copepod reproduction and development in the same area several years before, found no reflection of egg production rates in seasonal distribution patterns and suggested a greater importance of mortality rather than birth for population development, as well.

Mortality factors differed somewhat between species and also between developmental stages (MANUSCRIPT). Temperature exerted the highest impact on total mortality of all species, although this effect was not seen in the correlation of stage-specific mortalities. The strong temperature effect on mortality was already found by Hirst et al. (2007) for young developmental stages (eggs-nauplii stage NII) of *Calanus helgolandicus*. Hirst and Kiørboe (2002) demonstrated that longevity of adults is reduced at high temperatures, due to the thermal costs of an increased metabolism. Thus, a physiological cause for high total mortality with increasing temperature was also assumed in the present study.

Predation of chaetognaths (*Sagitta* spp.) and female copepods might account for the total mortality as well as for mortality of mostly older developmental stages in *A. clausi* and *T. longicornis* (MANUSCRIPT). With respect to adult copepods as predators this result was unexpected, as the feeding efficiency on the own offspring declines with ascending developmental stage of the prey, due to larger size and/or higher escape capabilities (Landry 1978, Londsdale et al.1979, Daan et al. 1988). Abundance of fish larvae was correlated with the mortality of copepodite stages CIII-adult in *T. longicornis* and *Centropages* spp.. These species were larger in size compared to *A. clausi*. Hence, although they had a relatively lower abundance, they could be easier detected by visual oriented predators, such as fish larvae. Abundance of hydromedusae and ctenophores did not influenced mortality of copepods during this study, although other investigations had demonstrated the potential of that these groups to decimate copepod populations significantly, when they were abundant (e.g. Daan 1986, 1989, Pagés et al.1996). And they were as abundant as chaetognaths (MANUSCRIPT). An effect of hydromedusae is dependent on abundance as well as species composition, as it is assumed, that mostly anthomedusae (ambush predators) were successful in feeding on copepods and their nauplii, whereas leptomedusae (cruising predators) prefer soft-bodied prey, such as chaetognaths (Purcell and Mills 1988, Costello and Colin 2002). Thus, an exact differentiation of predator species is also necessary, which was lacking in the plankton examination of the present study. The identification of factors influencing population sizes is extremely difficult, as always a combination of abiotic and biotic factors has to be considered. The understanding of the interactions of the different factors is still in progress and further work has to be done.

4.5 Inter- and intra-specific predation

4.5.1 Laboratory experiments

The laboratory study, emphasising on cannibalism in calanoid copepods, had clearly shown the capability of the calanoid copepod species to ingest all types of eggs and nauplii offered (PUBLICATION II). The feeding rates increased with increasing prey density. However, absolute values differed, depending on predator species, prey morphology, prey behaviour, as well as on the concentration of algae prey as alternative food. The maximal feeding rates varied between 22 (*A. clausi*) and 64 eggs fem^{-1} d^{-1} (*C. typicus*), and 16 (*A. clausi*) and 45 nauplii fem^{-1} d^{-1} (*C. hamatus*), with additional differences with respect to egg or nauplii type (PUBLICATION II). Regarding energy gain for the predator, the females under optimal feeding conditions ingested up to 22 % body C d^{-1} when feeding on eggs, and up to 29 % body C d^{-1} on nauplii (PUBLICATION II).

In general, eggs of *Centropages* spp. were less preyed on than eggs of *A. clausi* or *T. longicornis*. The spiny surfaces of these eggs (Fig. 4b) suggest have causing a worse handling, and thus, protecting the eggs against predation (PUBLICATION II). In nauplii feeding experiments, all predator species ingested much more *Centropages* spp. nauplii compared to the other two nauplii types. Indeed, the nauplii of *Centropages* spp. with a constant swimming behaviour differed from the jump-sink behaviour of *A. clausi* and *T. longicornis* nauplii (Titelman and Kiørboe 2003). The constant swimming caused constant hydrodynamic signals, which simplified the detection by predators. From mixed animal prey experiments, behaviour dependent predilections were more obvious. Ambush predators, such as *A. clausi* and *Centropages* spp. preferred more on motile prey (nauplii), whereas the cruising species *T. longicornis* ingested more eggs. Thus, the species-specific feeding habits of adults (Jonsson and Tiselius 1990) showed their effects. Additional algae food in concentrations of about 200 µg C L^{-1} reduced predatory feeding most significantly in *T. longicornis*; while in *C. typicus* feeding on young offspring was clearly enhanced.

In conclusion, the differences in laboratory feeding rates and predilections, also with respect to additional mono-culture algal prey, lighted up the complex interactions of concentration and usability of prey (e.g. Price and Paffenhöfer 1986), as well as predators and prey behaviour (Jonsson and Tiselius 1990, Titelman and Kiørboe 2003).

4.5.2 Seasonal impact of cannibalism in field

The results from the laboratory experiments and the stage-specific field abundances were the basis for the calculation of the potential seasonal impact of cannibalism in the field. For this approach, only feeding rates of single prey experiments were used. However, knowledge from mixed prey experiments was considered in the discussion.

I am aware of the difficulties encountered by transferring laboratory results to field conditions, especially with respect to the complexity and variability of natural food webs, the feasibility of laboratory designs, and the still partly known feeding ecology of copepods. Nevertheless, the results of my study provide theoretical maximum rates of cannibalism that are as realistic as field studies, which determine cannibalistic loss without using predatory feeding rates (e.g. Kiørboe and Nielsen 1994, Peterson and Kimmerer 1994). The laboratory feeding rates were corrected for prey and predator densities as well as for field temperatures to approximate more realistic conditions. For the calculation of cannibalistic feeding impact in field, the absence of alternative food was a prerequisite, a situation rarely encountered in the field. Hence, potential impact of female cannibalism might be slightly overestimated, as especially *A. clausi* and *T. longicornis* tended to reduce predatory feeding in the presence of sufficient algae food (PUBLICATION II).

The potential impact of cannibalism on prey abundance reached its maximum in summer 2004, in both egg and nauplii prey. At this time, the predator species were able to reduce the total calculated egg and nauplii density up to 100 and 150 % daily, respectively (Fig. 9).

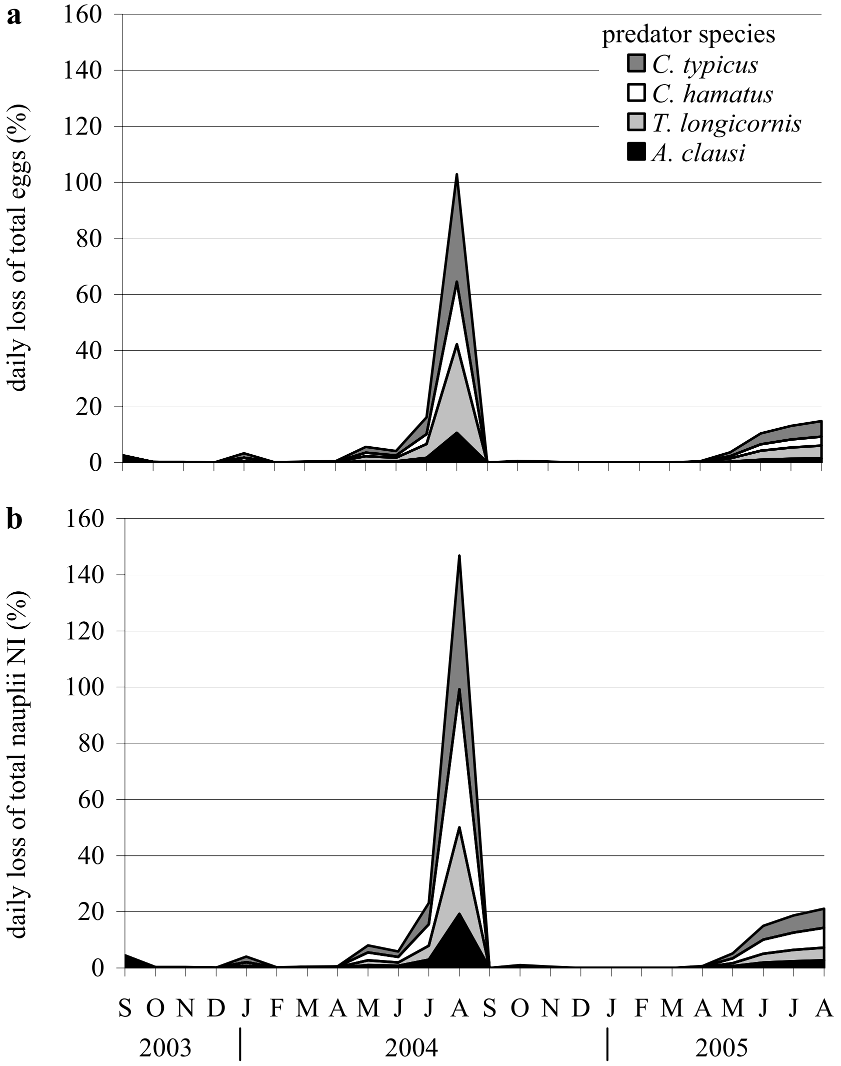

Fig. 9 Seasonal impact of cannibalistic feeding of adult females on copepod eggs (a) and young copepod nauplii (b)

This high predation pressure was restricted to a very narrow time-window. In summer 2005, the impact was much lower than in 2004. During the rest of the year, the daily loss of eggs or young nauplii due to cannibalism was less than 10 %. In the present study, the calculated maximum egg loss due to cannibalistic predation was in the upper range of values given by Ianora and Buttino (1990) and Peterson and Kimmerer (1994). They found a daily loss of eggs between 80 and 99 % during periods of intense breeding. Temporally, maximum loss of offspring in 2004 coincided with the high birth rates in July and August (MANUSCRIPT). This was also true for 2005, but then the impact was less than 20 %. There were annual differences in abundance of adult copepods, which could account for the different impact. Mean pooled abundance of all species during July and August 2004 was 424 ind m^{-3}. This was about four times higher than in 2005. Mortality rates of the egg-nauplii stage could not be related to copepod adult abundance. Only for older copepodite stages a relation between mortality and female abundance was found (MANUSCRIPT).

It has to keep in mind, that egg production rates of all four species were higher in 2005 (Fig. 7 and 8), which could account for higher offspring density. Another explanation, but not considered within the calculation of potential cannibalistic impact and not directly provable by this study, may be the differences in composition and concentration of phytoplankton biomass in 2004 and 2005, especially with respect to dinoflagellate biomass. Dinoflagellates were the only group with higher values in summer 2005 (Jul/Aug) (Fig. 2c). Total phytoplankton biomass in 2005 peaked first in May, about two and a half month earlier than in 2004. Maximum biomass was about four times higher in 2005 than in 2004. The timing of the dinoflagellate biomass peak coincided in both years, but with 145 µg C L^{-1} the concentration in July 2005, was about three times higher than in 2004.

The laboratory experiments with an alternative food source revealed a lower predatory impact in the presence of algae food in concentrations about 200 µg C L^{-1} in *A. clausi* and *T. longicornis* (PUBLICATION II). This threshold concentration was reached in both years during the reproductive period of the copepods, so that this was not a sufficient explanation for the annual differences of cannibalism. In conclusion, the lower cannibalistic impact on offspring in 2005 may be due to a lower density of potential predatory adults in conjunction with higher offspring density and a better food supply relative to copepod abundance.

In this approach, the temperature effect on female feeding activity was considered by correcting the feeding rates with the corresponding Q_{10} value. However, the temperature effect on swimming speed of the prey was not evaluated due to the lack of data. Potential feeding rates on non-motile prey, such as eggs, increase with increasing temperature, due to the higher swimming speed and the higher ingestion rates of predators (e.g. Kiørboe et al. 1982). Considering the temperature effect on nauplii, predation is more complex. Higher swimming speed of predator and prey boosts the encounter rates and thus, the potential predator feeding success. Otherwise, enhanced prey swimming activity and escape ability could negatively affect the predators` success in catching the prey, and this results in lower predation rates.

Another factor affecting predatory feeding was the morphology of the prey, as has been shown by the feeding on spiny eggs compared with others. For cannibalism field estimation of the present study, all egg and nauplii types were pooled, due to the low densities on species-level. Thus, the possibility of different feeding rates due to species-specific prey morphology was neglected. For further investigations on cannibalism prey morphology should be therefore taken into consideration.

In conclusion, around Helgoland Island the density of predators and prey was low most of time. Hence, cannibalism might be of low importance in the field due to low encounter rates, especially during winter. However, at times of high population density, the species were potentially able to reduce the abundance of young offspring significantly. Whether this really occurs in the field remains to be investigated, as so far not many data on detailed feeding ecology are available and the potential of selective feeding of copepods is still discussed (e.g. Knotz 2006, PUBLICATION II). Furthermore, in the field, potential food sources are manifold and the constituents, such as dinoflagellates, flagellates, ciliates, diatoms or detritus are much more abundant than eggs or nauplii. The relative energetic costs to feed on these components are lower than feeding on sparsely abundant eggs and nauplii. Anyhow, if adults encounter copepod eggs or nauplii and could catch them successfully, they will eat them.

5 CONCLUSIONS

The present study observed strong differences in the life-cycle strategies of the dominant calanoid copepod species *Acartia clausi*, *Temora longicornis*, *Centropages hamatus* and *C. typicus* in the German Bight, although they show a similar course of abundance and reproductive activity. The strategy of ceasing reproduction and hibernation of adult females, as found in *A. clausi*, competed successfully with a strategy of reproduction throughout the year combined with the production of resting eggs in *T. longicornis*, or with the strategy of *C. hamatus* with its virtual absence in winter and population built-up in spring by nauplii emerging from resting eggs. There is evidence to assume that the importance of *C. typicu*s in the copepod community around Helgoland Island increases, whereas the congener *C. hamatus* seems to back out. The latter is named to be restricted to colder waters. In the German Bight, the temperature is increasing since the last 60 years, and also a decline in abundance of *C. hamatus* was obvious. Hence, it could be assumed that *C. typicus* displaces *C. hamatus*.

Here, mortality was the factor that accounted for most of the variability in population sizes in all four species. This was not only due to predation by fish larvae or chaetognaths, but also cannibalism may cause a high proportion on mortality in several developmental stages. The theoretical approach demonstrated the potential of cannibalistic predation to reduce the population sizes markedly during times of intense breeding. However, the impact of cannibalism may be neglected during the rest of the year, as densities of potential predators and prey are to low to account for sufficient encounter rates.

It has to mentioned, that there is a high importance to consider both, reproduction and mortality in copepod communities due get realistic results of population dynamics. Therefore, I stresses the importance of high frequency sampling resolution and detailed investigations down to the species-level. The consideration of these differences in future investigations will advance our understanding of copepod ecology. The continuation of high frequency time series sampling and analyses provide an essential basis to detect changes in species composition and could aid in identifying the underlying factors.

6 PUBLICATIONS

PUBLICATION I

Wesche A, Wiltshire KH, Hirche HJ (2007) Overwintering strategies of dominant calanoid copepods in the German Bight, southern North Sea. Mar Biol 151:1309-1320

The initial idea originates from the third author and myself. Sampling, analysing and interpredation of the data as well as all experiments were done by myself. The second author provided data on hydrography and phytoplankton. I wrote the manuscript, which was improved by the co-authors.

PUBLICATION II

Wesche A, Boersma M, Hirche HJ (submitted with positive reviews) Inter- and intraspecific predation of calanoid North Sea copepods on young offspring – and experimental approach

The initial idea originates from the third author and myself. I planned, conducted and analysed all experiments. The co-authors helped with interpreting the data and improved the manuscript I wrote.

MANUSCRIPT

Wesche A, Hirche HJ, Boersma M (submitted) Seasonal birth and mortality rates of calanoid copepods in the German Bight (Southern North Sea)

The initial idea originates from M. Boersma and myself. Sampling, analysing, experiments and interpreting the data were done by myself. Data on hydrography, phytoplankton and partly zooplankton abundances were provided by the Biologische Anstalt Helgoland. I wrote the manuscript, which was improved by the co-authors.

OVERWINTERING STRATEGIES OF DOMINANT CALANOID COPEPODS IN THE GERMAN BIGHT, SOUTHERN NORTH SEA

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RESEARCH ARTICLE

Overwintering strategies of dominant calanoid copepods in the German Bight, southern North Sea

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Abstract Abundance, stage composition and reproductive parameters (egg production, egg viability, proportion of spawning females) of the four copepod species *Acartia clausi, Centropages hamatus*, *C. typicus* and *Temora longicornis* were measured at the long term sampling station Helgoland Roads (German Bight, southern North Sea) from September 2003 to May 2004 to study their overwintering strategies. *A. clausi* was overwintering as females with arrested reproduction from November to January. *T. longicornis*, which is known to produce resting eggs in the North Sea, had a pelagic population with all developmental stages present during winter and reproductive rates closely related to food concentrations. Although their females produced eggs in response to ambient food conditions, both *C. hamatus* and *C. typicus* were rare in the pelagic. The *C. hamatus* population returned in May, probably from resting eggs, whereas *C. typicus* depended on advection. The *Centropages* species seemed to be less adapted to pelagic life in winter than *A. clausi* and *T. longicornis*. Sporadic occurrence of large numbers of nauplii and young copepodids of *A. clausi* and *Centropages* spp. pointed to different overwintering strategies or more successful survival in adjacent regions and advection of them into the waters around Helgoland island. While *A. clausi* was decoupled from environmental conditions in late autumn and winter, the other species were able to respond to variations in the food environment. Thus, egg production of *T. longicornis* increased during an unusual autumn diatom bloom.

Introduction

In temperate seas, water temperature and plankton biomass show a pronounced seasonality. In the south-eastern North Sea surface water temperature ranges between −1°C in winter and about 20°C in summer (Otto et al. 1990). Phytoplankton biomass in winter is low and consists mainly of small flagellates, whereas values up to 1,000 μg C l^{-1} are found in spring, mostly dominated by diatoms (Hickel et al. 1992).

Zooplankton growth and reproduction generally peak in spring, when temperature and phytoplankton biomass increase. Small calanoid copepods (*Acartia* spp., *Temora longicornis, Centropages hamatus, C. typicus* and *Pseudocalanus elongatus*) dominate the zooplankton population, with up to 85% of abundance in spring and summer (Krause et al. 1995). In winter their abundance is very low (Greve et al. 2004).

Little is known on the overwintering strategies of small calanoid copepods and the factors controlling it. Due to hydrographic and food conditions, winter represents a season where these copepods have to survive in an adverse environment. With respect to food, microzooplankton and detritus might be important for copepod diet in times of low phytoplankton biomass (Marshall and Orr 1958) and cannibalism could also play a role (Landry 1978; Daan et al. 1988; Ohmann and Hirche 2001; Sell et al. 2001). Another strategy to bridge

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adverse conditions is dormancy, defined as a state of suppressed development (Danks 1987). In copepods, dormancy may occur in various ontogenetic stages, from resting eggs to arrested development in copepodids and adults (Dahms 1995; Marcus 1996; Hirche 1998). In the southern North Sea, some species disappear completely from the water column for several months (Hickel 1975; Fransz et al. 1991). For example, *C. hamatus*, which is only present as resting eggs on the sea floor during winter months (Engel and Hirche 2004). In contrast, *T. longicornis* is found as both resting eggs and pelagic stages (Engel and Hirche 2004; Halsband and Hirche 2001).

Hay (1995) pointed out, that a combination of producing hibernating stages and low productivity will maximize success to bridge adverse conditions. Species specific strategies may result in different overwintering success under changing environmental conditions. Thus in the North Sea, temperature has been increasing by 1.1°C since 1962 (Wiltshire and Manly 2004). The hydrography of the North Sea has changed (Beare et al. 2002), potentially due to a climate-related increased inflow of Atlantic water into the northern North Sea (Reid et al. 2003). An increase in North Sea colour index has been reported by Edwards et al. (2002). Wiltshire and Manly (2004) related a shift in phytoplankton succession to the warming of the autumn (October–December) temperatures. The mean diatom day of the algal spring bloom is delayed and shifted to the end of the first quarter of the year (Wiltshire and Manly 2004). The overall zooplankton community has shown a considerable shift since the 1990s, mainly due to the presence of sub-tropical species. Copepod abundance, which dominated the zooplankton community from the 1950s to the late 1970s, was declining; instead, meroplankton became dominant (Edwards et al. 2005). According to Edwards and Richardson (2004) temperate marine environments may be particularly vulnerable to phenological changes caused by climatic warming because the recruitment success of higher trophic levels is highly dependent on synchronization with pulsed planktonic production. In terms of marine phenological changes and climate, the plankton of the North Sea has been extensively studied using Continuous Plankton Recorder data (Edwards and Richardson 2004). It was found that the plankton community was responding to changes in sea surface temperature by adjusting their seasonality. More importantly the response to climate warming varied between different functional groups and trophic levels, leading to mismatch (Edwards and Richardson 2004).

So far causative explanations for different responses on the species level are rare. Abiotic stress should affect co-occurring species with different life cycle strategies differentially. For example species with overwintering strategies controlled by instrinsic processes like dormancy should react differently from those with just temperature and food dependent development. To understand phenology, detailed knowledge on its controls is a prerequisite. In this study we investigated the population dynamics of four dominant copepod species at the long term sampling station Helgoland Roads at Helgoland island (German Bight, southern North Sea) from autumn to spring to analyse their overwintering strategies. Thereby we built on earlier studies by Halsband and Hirche (2001) and Engel and Hirche (2004), but sampled with a higher temporal resolution during the winter months. In addition to reproductive parameters (egg production rate (EPR), proportion of spawning females, egg viability) and prosome length we determined stage composition with emphasis on the abundance of young developmental stages as indicators of successful growth.

Materials and methods

Study area

The long term sampling station Helgoland Roads is located between the main island Helgoland and the sand dune island (54°11.3′N, 7°54.0′E) (Fig. 1). Water depth varies tidally between 5 and 10 m. The island is situated in the centre of the German Bight, about 65 km off the German coast. The hydrography of the German Bight and specifically around Helgoland island is influenced by waters of different origins. Water of high salinity, which enters the North Sea from the Atlantic via the English Channel in the south and the Fair Isle Current in the north reaches the island from the central North Sea, west from Helgoland. The source of low salinity water comes from coastal currents north and northeast from Helgoland (Banner et al. 1980; Otto et al. 1990). In autumn and winter the influence of Atlantic water is more important than in spring and summer (Otto et al. 1990). Due to strong tidal currents and the shallow depth the water column around the island is permanently mixed (Radach et al. 1990). Very cold winters, with a monthly minimum temperature of −1°C or less, occurred about every 10 years up to 1944, but only once since 1960 (Wiltshire and Manly 2004).

Sampling

Surface water samples for temperature, salinity, phytoplankton composition and biomass were collected on all workdays at Helgoland Roads using a bucket. Surface water temperature was measured immediately.

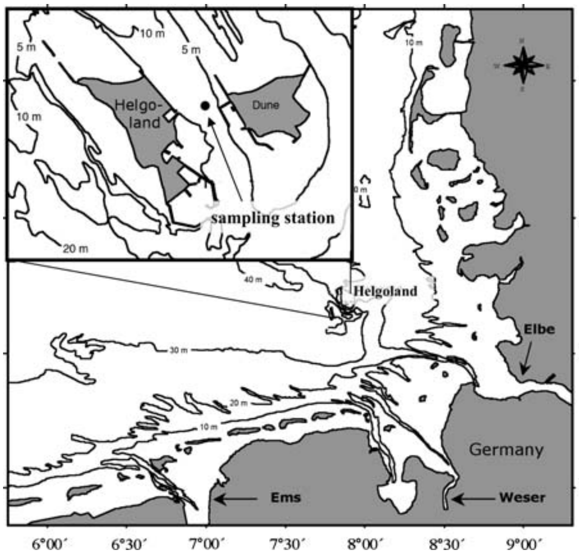

Fig. 1 Map of the German Bight, Helgoland island and the long term sampling station Helgoland Roads (54°11.3′N, 7°54.0′E)

The sample was gently mixed and sub-sampled into a glass bottle. A phytoplankton subsample was preserved with Lugols solution. Sub-samples (25 ml) were counted to species level using the Utermöhl method and converted into carbon content with the program 'Count' (Tripos Inc., Germany), which works on the basis of calculations by Hillebrand et al. (1999).

Zooplankton was collected on 49 days from September 2003 to May 2004 in the morning, at least twice per month in vertical hauls from near the bottom to the surface. A Nansen net (0.35 m^2 opening area, 150 μm mesh size) was used for sampling adult copepods and copepodids and an Apstein net (0.023 m^2 opening area, 55 μm mesh size) for nauplii. Volumes of water filtered were measured using calibrated flow meters fitted in the net openings. Net samples were preserved immediately in 4% borax buffered formalin-seawater solution until analysis in the laboratory. Sub-samples of at least 150 copepods or nauplii were analysed for species composition except for two cases, where the entire sample contained less then 150 individuals. Calanoid copepods were identified to species level and stage (adults, copepodids CI/II, CIII, CIV/V, nauplii) except for *Acartia* spp., where only adult females were determined to species level. Nauplii of *C. hamatus* and *C. typicus* were not distinguished. The prosome length of at least 50 preserved females was measured once a month with a video-image digitising system (NIH Image 1.55) to the nearest 20 μm.

Reproduction

Egg production rate and proportion of spawning females of the four dominant calanoid species *Acartia clausi*, *C. hamatus*, *C. typicus* and *T. longicornis* were determined at least four times per month between September 2003 and May 2004. Live females were collected by oblique net tows (Nansen net, mesh size 280 μm and Calcofi net, mesh size 500 μm) at Helgoland Roads. Samples were brought to the laboratory within 1 h and 30 active females per species were gently sorted with a pipette under a binocular microscope and placed individually in cell wells (Corning) filled with 10 ml of 55 μm prefiltered seawater. The wells were incubated at ambient temperature and light regime in an incubator chamber (WTB Binder). After 24 h, females were removed and all eggs and eggshells were counted. Egg production rates (EPR) were calculated as the number of eggs spawned per female per day (eggs fem^{-1} d^{-1}). To study hatching success, eggs were incubated in cell wells at in situ temperature and hatching was controlled daily for up to 10 days after spawning.

Data analysis

Stage specific abundance data of the four copepod species were log transformed (log + 1) to show low abundances clearly. Temperature, salinity and phytoplankton components biomass were tested for autocorrelation. They were fitted to an ARMA model (Box and Jenkins 1976) to eliminate autocorrelation. Further analyses were done with the residuals of the fitted environmental data. Egg production rate, hatching success and proportion of spawning females had to be excluded from test of autocorrelation, because they did not fulfil the condition of time series analyses of regular time intervals between successive values. Sets of environmental and reproduction parameters were grouped by seasons and tested for significant seasonal differences by non-parametric Kruskal–Wallis test (Kruskal and Wallis 1952). Seasons were defined as follows: autumn, September–November; winter, December–February; spring, March–May. Egg production was correlated with the residuals of temperature and total phytoplankton biomass (PPC) by Pearsons Product Moment Correlation. All statistical analyses were performed with STATISTICA 6 (StatSoft Inc., Tulsa, OK, USA).

Results

Hydrography

Water temperature decreased from 18°C in September to a minimum of 3°C in March (Fig. 2a). Thereafter

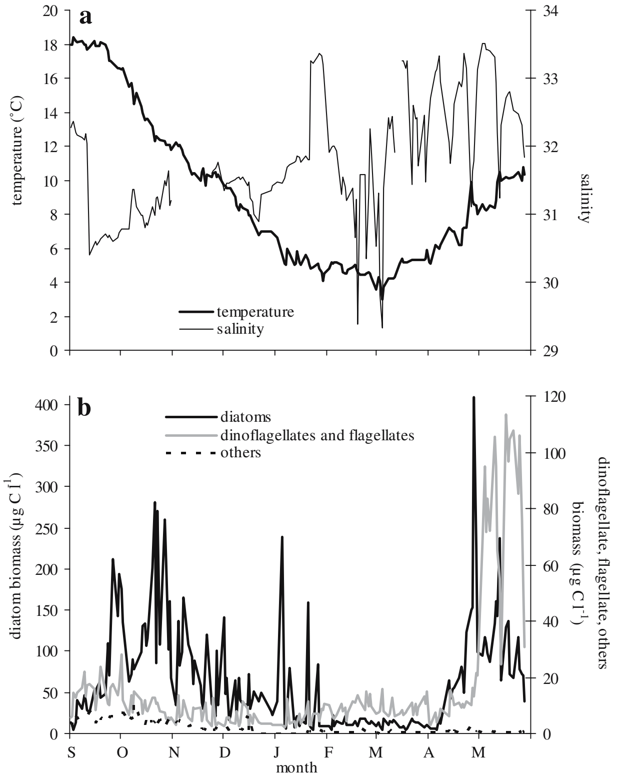

Fig. 2 Seasonal cycles of temperature and salinity (**a**) and phytoplankton biomass (**b**) at Helgoland Roads. *others*: ciliates, silicoflagellates, coccolithophorids and *Noctiluca scintillans*

temperature increased continuously to 10.4°C until the end of the study. Salinity showed strong variations with extremes of 29.3 (4th March) and 33.5 (3rd and 4th May). The lowest salinity was associated with the lowest temperature of 3°C on 4th March. The Kruskal–Wallis tests with residuals of temperature and salinity gave significant differences only in temperature between autumn and spring ($z = 2.97$) and winter and spring ($z = 2.91$) ($H_{2,185} = 11.51$, $P < 0.01$).

Phytoplankton

The phytoplankton consisted mainly of diatoms, flagellates and dinoflagellates (Fig. 2b). An autumn bloom of diatoms peaks with up to 250 µg C l^{-1} in October and was followed by a minimum period with less than 25 µg C l^{-1} from February to April, interrupted by strong short peaks in January (Fig. 2b). The maximum diatom carbon of 408 µg C l^{-1} was observed at the end of April. Dinoflagellates and flagellates were present with low biomass until May, where they became abundant and amounted to nearly half of the phytoplankton biomass (Fig. 2b). Ciliates, silicoflagellates and coccolithophorids (combined as ‘others’) were present at mentionable numbers only from September to December. No significant differences between seasons within phytoplankton components were seen, after elimination of autocorrelation.

Copepod community structure and abundance

The copepod community in autumn was dominated by cyclopoid and harpacticoid copepods, which contributed more than 70% of the copepod population (Fig. 3a). While cyclopoid and harpcaticoid abundance decreased, from December on calanoid copepods became abundant and reached a proportion of more than 90% of the copepod population at the end of March. Total numbers of copepods decreased from about 7,000 ind m^{-3} in autumn to less than 1,000 ind m^{-3} in the winter months (Fig. 3b). Within the calanoid copepods we focused on four species (*A. clausi*, *C. hamatus*, *C. typicus*, *T. longicornis*). *Paracalanus parvus, Pseudocalanus elongatus* and *Calanus* spp. were combined as ‘other calanoids’ and were dominant from September until December (Fig. 4a). Individual numbers of the species investigated were below 1,000 ind m^{-3} from September until May, dominated by *A. clausi* and *T. longicornis* (Fig. 4b). The abundance of the two *Centropages* species was always low (max. 385 ind m^{-3}).

Stage specific field abundances for the four copepod species were given as log transformed data (Fig. 5). For better understanding we gave the not transformed abundances in ind m^{-3} additionally in the text.

Nauplii

Nauplii of all species occurred during the entire study period, except in October and November, when *Centropages* spp. nauplii were absent (Fig. 5). Most of time nauplii outnumbered the other stages by far. They were usually dominated by *Acartia* spp. and *T. longicornis*. During autumn and winter months, their log abundance fell to less than 3.3 ind m^{-3} (<2,000 ind m^{-3}). In spring, there was a strong increase in abundance in these two species, with peaks of log abundance of about 4.2 ind m^{-3} (maximum abundance 14,290 and 13,751 ind m^{-3}, respectively). For *Centropages* spp. nauplii highest log abundance of 3.3 ind m^{-3} (1,855 ind m^{-3}) was observed in October, while most of the time, their log number was less than 3 ind m^{-3} (<700 ind m^{-3}).

Copepodids and adults

Acartia clausi

Three *Acartia* species have been reported from the North Sea: *A. clausi*, *A. longiremis* and *A. bifilosa*, with the first being predominant (Krause et al. 1995). As all

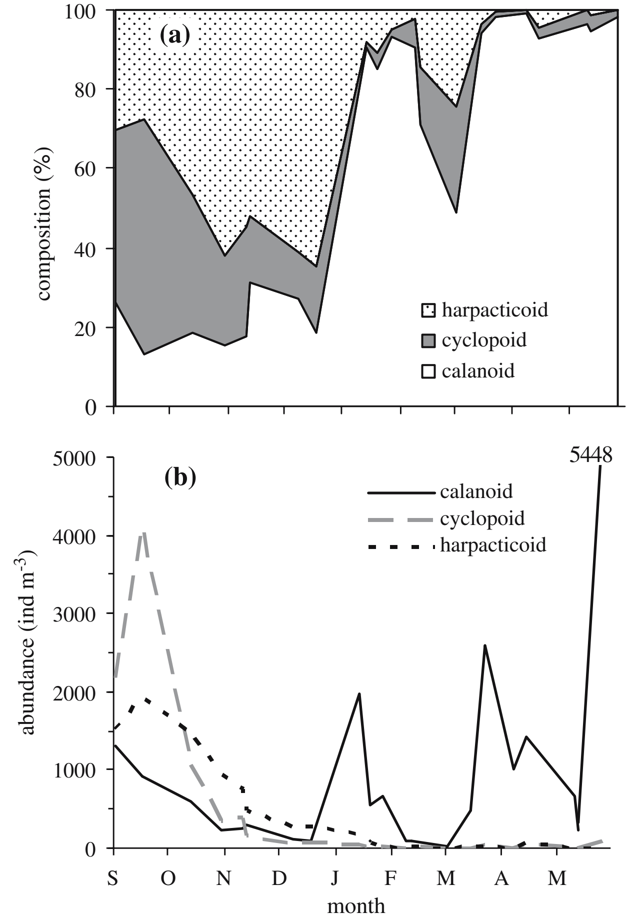

Fig. 3 Composition (**a**) and abundance (**b**) of the copepod community at Helgoland Roads

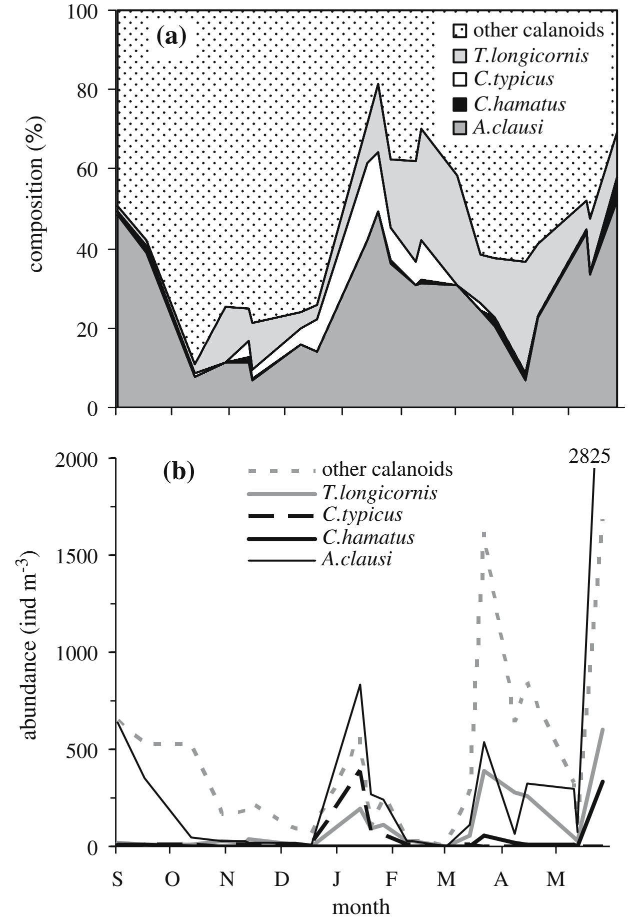

Fig. 4 Composition (**a**) and abundance (**b**) of calanoid copepods at Helgoland Roads. others: *Paracalanus parvus*, *Pseudocalanus elongatus*, *Calanus* spp.

females determined in this study were *A. clausi*, we assumed the other stages belonging to this species, too. Copepodids and adults of *A. clausi* dominated the calanoid copepods (Fig. 4a, b). Their winter population consisted of older stages (CIV to adults) (Fig. 5). The log abundance of CIV and adults together decreased from 2.6 ind m^{-3} (400 ind m^{-3}) in September to 1 ind m^{-3} (10 ind m^{-3}) in December, showed a short peak of about 2.8 ind m^{-3} (695 ind m^{-3}) in January and increased from April up to 3.1 ind m^{-3} (1,172 ind m^{-3}). From September to January, no adult males were observed. Afterwards the sex ratio was 1:1. Early copepodite stages (CI to III) became abundant in spring (log abundance 3.5 ind m^{-3}, corresponds to 2,992 ind m^{-3}).

Temora longicornis

Temora longicornis was second in abundance (Fig. 4a, b). Adults were present throughout the investigation, from September until March with log numbers of 1.6 ind m^{-3} (<40 ind m^{-3}) (Fig. 5). Abundance of adults increased from April with a log maximum of 2.1 ind $^{-3}$ (128 ind m^{-3}) interrupted by a short decline at the beginning of May. The sex ratio was approximately 1:1. Copepodite stages CI to V showed low numbers until March, except a peak in January of 2.2 ind m^{-3} (162 ind m^{-3}). In March, their log abundance increased and reached numbers of 2.7 ind m^{-3} (491 ind m^{-3}) in May.

Centropages hamatus and Centropages typicus

Copepodids and adults of *Centropages* spp. were less in numbers than the other species (Figs. 4, 5). Individuals of *C. hamatus* were almost absent from October until the middle of March, only a few adults occurred in September and January (log abundance 0.5 ind m^{-3}, corresponds to 3 ind m^{-3}). From March log abundance of all stages together increased to a maximum of 2.4 ind m^{-3} (246 ind m^{-3}) in May. *C. typicus* also occurred only sporadically. An abundance peak of all stages was observed in the beginning of January (log abundance 2.6 ind m^{-3}, corresponds to 369 ind m^{-3}), consisting mostly of older copepodite stages (CIII and CIV/V, log abundance

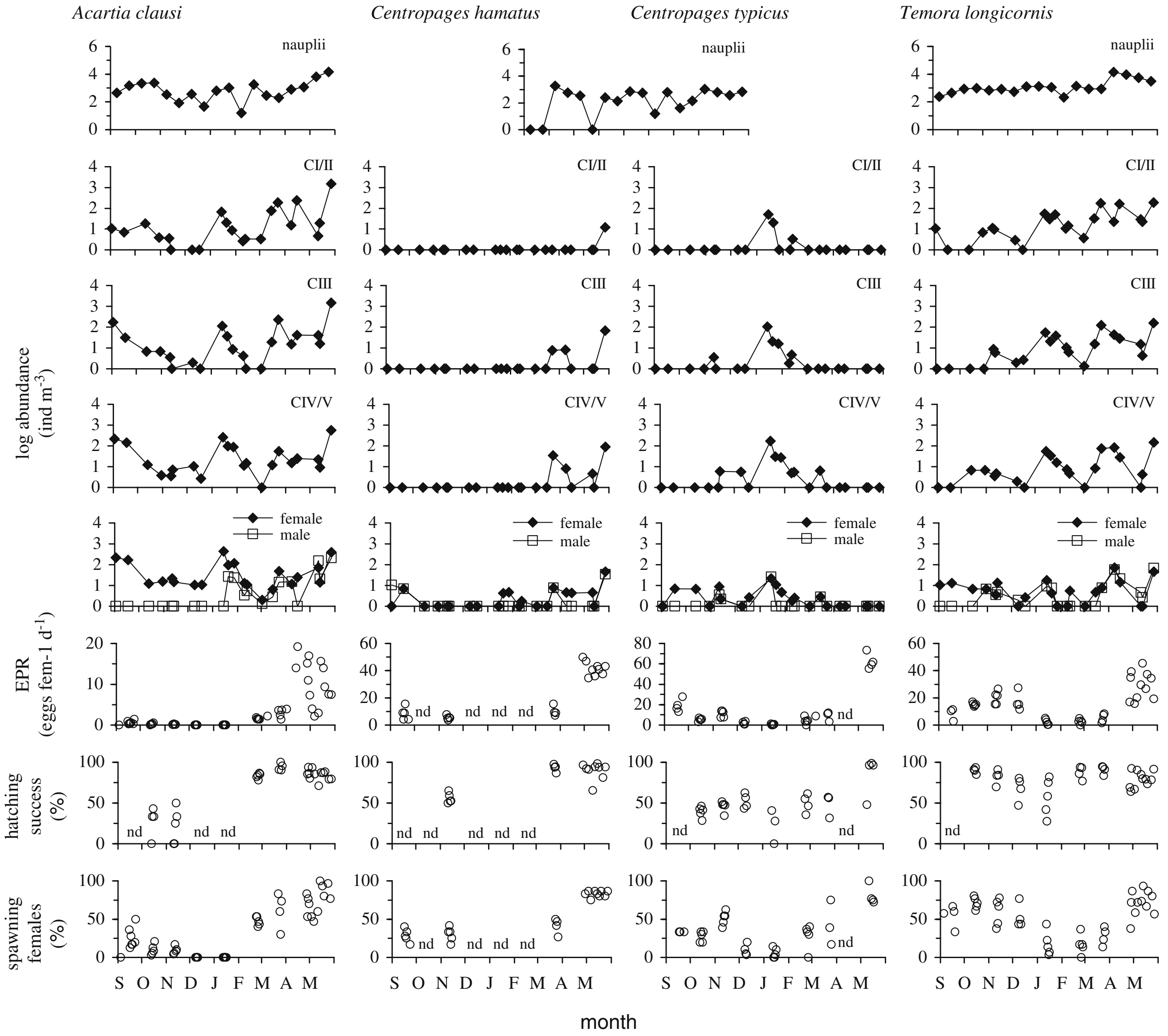

Fig. 5 Stage specific log abundances and reproduction parameters of four copepod species at Helgoland Roads. Note different scales. *nd* no data

2.4 ind m^{-3}, corresponds to 274 ind m^{-3}). The adult sex ratios of *Centropages* spp. were close to 1:1.

Reproduction and female size

Egg production and female sizes showed a general seasonal pattern of low values during autumn and winter and highest values in spring, but there were species specific characteristics (Figs. 5, 6).

Acartia clausi

Acartia clausi showed a pattern of discontinued reproduction with a clear disruption during winter and a springtime recovery (Fig. 5). There was no response of egg production to the autumn bloom. Egg production rate (EPR) was zero in December and January (Fig. 5). At the end of February, EPR began to increase suddenly, although there were no differences in the food environment to the previous months. Maximum EPR was reached in April with 19 eggs fem^{-1} d^{-1} and a proportion of spawning females of 80%. Differences in EPR and proportion of spawning females were significant between autumn and spring, and spring and winter (Table 1). Hatching success in spring was also different to that in autumn (Table 1). There was no significant correlation between temperature or phytoplankton carbon and EPR (Table 2). Hatching success

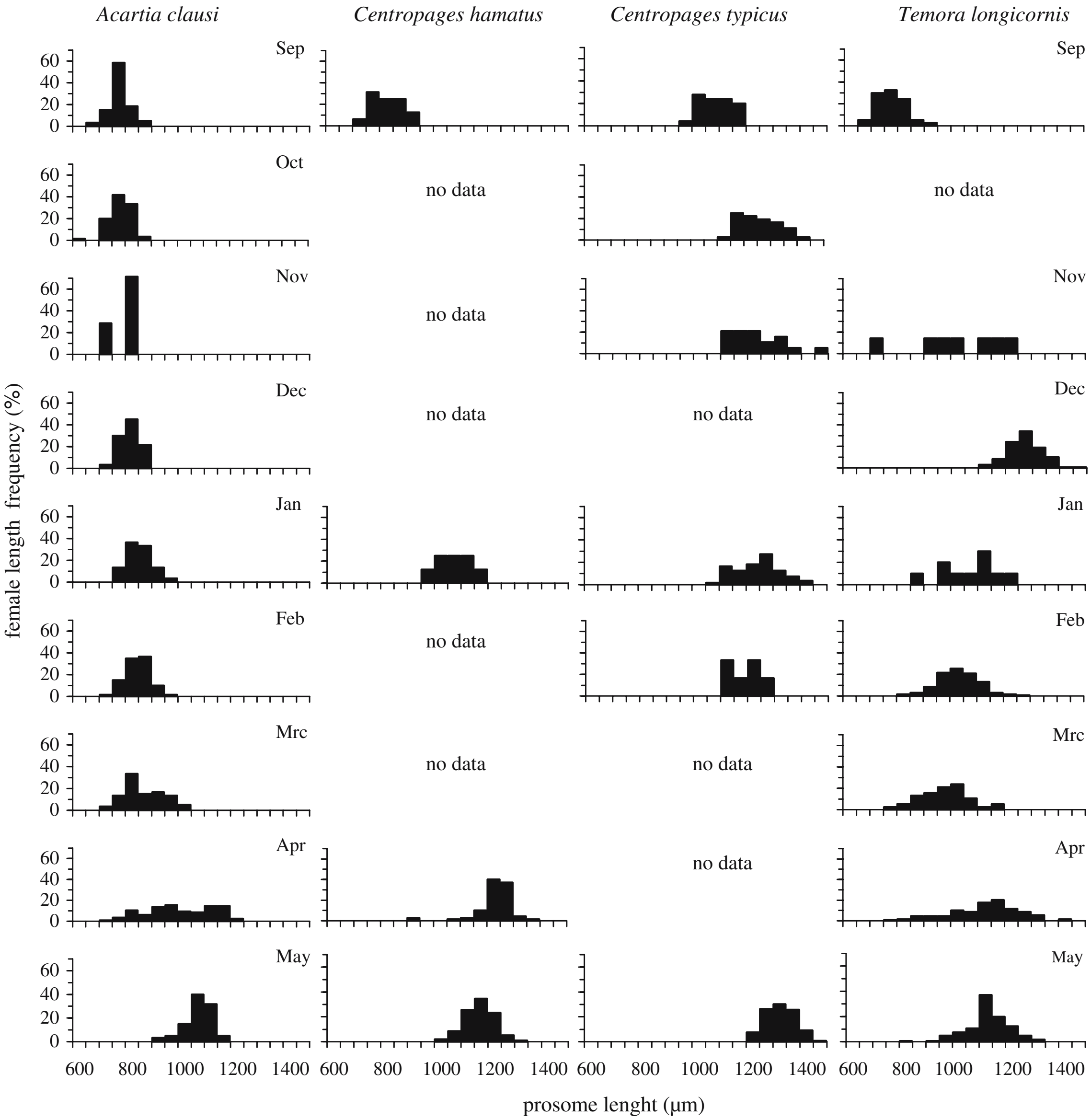

Fig. 6 Female length frequency distribution of four copepod species at Helgoland Roads

was low during winter (<40%), but reached more than 80% in spring. It differed significantly between spring and autumn (Table 1). Female size remained nearly unaltered with a mean prosome length (PL) of 824 µm from September to February (Fig. 6). From March on, larger females appeared. The largest females with 1,079 µm were found in May.

Temora longicornis

Temora longicornis reproduced continuously throughout the study period, but EPR showed no coupling to temperature or phytoplankton carbon (Table 2). EPR up to 27 eggs fem^{-1} d^{-1} was reached in November and December, when the proportion of spawning females was about 60% (Fig. 5). From January to March, egg production declined to less than 10 eggs fem^{-1} d^{-1} and only 20% of females were spawning. Afterwards, EPR increased to 45 eggs fem^{-1} d^{-1} and nearly 80% of females produced eggs. Egg production and proportion of spawning females were different between autumn and winter, and winter and spring (Table 1). Mean hatching success was always more than 60% with highest level of 90% in spring, but there were no significant differences between seasons (Table 1). *T. longicornis* had the tendency to larger females during spring, although the largest females with 1,199 µm PL were observed in December (Fig. 6). Monthly mean female PL varied between 774 and 1,199 µm.

Table 1 *Acartia clausi*, *Centropages hamatus*, *Centropages typicus* and *Temora longicornis*. Seasonal comparison between reproduction parameter by Kruskal–Wallis test

Season	*Acartia clausi*			*Centropages hamatus*			*Centropages typicus*			*Temora longicornis*		
	EPR (52)***	Spawn (52)***	Hatch (34)***	EPR (23)***	Spawn (23)***	Hatch (18)**	EPR (36)***	Spawn (36)***	Hatch (31)*	EPR (42)***	Spawn (42)**	Hatch (36)ns
Autumn versus winter	ns	ns	ns	nd	nd	nd	3.62	2.69	ns	2.47	3.26	ns
Autumn versus spring	4.84	4.73	4.63	3.60	3.66	3.20	ns	ns	2.42	ns	ns	ns
Winter versus spring	5.28	5.14	ns	nd	nd	nd	4.02	3.82	ns	3.70	3.11	ns

Numbers in parantheses, Significance levels $*P < 0.05$; $**P < 0.01$, $***P < 0.001$

ns not significant, *nd* no data, *EPR* egg production rate, *spawn* proportion of spawning females, *hatch* hatching success

Table 2 Correlation coefficients (*r*) between egg production rate (EPR) of four copepod species and residuals of temperature (*T*) and total phytoplankton biomass (PPC) at Helgoland Roads

	Acartia clausi	*Centropages hamatus*	*Centropages typicus*	*Temora longicornis*
EPR/*T*	0.021 (52)	0.159 (23)	0.353* (36)	−0.025 (42)
EPR/PPC	0.199 (52)	−0.251 (23)	0.189 (36)	−0.011 (42)

Sample size in parentheses

Significance levels $*P < 0.05$

Centropages hamatus and Centropages typicus

Egg production of *C. hamatus* was low in autumn and only 30% of the females produced eggs on the few dates where experiments were conducted (Fig. 5). In spring, reproduction increased and reached values up to 49 eggs fem^{-1} d^{-1} in May with a proportion of spawning females of 80% and hatching success more than 90% (Fig. 5). Egg production, proportion of spawning females and hatching success of *C. hamatus* differed significantly between autumn and spring (Table 1), but no correlation between EPR and temperature or phytoplankton was seen (Table 2). Female size varied between 824 μm in September and 1,266 μm in April (Fig. 6).

Centropages typicus showed egg production of less than 20 eggs fem^{-1} d^{-1} from September to March. The maximum EPR of 73 eggs fem^{-1} d^{-1} occurred in May. EPR and proportion of spawning females were significantly different between autumn and winter, and winter and spring (Table 1). There was a significant correlation between EPR and temperature (Table 2). The percentage of spawning females varied between 5% in January and 81% in May. Hatching success varied from 27 to 62% from October to April and reached its maximum of 99% in May. Differences in hatching success were seen between autumn and spring (Table 1). Females of *C. typicus* were the largest ones with a maximum mean PL of 1,324 μm, occurring in May (Fig. 6). Smallest females with 1,087 μm appeared in September.

Discussion

Harpacticoids and cyclopoids dominated the copepod community of the southern German Bight in autumn, but from December on calanoids became the most important group, confirming results of previous studies (Fransz et al. 1991; Krause et al. 1995; Halsband and Hirche 2001; Halsband-Lenk et al. 2004). This predominance indicates proper adaptations to winter conditions in the pelagic.

We distinguished different overwintering strategies in each of the species of calanoid copepods investigated around Helgoland island, using stage composition together with reproductive parameters and female prosome length.

Acartia clausi was the most abundant calanoid during the study. Its reproductive parameters mirrored very closely the observations by Halsband and Hirche (2001) during the winter 1995/96, although temperatures then were significantly lower. In both studies, females were the most frequent stage (nauplii were not studied by Halsband and Hirche 2001), followed by copepodite stages CIV/CV. Spawning activity was low in autumn and zero in December and January. Number of spawning females and egg viability increased conspicuously in February. Low hatching success in autumn could relate to the scarcity of males, as e.g. *Acartia tonsa* one mating is usually not sufficient (Wilson and Parrish 1971). Otherwise, the complete cessation of reproductive activity at the end of autumn during a time when food was available and initiation of egg production during a time of lowest food concentrations indicate instrinsic control, and an arrested reproductive dormancy (Hirche 1998). In this case low hatching success could be a result of preparation of the gonads for dormancy. A female diapause was described for the congener *Acartia longiremis* in a North Norwegian fjord (Norrbin 2001). The factors causing the arrested reproductive activity are not known. In other regions like the Mediterranean *A. clausi* reproduces year round, with winter and spring as the main spawning season (Gaudy 1972; Ianora and Buttino 1990). As temperatures are not too different then from autumn temperatures in the North Sea, temperature is not a likely cue. Closer examination is needed to identify the nature of this dormancy in *A. clausi.* Female prosome length further supports the concept of an overwintering strategy based on reproductively inactive females, as it remained rather constant from September to April. In contrast, in the Mediterranean females size changes continuously, also during the winter (Riccardi and Mariotto 2000).

The general strategy is, however, obscured by the irregular occurrence of relatively large numbers of younger copepodids and nauplii on several occasions, but especially in January. From this time on also slightly larger females were present. The lack of a clear stage succession together with the reproductive inactivity excludes local development, but rather points to advection, the more so, as in January strong changes in salinity were recorded. Thus, these individuals originate either from adjacent regions where *A. clausi* has another overwintering strategy, or they represent offspring of the congeners *A. longiremis* and *A. bifilosa*. As nauplii and young copepodids of *Acartia* spp. were not determined to species level no clear assumption could be made. Evidence of resting eggs of *Acartia* spp. as a source of nauplii is missing in the Atlantic and the North Sea (Naess 1996; Engel and Hirche 2004). However, the congener *A. bifilosa* is known to produce resting eggs (Castro-Langoria and Williams 1999), but is usually rare in the southern North Sea (Krause et al. 1995).

Reproductive parameters clearly indicate the end of February as the beginning of the new growth period around Helgoland island. The first new generation was completed then by April, as indicated by a different female size distribution. This period corresponds well with developmental times at the respective temperatures derived from laboratory rearings (Klein Breteler and Schogt 1994).

In contrast to *A. clausi*, stage composition of *T. longicornis* was characterised by the almost permanent presence of all stages throughout the investigation. Females produced eggs at much higher rates than *A. clausi*. Egg production followed closely the seasonal cycle of phytoplankton; low rates were only found in January and February. From September to March, hatching success and the number of spawning females was almost higher than in *A. clausi*. Female size increased already in November, indicative of a new generation developed at lower temperatures. As the reproductive parameters were very similar in 1995/96 (Halsband and Hirche 2001), we conclude that the overwintering strategy of *T. longicornis* in the German Bight be characterised in general by active growth and reproduction in response to its nutritional environment. Thus, it was the only species, which responded to the late autumn peak in diatom biomass with enhanced reproductive activity. However, *T. longicornis* is also known to produce resting eggs in the North Sea (Lindley 1986, 1990; Engel and Hirche 2004). The strong increase in nauplii abundance observed one month before the spring bloom and the maximum egg production may at least in part originate from resting eggs. According to Castellani and Lucas (2003) resting eggs of *T. longicornis* were mainly produced during spring and late summer, at the peak of the reproductive season. We found no clear evidence of a higher production of resting or diapause eggs during spring; the hatching success did not decrease. Thus, resting eggs have to be produced later in season. The mixed strategy of active growth and low reproduction in winter together with the production of resting eggs may minimise mortality from predation pressure, prevent intraspecific competition (Engel and Hirche 2004) and ensures the survival of the population during extremely severe winters.

In *C. hamatus* copepodids were almost completely absent from October 2003 until March 2004. Adults were extremely rare from September onwards and recurred in February. Whenever females were available in the samples they produced eggs. Egg production was moderate until November and in April, but increased rapidly in May, as reported before by Halsband and Hirche (2001). In the German Bight around Helgoland island (Engel and Hirche 2004) as in other locations of the North Sea (Lindley 1986, 1990) *C. hamatus* overwinters mainly through resting eggs. As nauplii of the congener *C. typicus* were not distinguished here we could not prove emergence from resting eggs. The overwintering of *C. hamatus* in the southern North Sea resembles the mixed strategy of *T. longicornis*, but the survival of the pelagic population seems to be less successful, was it due to inadequate food conditions, or to predation. In contrast, *C. hamatus* in the Kattegat (Kiørboe and Nielsen 1994), the English Channel (Le Ruyet-Person et al. 1975) and the Irish Sea (Castellani and Lucas 2003) is abundant in winter and reproduces throughout the year. So, the few individuals found during winter might be advected into the waters around Helgoland.

Centropages typicus has been considered as a sporadic immigrant in the North Sea or was not mentioned in earlier studies (e.g. Rae and Rees 1947; Wiborg 1955; Fransz 1975; Hickel 1975). However, in recent years it becomes more abundant, especially from late summer to winter (Hay 1995; Halsband-Lenk et al. 2004). Lindley and Reid (2002) suggested population centres of *C. typicus* in the German and the Southern Bights, persisting throughout the winter. Halsband and Hirche (2001) observed this species between September and January also around Helgoland island. During this study it was found only sporadically and was absent in 9 out of 21 quantitative vertical tows. Stage composition was not consistent and did not show a succession of stages, but included different combinations of stages. Large abundances of all stages were observed on two occasions in January, probably due to advection. Advection from adjacent regions would underline the existence of pelagic winter population in northern and western regions (Lindley and Reid 2002). The female size shift from September to October indicated the arrival of another generation, which then persisted throughout this study. Egg production continued during winter with the exception of January, when no eggs were laid. Hatching success was never higher than 50% until May. This is in contrast to the other species investigated, which showed shorter periods of low hatching success. In May, when egg production increased dramatically, also hatching success was high. So far, no indication of resting eggs was found for *C. typicus* (e.g. Ianora and Scotto di Carlo 1988; Miralto et al. 1995; Engel and Hirche 2004). Lindley (1990) supposed dormancy of such eggs in sediments, but in experiments much less nauplii hatched compared to its congener *C. hamatus*. Thus, there seems to be no specific adaptation to winter conditions and the population continues its development during winter depending on food conditions. Due to unfavourable conditions it is dying off before the end of winter.

In their review on the phytoplankton dynamics of the North Sea, Reid et al. (1990) pointed to the great complexity of phytoplankton dynamics in the North Sea and the fact that algal successions and blooms often do not follow classical patterns. This applies also to the period of our investigation. The phytoplankton succession in 2003 was rather unusual. While mostly phytoplankton carbon drops to below 30 μg C l^{-1} in late summer and remains very low until April of the following year, the autumn bloom in 2003 was associated to a relatively high phytoplankton biomass until the end of December. Our data showed that only one copepod species could benefit from this opportunity. As the pelagic population of *T. longicornis* perpetuates actively during the winter, it was able to respond to the autumn bloom with an increased reproductive activity. The fact that it also has resting eggs on the sea floor as an additional safeguard illustrates the risk of a pelagic strategy without adaptation. Female *C. hamatus* and *C. typicus* seemed also to possess the potential to reproduce when food is sufficient, but their mortality was obviously so high that the pelagic populations died off during winter. Finally, in *A. clausi* reproduction is decoupled from environmental changes during autumn and winter. However, their late winter arousal should make especially this species sensitive to the timing of the spring bloom.

The general picture of overwintering strategies we found was disturbed by sudden abundance peaks consisting often of very young stages. The most conspicuous peak was observed in January and affected the stage compositions of all species except *C. hamatus*. It was most likely associated with an advective event from the western or northern parts of the North Sea, typical in winter at Helgoland Roads (Banner et al. 1980; Otto et al. 1990), as seen in the continuous increase in salinity during our study. Advection of populations with different stage composition indicates, that the overwintering strategies observed here are effective only on a regional scale, and that other strategies are in effect of adjacent areas.

So far, overwintering of calanoid copepods in the southern German Bight is controlled and affected by a combination of several factors, whose impacts are species specific. Within this, food, temperature and advection seemed the most important factors. Certainly more synoptic observations on a larger regional scale during winter are needed to understand the strategies and their control in the North Sea.

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INTER- AND INTRASPECIFIC PREDATION OF CALANOID NORTH SEA COPEPODS ON YOUNG OFFSPRING – AN EXPERIMENTAL APPROACH

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INTER- AND INTRASPECIFIC PREDATION OF CALANOID NORTH SEA COPEPODS ON YOUNG OFFSPRING – AN EXPERIMENTAL APPROACH

ABSTRACT

Predatory feeding of adult female copepods (*Acartia clausi*, *Centropages hamatus*, *Centropages typicus*, *Temora longicornis*) on their own and other species´ eggs and young nauplii was investigated in bottle incubation experiments with different densities of single animal prey, mixtures of animal prey and in the presence of diatoms. Predation on eggs and nauplii occurred in all species. Maximal egg predation rates varied between 7 and 64 eggs fem^{-1} d^{-1}. Ingestion of *Centropages* spp. eggs was lowest, evidently due to the spiny egg surface. Maximal feeding rates on nauplii ranged from 5 to 45 nauplii fem^{-1} d^{-1}. *T. longicornis* preferred eggs, when eggs and nauplii were offered together at the same densities, the other predators selected nauplii. All predators preferred *T. longicornis* nauplii when they were offered together with *Centropages* spp. nauplii. At diatom concentrations below 60 µg C l^{-1}, predation on *T. longicornis* eggs by *A. clausi, T. longicornis* and *C. typicus* was nearly doubled. At a diatom concentration of about 200 µg C l^{-1} predation on eggs by *A. clausi* was unaltered, by *T. longicornis* less and by *C. typicus* higher than without algae. Feeding on nauplii in the presence of 60 µg C l^{-1} diatoms was unaffected in *A. clausi* and *C. hamatus*, reduced in *T. longicornis* and enhanced in *C. typicus*. Calculated predation rates using field abundances of predators and prey, varied between 0.3 and 2.1 % d^{-1} of eggs, and 0.4 and 3.3 % d^{-1} of nauplii eaten by females in November and May, respectively.

KEY WORDS: Predation, copepods, North Sea, *Acartia clausi*, *Centropages hamatus*, *Centropages typicus*, *Temora longicornis*

INTRODUCTION

Copepods are a major component of the marine zooplankton and play a key role in transfer of energy to higher trophic levels. Earlier concepts of a strict separation of feeding strategies of herbivorous and carnivorous copepod species have undergone drastic revisions in the few last decades. It is now generally accepted that most of the previous "herbivorous" species feed on a large range on particles including their own offspring (Heinle 1970, Paffenhöfer & Knowles 1980, Kleppel 1993).

Quantitative measurements of feeding on nauplii by several marine copepod species (reviewed in Bonnet et al. 2004), and predation on copepod eggs by *Calanus helgolandicus* (Kang & Poulet 2000, Bonnet et al. 2004), *Metridia lucens* and *Centropages typicus* (Sell et al. 2001) have shown the capabilities of all species investigated to ingest animal prey. Often the presence of empty or crumpled egg-shells in experimental containers (e.g. Ianora & Poulet 1993, Ceballos et al. 2006) or differences between egg production rates and abundance of nauplii in the field in the absence of other predators (Peterson & Kimmerer 1994, Liang & Uye 1996, Ohman & Hirche 2001) have been interpreted as results of cannibalism.

The risk of being eaten by copepods declines with ascending developmental stage, due to larger size and/or higher escape capability (Landry 1978, Lonsdale et al.1979, Daan et al. 1988). Individual survival might be facilitated by feeding of older stages on conspecific early life stages, when other food is scarce and population density is high (Heinle 1970, Daan et al. 1988, Ianora & Buttino 1990, Ohman et al. 2002).

In the southern North Sea, small copepod species are an important component of the zooplankton. The calanoids *Acartia clausi*, *Temora longicornis*, *Centropages hamatus*, *C. typicus* and *Pseudocalanus* spp. contribute up to 85% of total zooplankton abundance (Hickel 1975). Population density and reproductive activity of these copepods are higher in spring and summer, when primary production is at its highest level (Hickel et al. 1992), than in autumn and winter (Fransz et al.1991, Wesche et al. 2007). Predation by fish and their larvae (e.g. Nielsen & Munk 1998, Voss et al. 2003) and other invertebrates (Daan 1986, 1989, Barz & Hirche 2007) may seasonally affect the population size, but inter- and intraspecific predation within the copepod community could be an important mechanism controlling abundance as well (e.g. Ianora & Buttino 1990, Petersen & Kimmerer 1994). In the German Bight the occurrence and significance of inter- and intraspecific predation has not been studied, although it is known for the dominant species from other regions (e.g. Landry 1978, Conley & Turner 1985, Daan et al. 1988, Sell et al. 2001). The aim of the present study was to determine the potential of carnivorous feeding by the four free-spawning copepod species, *A. clausi*, *T. longicornis*, *C. hamatus* and *C. typicus* on their offspring. In the laboratory the functional response of ingestion rate to different concentrations of eggs and young nauplii in the presence and absence of alternative food was studied. The results are discussed with respect to predator and prey behaviour as well as food conditions and copepod field abundances.

MATERIAL AND METHODS

Collection of predators and rearing of prey

Copepods were caught in oblique net hauls (280 µm Nansen net and 500 µm Calcofi net) at the station Helgoland Roads (54° 11.3` N, 7° 54.0` E; German Bight, southern North Sea) between May and August in 2004 and 2005. In the laboratory, active swimming and intact adult females of *Acartia clausi*, *Centropages hamatus*, *Centropages typicus*, and *Temora longicornis* were sorted within 2 h into 1000-ml beakers filled with 55 µm prefiltered seawater. Females to be used as predators were acclimated for 48 h at 10°C without food to avoid spawning during the experiments and to standardise feeding history. To obtain eggs and nauplii as prey, other females were kept at 15°C and fed ad libitum with the cultured cryptophyte *Rhodomonas* sp. Eggs were removed at least every 3 h and stored at 4°C for less than 24 h prior to egg-feeding experiments, to prevent hatching during the experiments. To obtain nauplii as prey, eggs were incubated in Petri dishes at 15°C for hatching. Nauplii were used at stage II.

Incubation

General set-up

The experimental flasks (640 ml) were filled with 0.45 µm prefiltered seawater and different densities and combinations of prey. Four approximately equally-sized females of one species were used as predators per flask (corresponds to 6.25 predators per liter). All animal components were individually placed into the flasks with a wide pipette. The flasks were covered tightly with plastic film, closed and incubated for 6 h on a slowly-rotating plankton wheel (1 to 2 rpm) at 10°C and dimmed light. Experiments were run with at least two replicates for each density. Two to three control flasks per prey abundance without predators were set up. Visual examination at the end of the experiment ensured that the females were still alive. Experiments were terminated by pouring the bottle content over a 50 µm sieve, rinsing the material retained with filtered seawater into plastic dishes and immediate preservation in 4% formaldehyde seawater solution. As especially eggs of *T. longicornis* tended to stick to the walls of experimental equipment, flasks, sieves, dishes and pipettes were rinsed three times. In naupliar experiments, Rose Bengal solution was added to stain the nauplii and improve the recovery of the animals. Females, eggs and nauplii were counted under a dissecting microscope. For size determination, all females, 100 eggs and 50 nauplii per species were measured.

The experiments were separated into single and mixed animal-prey experiments, and experiments with a mixture of animal and algae prey (Table 1). Special set-ups were described below.

Single animal-prey experiments

Prey was offered in densities of 30, 60, 90, 120,150,180 and 210 eggs per flask, and 20, 40, 60,80 and 100 nauplii per flask. The lowest densities were in the range of densities found in the southern North Sea during the reproductive peak (Wesche et al. 2007; Daan et al. 1988). Each species was fed its own eggs and nauplii and those of all other species. Eggs and nauplii of the two *Centropages* species (C_{Egg}, C_{Naup}) were relatively similar in morphology and swimming behaviour (nauplii). Thus, *C. typicus* eggs and nauplii were used exemplary due to a better availability.

Mixed animal-prey experiments

Mixed prey experiments were conducted for *A. clausi*, *C. typicus* and *T. longicornis* as predators. Prey combinations of *A. clausi* eggs (A_{Egg}) and *T. longicornis* nauplii (T_{Naup}) (94:94 l^{-1}) and nauplii of *T. longicornis* (T_{Naup}) and *Centropages* spp. (C_{Naup}) (63:63 l^{-1}) were tested.

Animal-prey and diatom experiments

To determine the predation rates on eggs and nauplii in the presence of phytoplankton, experiments were conducted with the addition of laboratory-cultured, single cells of the diatom *Thalassiosira weissflogii* (Ø 10-16 µm). The cell carbon content of the diatom culture was measured by filtering 30 ml of diatom culture (n = 3) onto combusted Whatman GF/C-filter before the experimental series. Filters were stored at –20°C and analysed with a Fison EA 1108 CHN analyser. Cell number and cell size of the culture were determined with a CASY particle counter (Schärfe Systems, Reutlingen, Germany) prior each experiment. The initial diatom concentration in the egg experiments was set-up in 0, 30, 60 and 200 µg C l^{-1}. In experiments with nauplii one diatom concentration of 60 µg C l^{-1} was used.

To obtain the initial diatom concentration required in the flasks, a calculated volume of diatom culture was added to beakers filled with 3000 ml of 0.45 µm filtered seawater. Beakers were gently stirred and the diatom-seawater solution was added into the flasks. Two unfixed replicates of the initial algae concentration were measured with the CASY particle counter before and after filling the flasks. The abundances of T_{Egg} and C_{Naup} prey was 70 and 94 l^{-1}. For each diatom concentration three replicates and three controls without predators were set up. When terminating experiments, eggs or nauplii were separated from diatoms by pouring the bottle content over a 50 µm sieve. The final diatom concentration was measured from two unfixed replicates of each flask with the CASY particle counter.

Data analysis

Data on female, egg and naupliar size were transformed into carbon units using available equations and conversion factors. Relationships of dry weight (DW in µg) to prosome length and total length are given in Hay et al. (1991) for nauplii and females of *A. clausi*, *T. longicornis* and *C. typicus*. For *C. hamatus* females, the equation of Klein Breteler et al. (1982*)* was used. Carbon content of females, nauplii and eggs was assumed to be 44.7% of DW (Båmstedt 1986). For converting egg sizes into carbon content, the carbon-volume relationship of $0.14*10^{-6}$ µg C μm^{-3} was used (Kiørboe et al. 1985).

Predation on animal prey was calculated as the number of prey removed after 6 h compared to initial prey density. Ingestion rates were determined according to Kiørboe et al. (1982) and standardised to daily feeding rates. Clearance and ingestion rates on diatoms were determined according to Frost (1972). For mixed animal-prey, selectivity indices were calculated with the equation of Ivlev (1961) with values ranging from –1 (strong negative selection) to +1 (strong positive selection), and 0 indicating no selection.

Statistical analysis

For statistical analysis, we combined densities of the single prey experiments to three mean prey abundances to compensate missing values. In egg-feeding experiments, the densities were combined into the classes low, 30 to 60 eggs flask^{-1}; mid, 90 to 120 eggs flask^{-1} and high, 150 to 210 eggs flask^{-1}. In naupliar-feeding experiment the classes were low, 20 naup flask^{-1}; mid, 40 to 60 naup flask^{-1} and high, 80 to 100 naup flask^{-1}. Data sets were tested for equality of variances by Levene´s test (Levene 1960) and when necessary square root transformed to obtain normality. Three-way ANOVAs and post hoc Tukey´s Honestly Significant Differences (HSD) tests for unequal sample size were used to compare the ingestion rates with respect to predator species, egg- or naupliar species and prey density.

The influence of additional diatom food on ingestion of eggs and nauplii was tested with an unpaired t-test. All statistical analyses and were performed with STATISTICA 6 (StatSoft Inc., Tulsa, OK, USA).

RESULTS

Predators and prey

Female, egg and naupliar size and carbon content differed between species (Table 2). *Acartia clausi* was the species with the smallest females, eggs and nauplii, whereas the largest females belong to *Centropages typicus*. *Temora longicornis* had the largest eggs and young nauplii. The surfaces of A_{Egg} and T_{Egg} were smooth, whereas that of C_{Egg} was covered with small spines. Swimming and feeding behaviour of females differed between ambush predators (*A. clausi*, *C. hamatus* and *C. typicus*) and cruising predators (*T. longicornis*), according to Jonsson & Tiselius (1990). Nauplii were classified as jump-sink nauplii (*A. clausi*, *T. longicornis*) and swim nauplii (*Centropages* spp.), using the categories of Titelman & Kiørboe (2003).

Single prey experiments

The field-dependent availability of predators and prey made it necessary to combine experiments to get the series of concentrations considered.

Predation on eggs and nauplii occurred in all predator species (Figs. 1, 2). The ingestion rates increased with increasing prey densities over the entire range of densities offered for all prey and predator species examined. *A. clausi* showed the lowest predation rates on eggs and nauplii (max. 22 T_{Egg} fem^{-1} d^{-1}, 16 C_{Naup} fem^{-1} d^{-1}), whereas the two *Centropages* species mostly had the highest feeding rates (max. 64 A_{Egg} fem^{-1} d^{-1}, 45 C_{Naup} fem^{-1} d^{-1}). Ingestion rates were significantly affected by predator and prey species, as well as prey density (Table 3, 4). The interaction of predator and prey species, and in naupliar experiments also the interaction of predator species and prey density was significant. Regarding predator specific ingestion rates, the post hoc test revealed significant differences of egg species dependent predation rates for *T. longicornis* and *C. hamatus*, which ingested significantly more T_{Egg} than C_{Egg} ($p < 0.05$); *C. hamatus* also showed significantly higher ingestion of T_{Egg} than of A_{Egg} ($p < 0.05$). Although predation rates on C_{Naup} were highest in all predator species compared to A_{Naup} and T_{Naup} (Fig. 2), they were only significantly different in *A. clausi* and *C. hamatus*; both ingested more C_{Naup} than A_{Naup} ($p < 0.05$, $p < 0.001$) and T_{Naup} ($p < 0.001$).

Mixed animal-prey experiments

Six experiments were conducted, three with a combination of A_{Egg} and T_{Naup}, and three with T_{Naup} and C_{Naup} fed to females of *A. clausi*, *T. longicornis* and *C. typicus*. When offered A_{Egg} and T_{Naup}, *T. longicornis* showed a positive selection for A_{Egg} (Fig. 3a), while *A. clausi* and *C. typicus* preferred naupliar prey. When two nauplii species were offered, all species showed a preference for T_{Naup} (Fig. 3b).

Animal-prey and diatom experiments

Carbon content of *Thalassiosira weissflogii* was determined as 124 ± 3.3 pg C cell^{-1}. Predation on T_{Egg} in the presence of diatoms occurred in all predator species (Fig. 4), and was nearly doubled up to diatom concentrations of about 36 µg C l^{-1} (*A. clausi*), 34 µg C l^{-1} (*T. longicornis*) and 62 µg C l^{-1} (*C. typicus*). At higher diatom concentrations the ingestion of eggs decreased in all species. In *A. clausi* no significant difference of egg ingestion between high and zero diatom concentration was seen. Also the clearance rate on diatoms in combination with eggs was unaltered. Feeding of *T. longicornis* on eggs at highest diatom concentration was significantly lower than that without diatoms (df = 4, t = -4.7, $p < 0.01$). Diatom clearance rate was highest at a concentration of 34 µg C l^{-1}. In *C. typicus*, ingestion of eggs stayed significantly higher at the highest diatom concentration than without algae (df = 4, t = 3.5, $p < 0.05$).

Ingestion of C_{Naup} by *A. clausi* and *C. hamatus* was unaffected by diatom food (Fig. 5a), but significantly higher clearance rates on diatoms in the absence of nauplii were seen in both species (Fig. 5b). Predation on C_{Naup} in the presence of diatoms was significantly enhanced in *C. typicus* and reduced in *T. longicornis* (Fig. 5a). Clearance rates on diatoms by these two copepods showed no significant differences in the presence or absence of nauplii (Fig. 5b).

DISCUSSION

Experiments

All copepod species investigated fed on eggs and young nauplii of all prey types offered. As in other studies (Bonnet et al. 2004), there were no signs of barriers that would prevent inter- and intraspecific predation. However, there were significant differences in the rates of ingestion of eggs and nauplii of different species, and also between predators, and the presence of phytoplankton had also an effect.

Ingestion of eggs and nauplii followed a functional relationship, which varied widely between egg species and predator species. The eggs of *T. longicornis* were preferred prey by all copepod species tested, most likely due to their larger size. The eggs of *Centropages* spp. were the least ingested by all species. As its size is intermediate between *A. clausi* and *T. longicornis* eggs, size selectivity does not explain this difference. Rather the small spines covering the surface of the eggs of *Centropages* spp. may protect them against predation. Earlier studies have shown that predator perception and escape behaviour (Fields & Yen 1997, Titelman & Kiørboe 2003) by the prey and feeding habits of predators determine the interaction of both (Jakobsen et al. 2005). Nauplii of *Centropages* spp. were ingested at the highest rates in single-prey experiments. Again, size cannot explain this preference, as nauplii of all species investigated differed only slightly in size and *Centropages* nauplii are intermediate in size. Thus, differences in naupliar motility and behaviour might cause the different preferences for naupliar species. Indeed, nauplii of both *A. clausi* and *T. longicornis* perform a jump-sink swimming pattern where they swim only occasionally and perform strong escape jumps (Titelman & Kiørboe 2003). In contrast, the almost constantly swimming *Centropages* spp. nauplii may require stronger hydrodynamical signals for eliciting an escape response and are more easily detected by predators. Interestingly, nauplii of *T. longicornis* were the poorest escapers when compared to *Acartia tonsa* and *Eurytemora affinis* (Green et al. 2003, Titelman 2001, Titelman & Kiørboe 2003).

The influence of different feeding habits of adult copepods on food selectivity is more relevant in the experiments with mixed prey. Jonsson & Tiselius (1990) separated copepods into ambush and cruising predators. With the slow sinking behaviour interrupted by short jumps, ambush predators have the advantage of not being detected until they attack (Jonnson & Tiselius 1990, Kiørboe et al. 1999). Thus they are considered more effective in capturing motile prey like nauplii. Our results are in accordance with this assumption. The ambush feeders *A. clausi* and *C. typicus* showed a positive selection for motile nauplii over non-moving eggs when both prey types were offered; the cruising predator *T. longicornis* showed a positive selection for eggs, when eggs and nauplii were offered at the same density. According to Paffenhöfer & Knowles (1980) and Jonsson & Tiselius (1990) cruising species with their constant, strong and wide feeding currents feed on whatever prey comes according to its relative abundance if is not fast enough to escape. Otherwise, the constant hydrodynamical signal derived from such behaviour makes them more detectable by nauplii, which may escape before the copepod attacks.

When two naupliar species were offered all predators showed a more or less distinct preference for the jump-sink *T. longicornis* nauplii over the constantly swimming *Centropages* spp. nauplii. This is in sharp contrast to our single prey experiments, where *Centropages* spp. nauplii experienced the largest predation pressure. Apparently predators react differently in the presence of one or two prey behavioural patterns, but this requires further study.

A clear example of an additional effect of combining prey items is evident in our experiments with mixtures of diatoms and *Temora* eggs. The enhanced ingestion of eggs at diatom concentrations below 60 μg C l^{-1} may be due to an increased feeding activity, which causes higher encounter rates. Small algae are mostly detected by chemoreceptors located at the antennae of the copepods (Poulet et al. 1986) and may have stimulatory or inhibitory effects on feeding (Alstyne 1986, Huntley et al. 1986). In our study, the diatom *Thalassiosira weissflogii* seemed to be stimulatory because all species increased their feeding activity. However, when diatom concentrations reached 40 µg C l^{-1} the feeding on eggs declined rapidly in *A. clausi* and *T. longicornis*.

When nauplii instead of eggs were combined with diatoms the ingestion of nauplii by *A. clausi* and *C. hamatus* was unaffected by diatoms, but clearance rates on algae were enhanced in the absence of nauplii. This may be due to a switching behaviour in feeding modes as known already for *A. tonsa*, which may alternate between feeding-current-generating and ambush-feeding modes, when small-sized phytoplankton is present above a certain concentration (Jonsson & Tiselius 1990, Kiørboe et al. 1996). In contrast, clearance rates remained unaltered in *T. longicornis* and *C. typicus*, but ingestion of nauplii changed in these species. In *T. longicornis* it decreased, while in *C. typicus* it increased significantly, confirming the observations in combinations of eggs and diatoms for the latter species. It was the only species where the presence of phytoplankton stimulated both, ingestion of eggs and nauplii.

In situ predation

The relevance of inter- and intraspecific predation in the German Bight copepod population according to our observations depends not only on the abundances and predators and prey species, but also on the phytoplankton density. The information on natural density of eggs and nauplii in the southern North Sea is sparse. In winter, pooled egg abundance of the species studied herein ranged from 0 to 1 l^{-1}, and nauplii from 0.6 to 5 l^{-1}; in May during the main reproductive period (Halsband & Hirche 2001) up to 35.7 eggs and 20.4 nauplii l^{-1} were found (Wesche et al. 2007). Applying the functional relationship from this study to pooled in-situ concentrations of eggs and nauplii in November 2003 and May 2004, the resulting ingestion rates of females were 0.09 and 2.76 % body C d^{-1} for eggs, and 0.04 and 3.39 % body C d^{-1} nauplii, respectively (Table 5), not taking into account the effect of phytoplankton concentration. We assume that our laboratory rates are realistic, as observations reported on the effect of starvation previous to the experiments are ambiguous. Yen (1983) and Tiselius (1998) found increased ingestion rates following starvation, while Bonnet et al. (2004) reported lower ingestion rates in starved specimens as compared to fed ones. It seems that inter- and intraspecific predation for females in the winter when resources are low is not a substantial food resource, but in summer, when the small copepods reproduce almost synchronously at a time when the spring blooms is finished (Halsband & Hirche 2001), they may well use carnivorous feeding to fuel oogenesis. Predation on the young stages is low in the winter, partly due to the low abundance of older stages. For pooled November maximum abundances of eggs, nauplii and females (Wesche et al. 2007) predation rates of 0.3 % d^{-1} for eggs and 0.4 % d^{-1} for nauplii respectively were found (Table 5). For maximum abundances in May the respective rates are 2.1 % d^{-1} for eggs and 3.3 % d^{-1} for nauplii (Table 5). Differential selectivity of predators and susceptibility for predation by prey may help explain community composition, but other invertebrate predators (Daan 1989, Barz & Hirche 2007) and fish (Nielsen & Munk 1998) are also important, not to forget about the modifying effect of ambient phytoplankton. Furthermore, only females were studied as predators and only eggs and nauplii stage II as prey. As previous studies have shown distinct shifts in behaviour during ontogeny (Green et al. 2003, Titelman & Kiørboe 2003) there is certainly need to expand further on these investigations.

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Figure captions

Fig. 1. *Acartia clausi*, *Temora longicornis*, *Centropages hamatus*, and *C. typicus*. Ingestion of three egg species. A_{Egg} = *A. clausi* eggs, C_{Egg} = *Centropages* spp. eggs, T_{Egg} = *T. longicornis* eggs. Note different scales

Fig. 2. *Acartia clausi*, *Temora longicornis*, *Centropages hamatus*, and *C. typicus*. Ingestion of three nauplii species stage II. A_{Naup} = *A. clausi* nauplii, C_{Naup} = *Centropages* spp. nauplii, T_{Naup} = *T. longicornis* nauplii. Note different scales

Fig. 3. *Acartia clausi*, *Temora longicornis*, and *C. typicus.* Selectivity indices (Ivlev 1961) of mixed prey experiments. a) *A. clausi* eggs (A_{Egg}) and *T. longicornis* nauplii (T_{Naup}) (94:94 l^{-1}), b) *T. longicornis* nauplii (T_{Naup}) and *Centropages* spp. nauplii (C_{Naup}) (63:63 l^{-1})

Fig. 4. *Acartia clausi*, *Temora longicornis*, and *C. typicus.* Ingestion of *T. longicornis* eggs at an initial density of 94 eggs l^{-1} and clearance of the diatom *Thalassiosira weissflogii* offered in three concentrations ± SD

Fig. 5. *Acartia clausi*, *Temora longicornis*, *Centropages hamatus*, and *C. typicus*. a) Ingestion of *Centropages* spp. nauplii (C_{Naup}) with and without the diatom *Thalassiosira weissflogii* (60 µg C l^{-1}). b) Clearance of *T. weissflogii* in the presence and absence of *Centropages* spp. nauplii (94 l^{-1}) (C_{Naup}). Unpaired t-tests. Significance level: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 1. *Acartia clausi*, *Temora longicornis*, *Centropages hamatus*, and *C. typicus*. Total number of experiments per species conducted with total number of experimental flasks in parentheses

	predator species			
experiment	***A. clausi***	***T. longicornis***	***C. hamatus***	***C. typicus***
I single prey				
eggs (3 species) (up to 7 concentrations 30 to 210 eggs flask^{-1})	5(51)	7(68)	5(45)	6(5)
nauplii (3 species) (up to 5 concentrations 20 to 100 nauplii flask^{-1})	5(43)	5(47)	5(44)	5(44)
II mixed animal prey				
A_{Egg} + T_{Naup} (60 : 60 flask^{-1})	1(4)	1(7)		1(3)
T_{Naup} + C_{Naup} (40 : 40 flask^{-1})	1(3)	1(7)		1(5)
III animal prey and diatom				
T_{Egg} constant + *Th. weissflogii* (60 eggs flask^{-1} + 4 diatom concentrations 0 to 200 µg C L^{-1})	2(12)	2(12)		2(12)
C_{Naup} + *Th. weissflogii* constant (60 nauplii flask^{-1} + 60 µg C l^{-1} diatom)	1(9)	1(9)	1(9)	1(9)

Table 2. *Acartia clausi*, *Temora longicornis*, *Centropages hamatus*, and *C. typicus*. Mean length and carbon content ± SD of females, eggs and nauplii, and egg morphology. Sample size in parentheses. [1]Female feeding behaviour according to Jonsson & Tiselius (1990); [2]Nauplii swimming behaviour according to Titelman & Kiørboe (2003)

species	**female behaviour[1]**	**female prosome length carbon content**	**egg diameter carbon content**	**egg surface**	**nauplii total length carbon content**	**nauplii behaviour[2]**
A. clausi	ambush	946 ± 102 µm (488) 5.92 ± 2.16 µg C	63 ± 4 µm (100) 18.33 ± 0.01 ng C	smooth	115 ± 11 µm (50) 41.40 ± 0.02 ng C	jump-sink
T. longicornis	cruising	1028 ± 137 µm (600) 15.85 ± 0.04 µg C	88 ± 8 µm (100) 49.94 ± 0.04 ng C	smooth	135 ± 37 µm (50) 53.13 ± 3.17 ng C	jump-sink
C. hamatus	ambush	1103 ± 138 µm (392) 10.30 ± 3.01 µg C	75 ± 6 µm (100) 30.93 ± 0.02 ng C	spiny	129 ± 21 µm (50) 65.52 ± 1.12 ng C	swim
C. typicus	ambush	1304 ± 47 µm (508) 15.25 ± 1.08 µg C				

Table 3 Three-way ANOVA testing the dependence of ingestion rates on predator species (*A. clausi, T. longicornis, C. hamatus* and *C. typicus*), egg-species (A_{Egg}, T_{Egg}, C_{Egg}) and prey concentration (low, mid, high); data as in Fig. 1, square root transformed

source of variation	**SQ**	**df**	**MQ**	**F**	**P**
predator species	152.41	3	50.80	61.05	<0.001
egg-species	21.40	2	10.70	12.86	<0.001
prey concentration	146.02	2	73.01	87.73	<0.001
predator * egg-species	22.50	6	3.75	4.51	<0.001
predator * concentration	9.90	6	1.65	1.98	ns
egg-species * concentration	6.66	4	1.66	2.00	ns
predator * egg-species * concentration	9.70	12	0.81	0.97	ns
residual	155.62	187	0.83		

Table 4 Three-way ANOVA testing the dependence of ingestion rates on predator species (*A. clausi, T. longicornis, C. hamatus* and *C. typicus*), nauplii-species (A_{Naup}, T_{Naup}, C_{Naup}) and prey concentration (low, mid, high); data as in Fig. 2, square root transformed

source of variation	**SQ**	**df**	**MQ**	**F**	**P**
predator species	61.03	3	20.34	45.82	<0.001
nauplii-species	16.36	2	8.18	18.42	<0.001
prey concentration	98.62	2	49.31	111.07	<0.001
predator * nauplii-species	9.13	6	1.52	3.43	<0.001
predator * concentration	3.89	6	0.65	1.46	ns
nauplii-species* concentration	7.24	4	1.81	4.08	<0.001
predator * nauplii-species * concentration	4.60	12	0.38	0.86	ns
residual	65.26	147	0.44		

Table 5 *Acartia clausi*, *Temora longicornis*, *Centropages hamatus*, and *C. typicus*. Maximum pooled abundances of females, eggs and nauplii in November 2003 and May 2004 (Wesche et al. 2007), and calculated predation rates from applied functional response of single prey experiments

	abundance (ind l^{-1})			**ingestion (prey fem^{-1} d^{-1})**		**ingestion (% body C d^{-1})**		**predation (%)**	
month	**females**	**eggs**	**nauplii**	**eggs**	**nauplii**	**eggs**	**nauplii**	**eggs**	**nauplii**
Nov	0.04	1.19	1.49	0.35	0.53	0.09	0.94	0.33	0.42
May	0.48	35.65	20.38	10.64	7.45	2.76	3.39	2.06	3.29

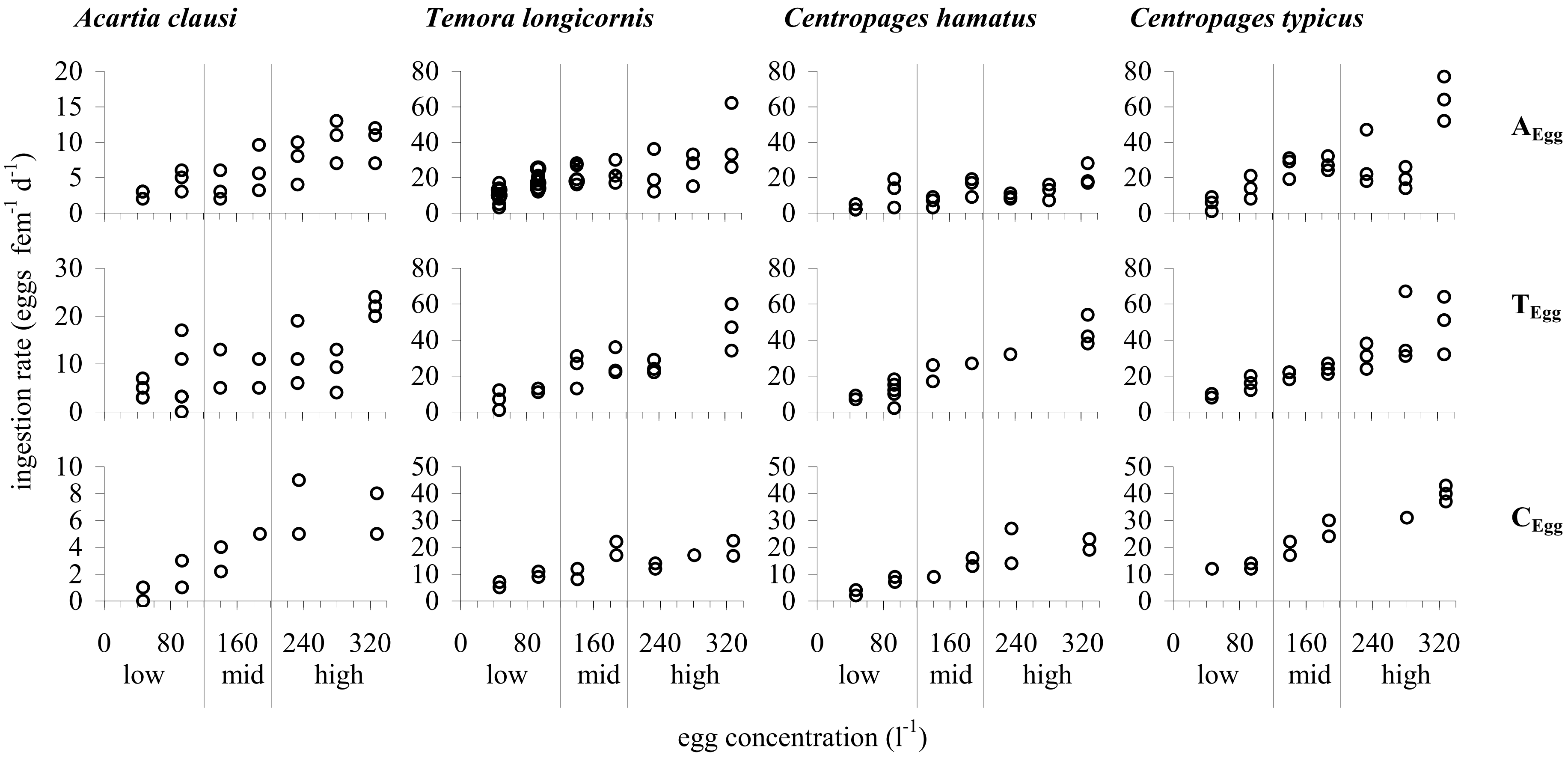
Acartia clausi
Temora longicornis
Centropages hamatus
Centropages typicus
A_Egg
T_Egg
C_Egg
ingestion rate (eggs fem-1 d-1)
0 5 10 15 20
0 10 20 30
0 2 4 6 8 10
0 20 40 60 80
0 10 20 30 40 50
0 80 160 240 320
low
mid
high
egg concentration (l-1)

Fig. 1

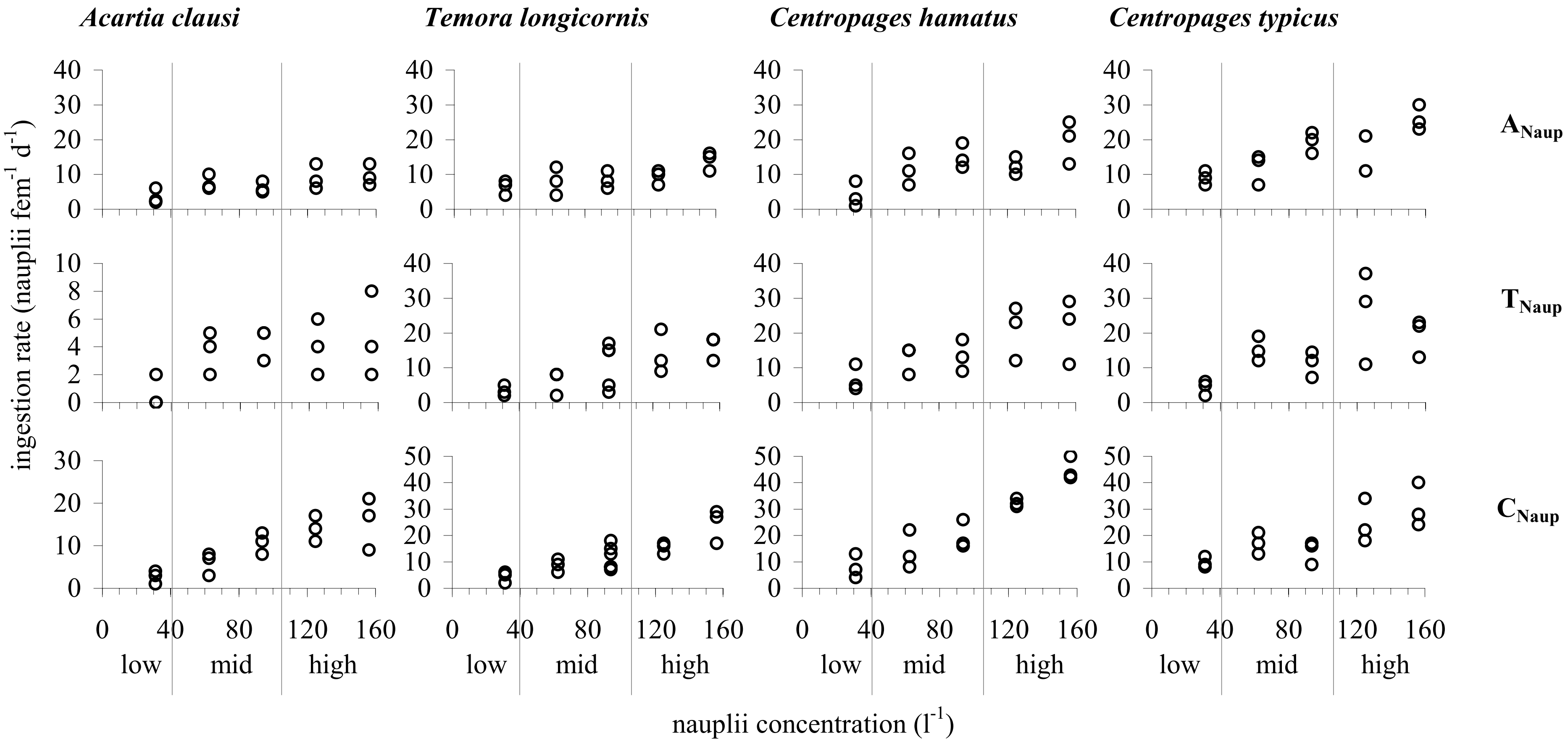
Acartia clausi
Temora longicornis
Centropages hamatus
Centropages typicus
ingestion rate (nauplii fem⁻¹ d⁻¹)
A_Naup
T_Naup
C_Naup
0
40
80
120
160
low
mid
high
nauplii concentration (l⁻¹)

Fig. 2

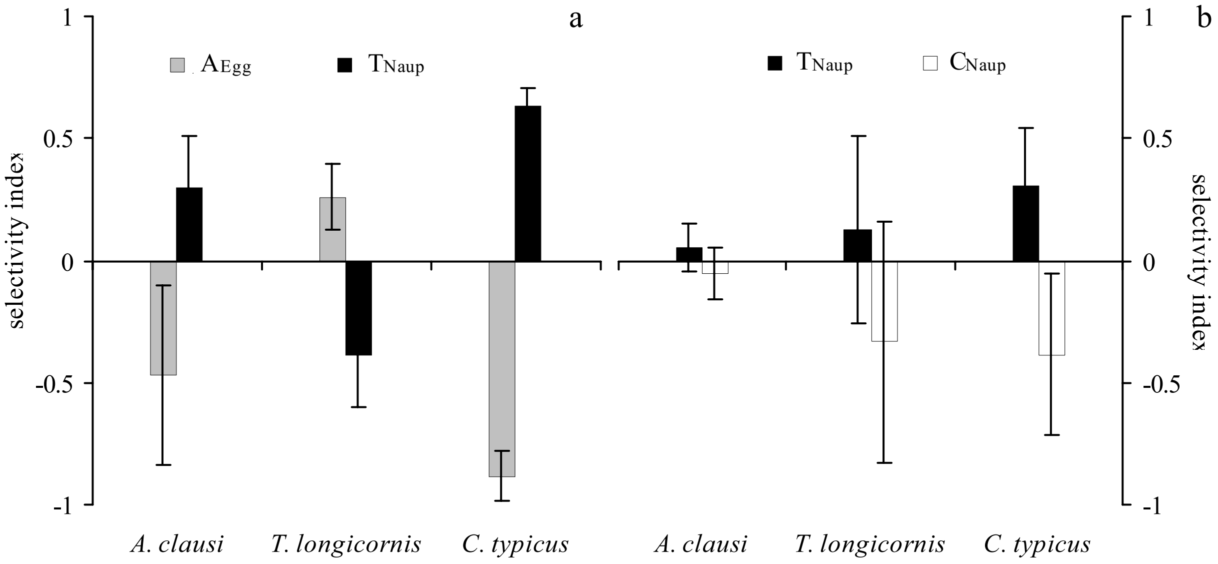
a
b
AEgg
TNaup
TNaup
CNaup
selectivity index
selectivity index
1
0.5
0
-0.5
-1
1
0.5
0
-0.5
-1
A. clausi
T. longicornis
C. typicus
A. clausi
T. longicornis
C. typicus

Fig. 3

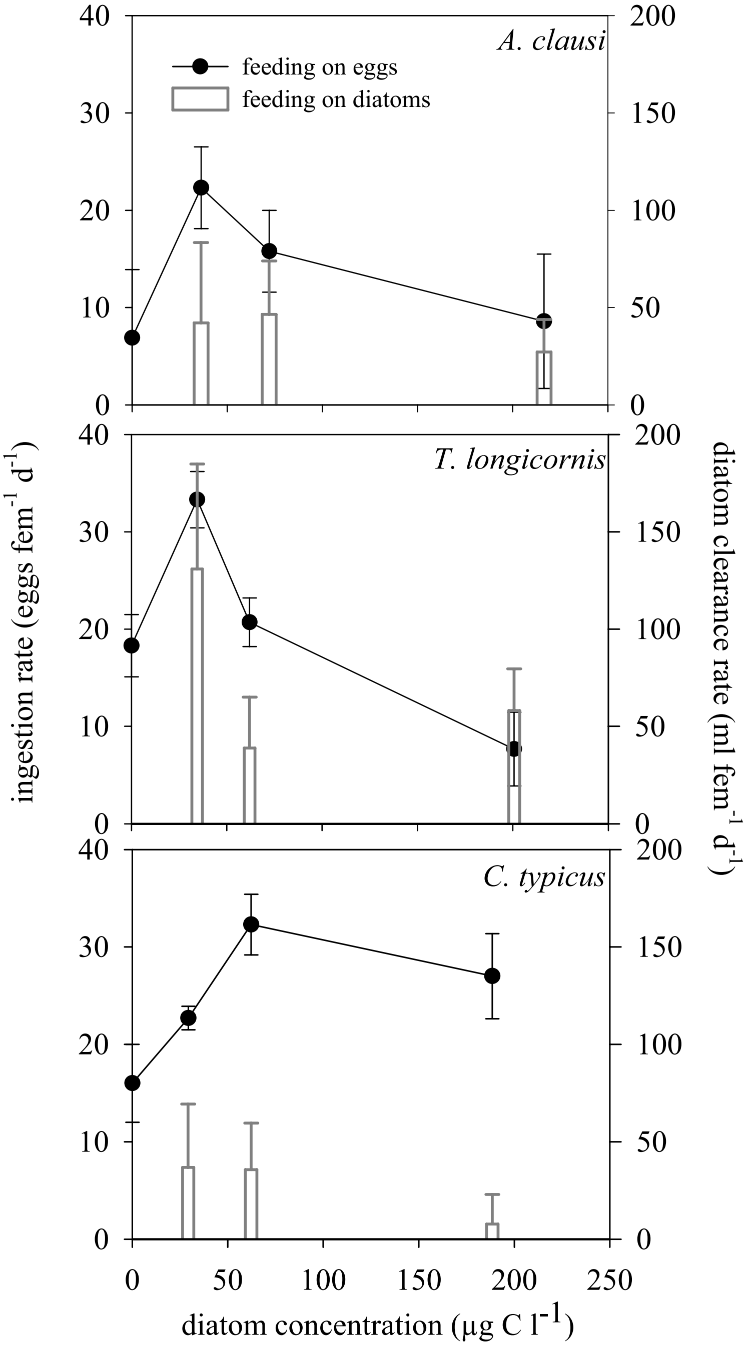
A. clausi
T. longicornis
C. typicus
feeding on eggs
feeding on diatoms
ingestion rate (eggs fem^{-1} d^{-1})
diatom clearance rate (ml fem^{-1} d^{-1})
diatom concentration (µg C l^{-1})
0
10
20
30
40
50
100
150
200
250

Fig. 4

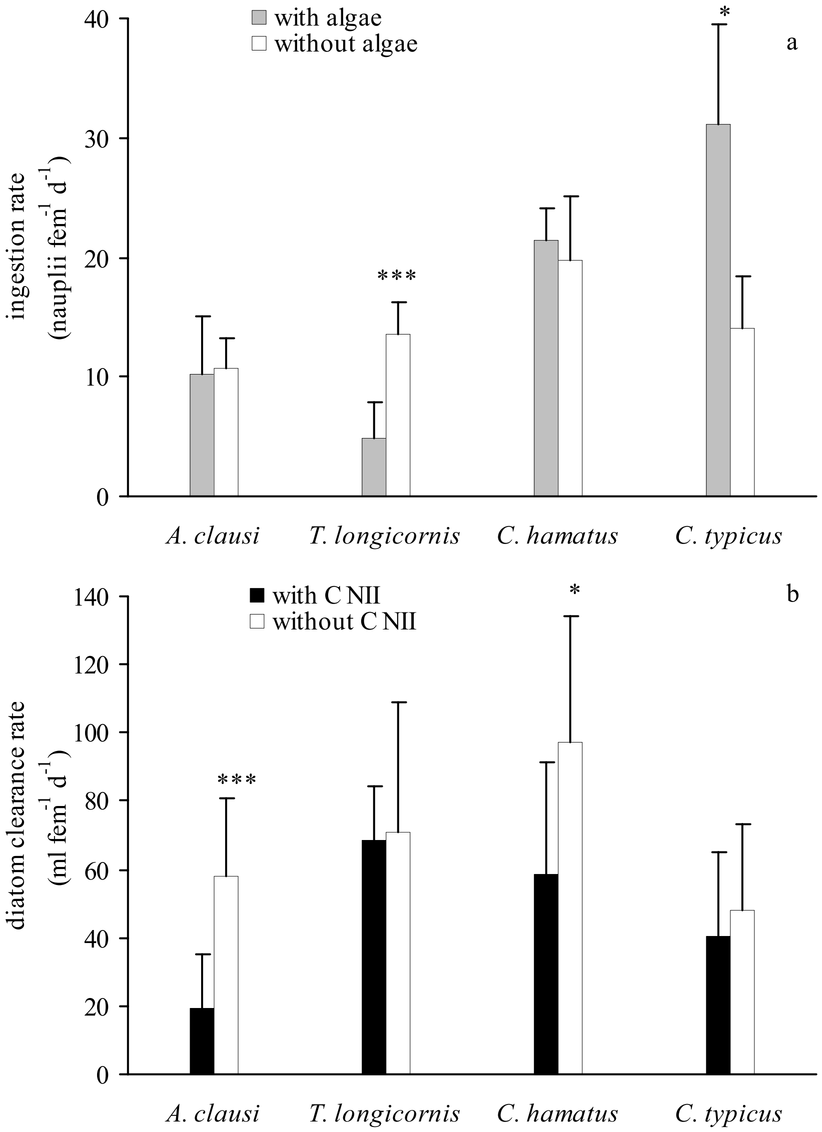
40
30
20
10
0
ingestion rate
(nauplii fem^{-1} d^{-1})
with algae
without algae
a
*
***
A. clausi
T. longicornis
C. hamatus
C. typicus
140
120
100
80
60
40
20
0
diatom clearance rate
(ml fem^{-1} d^{-1})
with C NII
without C NII
b
***
*
A. clausi
T. longicornis
C. hamatus
C. typicus

Fig. 5

SEASONAL BIRTH AND MORTALITY RATES OF CALANOID COPEPODS IN THE GERMAN BIGHT (SOUTHERN NORTH SEA)

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submitted to Journal of Plankton Research

Seasonal birth and mortality rates of calanoid copepods in the German Bight (Southern North Sea)

Abstract

This study presents seasonal birth and stage specific mortality rates of the dominant calanoid copepod species *Acartia clausi*, *Temora longicornis* and *Centropages* spp. in the central German Bight. Both rates showed a strong seasonal pattern. The instantaneous birth rate peaked during spring and summer with rates of 0.4 d^{-1} in *A. clausi*, 2.0 d^{-1} in *T. longicornis* and 1.1 d^{-1} in *Centropages* spp.. Birth rates were correlated with temperature, except in *A. clausi*. Dinoflagellate and ciliate biomass affected the birth rates of *A. clausi* and *Centropages* spp., whereas those of *T. longicornis* were correlated with flagellate and diatom biomass.

The highest stage specific mortality rate of *A. clausi* was estimated in the copepodite stage CI-CII (1.1 d^{-1}). *T. longicornis* showed highest mortality in the copepodite stage CIII (0.7 d^{-1}), whereas mortality for *Centropages* spp. was highest during the egg-nauplii, and copepodite stage CIII (0.6 d^{-1}). Mortality of older copepodids (CIV-adult) was lowest in all species, with maximum values of 0.2, 0.3 and 0.2 d^{-1} for *A. clausi*, T. *longicornis* and *Centropages* spp., respectively. Mortality of the egg and nauplii stage was low in comparison to the mortality rates in the older stages.

INTRODUCTION

Copepods constitute the majority of marine mesozooplankton (Verity and Smetacek, 1996). Their population abundance and distribution are influenced by physical (temperature, advection), physiological (temperature response, food requirements) and ecological conditions (food availability, predation) (Greve et al., 2004). In the German Bight (Southern North Sea), *Acartia clausi*, *Centropages hamatus*, *C. typicus* and *Temora longicornis* are the dominant free-spawning calanoid copepod species, which coomprise up to 80 % of total copepod abundance seasonally (Krause et al., 1995; Wesche et al., 2007). Population densities fluctuate seasonally, with a peak in summer and lower numbers during winter (Greve et al., 2004; Wesche et al., 2007).

Variability in the size of a population is the result of changes in birth and mortality rates within this population. Whereas the influence of external and internal factors for birth and growth rates has been relatively well established, the importance of mortality is most often neglected in studies of copepods population dynamics. Obviously, the main reason for the skewness in data is the relative ease with which one can establish egg production rates in combination with the difficulties attached to a proper assessment of mortality in natural populations. Numerous studies dealing with productivity and growth of populations in several species, from different regions are available, and in temperate regions, the reproductive activity of copepods could be related to temperature and phytoplankton biomass, with highest values in spring and summer, and a reduction in winter (e.g. Kiørboe and Nielsen, 1994; Halsband and Hirche, 2001; Wesche et al., 2007). The few studies on mortality were often restricted to egg and early nauplii stages or to relatively short sampling periods of a few weeks (Kiørboe and Nielsen, 1994; Petersen and Kimmerer, 1994; Ohman and Hirche, 2001). To our knowledge, the first annual study on mortality rates is given for *Calanus helgolandicus* by Hirst et al. (Hirst et al., 2007), who showed strong seasonal variability in mortality.

Copepods develop through successive, identifiable instars (egg, nauplii, copepodids, adults), which differ in their morphology, physiology (e.g. temperature and food requirements) (Mauchline, 1998), and their swimming and escape behaviour (Jonsson and Tiselius, 1990). Thus, mortality is likely to vary also with developmental stage due to different physiological requirements and capabilities to deal with adverse conditions, and also as a result of differences in vulnerability to predation. Copepods are the major food source for several fish and their larvae (e.g. Nielsen and Munk, 1998), jelly fish (e.g. Daan, 1986, 1989; Barz and Hirche, 2005) or chaetognaths (e.g. Szyper, 1978; Álvarez-Candena, 1993). Furthermore, copepods themselves can act as predators. Several species have shown a regulatory capability within their population by feeding of older stages on the own offspring during high population density and food scarcity (e.g. Heinle, 1970; Daan et al., 1988; Ianora and Buttino, 1990).

The most straightforward way to estimate mortality of different stages is to use a very high resolution sampling strategy, with sampling intervals short enough to separate mortality from changes in the stage class structure through growth and reproduction. In most temperate copepod species this would require almost daily sampling, and as a result this strategy is not possible when the aim of the study is to establish seasonal changes in mortality, but can be used in shorter scale experiments or sampling campaigns (Ohman and Hirche, 2001). Alternatively, one can use the method developed by Aksnes and Ohman (Aksnes and Ohman, 1996). Under the assumption that the population is in a stable stage structure, one can use the relative amounts of the different stages, in combination with the relative duration of these stages to estimate disappearance rates between the different stages. Obviously, variation in the estimates can be large at times, but averaging several samples could give a good estimator of mortality rates of the different stages.

The objective of this study was to investigate seasonal differences in both birth and mortality rates, link these to environmental conditions, such as temperature, food (biomass and composition), and predator abundance, and assess whether production or loss drive the changes in population densities of copepods. Hence, we studied birth and stage specific mortality rates of the dominant calanoid copepods in the German Bight for a two year period.

MATERIAL AND METHODS

Birth rates

Instantaneous per capita birth rates (b) of the dominant calanoid copepod species *Acartia clausi*, *Temora longicornis* and *Centropages* spp. (*C. hamatus* and *C. typicus*) were determined at least four times per month (during spring and summer twice per week) with the equation of Edmondson (Edmondson, 1968):

$$b = \ln(E+1)/D$$

where b is the birth rate (d^{-1}), E is the proportion of density of viable eggs (m^{-3}) and individual number (m^{-3}), and D is the egg developmental time.

The two *Centropages* species were pooled, because the copepodite stages CI-CV were not distinguished to species-level, which lead to problems in the calculation of population increase rates. Thus, although both species differed slightly in their seasonal appearance they could not be considered separately.

Developmental time D was calculated using the equations of McLaren et al. (McLaren et al.,1969) (*A. clausi*), Corkett and McLaren (Corkett and McLaren, 1970) (*T. longicornis*) and McLaren et al. (McLaren et al., 1989) (*C. typicus*). The basis for the estimation of E were measurements of species specific egg production rates (EPR in eggs fem^{-1} d^{-1}), hatching success (%) and female field abundance (m^{-3}). For estimation of EPR 30 active females per species were collected from oblique net tows (Nansen net, mesh size 280 µm and Calcofi net, mesh size 500 µm) at Helgoland Roads. Females were placed individually in cell wells (Corning) filled with 10 ml of 55 µm prefiltered seawater. The wells were incubated at ambient temperature and light regime in an incubator chamber (WTB Binder). After 24 h, females were removed and all eggs and eggshells were counted. For estimation of hatching success the eggs were incubated at ambient conditions in the incubator chamber up to 10 days after spawning with daily inspection and counting of nauplii. EPR was corrected for hatching success to get the numbers of viable eggs.

Rates of population increase

Abundance of copepods was analysed two times per month from September to December 2003, and weekly from January 2004 to August 2005 between 8:00 and 10:00 in the morning, by vertical hauls with a Nansen net (0.35 m^2 opening area, mesh size 150 µm) from near the bottom to the surface. Volumes of water filtered were measured using a calibrated flow meter fitted in the net opening. Calanoid copepods were identified to species level and developmental stage (adults, copepodids CI-II, CIII, CIV-V).The rate of population increase r was computed with the equation of Paloheimo (Paloheimo, 1974):

$$r = (\ln N_{t+\Delta t} - \ln N_t)/\Delta t$$

where N_t and $N_{t+\Delta t}$ are the individual numbers at times t and t+Δt.

Before computation of the rates of population increase the counted data were smoothed using a three-point running mean.

Mortality rates

Total population mortality m was calculated by conversion of the relationship r = b – m:

$$m = b - r$$

where b is the instantaneous birth rate and r the rate of population increase.

Stage specific mortality rates were determined by using field abundances from the net samples (for eggs: calculated viable egg abundance) and the vertical life table approach by Aksnes and Ohman (Aksnes and Ohman, 1996):

$$r_i = n_i/n_{i+1}$$

(ratio of individual numbers of two consecutive developmental stages)

$$r_i = [\exp(m_i{*}D_i)-1]/[1-\exp(-m_i{*}D_{i+1})]$$

(mortality of two juvenile stages)

$$m_i = \ln(r_i+1)/D_i$$

(mortality of juvenile and adult stage)

where m_i is the stage specific mortality rate (d^{-1}) and D_i and D_{i+1} are the stage specific developmental times (in days) of two consecutive developmental stages.

Species and stage specific developmental times were calculated from generation and stage duration times. Generation times were determined using the monthly mean temperatures and the equations of McLaren (McLaren, 1978) for *A. clausi*, of Klein Breteler and Gonzales (Klein Breteler and Gonzales, 1986) for *T. longicornis* and of Liang et al. (Liang et al., 1996) for *Centropages* spp.. For the determination of stage specific duration times we assumed that the relative proportion of stage duration and the generation time is the same, regardless temperature (Corkett and McLaren, 1970; Landry, 1975). Thus, we divided mean stage specific duration from the literature (Klein Breteler et al., 1994 for *A. clausi*; Halsband-Lenk, 2001 for *T. longicornis* and *Centropages* spp.) by the given generation times. The stage specific developmental times were obtained by the multiplication of the calculated proportion of each developmental stage with the generation times we determined for each species and month.

Abundance fish larvae was provided by Malzahn and Boersma (Malzahn and Boersma, 2007) and abundance of chaetognaths, hydromedusae and ctenophores were determined from the 150 µm samples.

RESULTS

Birth

Instantaneous birth rates (b) of all species showed seasonal fluctuations with highest rates found from April to August and lower or zero ones during winter (Fig. 1). Maximal monthly b (average of 3-4 values of b per month) of 0.4, 2.0 and 1.1 d^{-1} were reached in *A. clausi*, *T. longicornis* and *Centropages* spp., respectively. The birth rates were strongly influenced by season, species and the interaction of both (Tab. I). Birth rates of *A. clausi* were significantly lower than those of the other species ($p < 0.01$), except in winter, where no differences between *A. clausi* and the other species were found. Differences between *T. longicornis* and *Centropages* spp. were only significant in summer ($p < 0.001$). Birth rates were strongly related to temperature, except those of *A. clausi* (Tab. II). Further correlation analyses with phytoplankton components were done with temperature corrected birth rates by using the residuals of temperature-birth rate regressions. The temperature corrected birth rates of *A. clausi* showed a positive relation to dinoflagellate, flagellate and ciliate biomass, whereas that of *T. longicornis* were correlated positively with salinity, flagellate, diatom and total phytoplankton biomass. In *Centropages* spp. significant negative effects of salinity and flagellate biomass, as well as positive effects of dinoflagellate and ciliate biomass were found.

Population increase

Population increase was highly variable between and within months and showed a strong variability between sampling dates, which was reflected in the high standard deviations (Fig. 2). Thus, a seasonal trend was not seen. Nevertheless, positive population growth was mostly found in spring and summer in all species, and in winter 2005 in *T. longicornis* and *Centropages* spp..

Mortality rates and predators

Total population mortality was high from early spring to summer for all species, and additionally in autumn 2003 for *T. longicornis* and *Centropages* spp. (Fig. 3). Highest monthly mean mortality values were 0.4, 2.0 and 1.2 d^{-1} in *A. clausi*, *T. longicornis* and *Centropages* spp., respectively, caused by the high instantaneous birth and the low population increase.

Total mortality varied with season, species and the interaction of both (Tab. III). In winter, no significant differences of species specific total mortality were found. Total mortality of *A. clausi* differed significantly from that of *T. longicornis* and *Centropages* spp., except in winter. Significant differences of mortality rates between *T. longicornis* and *Centropages* spp. occurred in summer and autumn. There was a positive correlation of total mortality with temperature in all species (Tab. IV). Mortality of *Centropages* spp. was positively affected by flagellate and negatively by ciliate biomass.

Fish larvae, chaetognaths, hydromedusae and ctenophores, as well as copepods themselves are known predators of several developmental stages of copepods. During the sampling period, abundances for *Sagitta* spp. (chaetognath) and gelatinous zooplankton (hydromedusae and ctenophores) peaked in summer and early autumn, whereas fish larvae occurred in much lower numbers and reached maximum values in early spring (Fig. 4). Only small numbers of chaetognaths, hydromedusae and ctenophores were persistent throughout the winter. Highest mean abundance of *Sagitta* spp. was 493 ind m^{-3} in September 2003. Hydromedusae and ctenophores together peaked with 1070 ind m^{-3} in August 2004, and fish larvae had 2.4 ind m^{-3} in February 2004. Total mortality of *T. longicornis* was positively correlated with abundance of the chaetognath *Sagitta* spp., while fish larvae, hydromedusae and ctenophores did not influence or were negatively correlated to total mortality rates of the copepods (Tab. IV). The abundance of adult female copepods of the species investigated showed also a significant effect on total mortality in *A. clausi* and *T. longicornis*.

With respect to stage specific mortality rates, there was a temporal shift in importance within the developmental stages (Fig. 5). The mortality rates for eggs and nauplii (egg-NVI) peaked in late spring (Apr-May), for young copepodite stages (CI-CII) in summer (Jul-Sep), and for older copepodids (CIII-adult) in autumn (Oct-Nov). In 2005, mortality of the copepodite stages CIII to adult was already high in June, and as high as or even higher than maximal mortality in 2004. The highest mortality rate of *A. clausi* with 1.1 d^{-1} was estimated in the copepodite stage CI-CII (Sept 2004). With 0.7 d^{-1} *T. longicornis* showed highest mortality in the copepodite stage CIII, whereas mortality for *Centropages* spp. accounted highest during the egg-nauplii, and CIII stage (0.6 d^{-1}). Mortality of older copepodite stages (CIV-adult) was the lowest of in all species, with maximum values of 0.2, 0.3 and 0.2 d^{-1} for *A. clausi*, T. *longicornis* and *Centropages* spp., respectively. Figure six showed a cumulative graph of the proportion of different stage specific mortality rates to better see the seasonal changes. For this figure all negative mortality rates (previous figure) were set to zero. It clearly implicated that the mortality rates of eggs and nauplii were most of the time fairly low in comparison to the mortality rates in the older stages, whereas mortality of copepodite stages CI-CIII was fairly high.

DISCUSSION

This is the first study presenting seasonal cycles of birth and stage specific mortality rates of *A. clausi*, *T. longicornis* and *Centropages* spp. from the German Bight. Results rely on a data set, with a nearly weekly basis over a two year period. There were strong seasonal differences in birth and mortality rates, as well as differences between the investigated species. In temperate regions, like the North Sea, the pronounced seasonal cycles in reproductive activity of copepods and the influence of temperature and phytoplankton biomass is generally accepted (e.g. Kiørboe and Nielsen, 1994; Peterson and Kimmerer, 1994; Halsband and Hirche, 2001; Wesche et al., 2007). The per capita birth rates of this study showed seasonal differences, with highest values found from April to August, and low ones during winter. In temperate regions, egg production rates peak in spring, whereas copepod abundance does not peak until August (e.g. Krause et al., 1995; Hernroth and Ackefors, 1979), which was also found in the present study.

T. longicornis and *Centropages* spp. were capable to renew their populations within one or two days most of the time, except in winter. Both species produced relatively high numbers of eggs with values of about 60 and 100 eggs fem^{-1} d^{-1}, respectively, mostly found during spring, when population size is still low (Wesche et al., 2007). Birth rates of *A. clausi* were always less than 0.5 d^{-1} and zero during winter. Maximal egg production found for *A. clausi* was only one third of that of *T. longicornis*, but with respect to individual numbers *A. clausi* is by far the dominant species around Helgoland Island (Wesche et al., 2007). *A. clausi* had the shortest calculated developmental times during the sampling period of the species investigated (Tab. VI), which could explain the high abundance of this species, despite the lower egg production rates.

Several studies have demonstrated that temperature and food are key factors controlling egg production and growth of calanoid copepods (e.g. Landry, 1978; Smith and Lane, 1985). Birth rates of *A. clausi* were independent of temperature, whereas that of *T. longicornis* and *Centropages* spp. were positively correlated with temperature. Wesche et al. (Wesche et al., 2007) supposed an intrinsic control of the reproductive activity of *A. clausi* in winter. Whether this might be true for the entire reproductive cycle have to be investigated in further studies.

The impact of specific phytoplankton components on the birth rates varied between species. Diatoms affected birth rates only in *T. longicornis*, whereas in *A. clausi* and *Centropages* spp. biomass of dinoflagellates and ciliates had positive effects on reproduction. Dinoflagellates (Miralto et al., 1995; Veloza, 2006) and ciliates (Bonnet and Carlotti, 2001) are known to have positive effects on fecundity of copepods and viability of eggs due to their high content of essential fatty acids, which would support our results.

The population increase of copepods is controlled through reproduction, mortality and by physical factors affecting their life. In this study, population increase varied strongly, had very high deviations and no seasonal trend was seen. The high variability of abundance between sampling dates illustrates the difficulties of sampling pelagic populations. Advection can never be excluded and always has to be considered in discussing and evaluating data. However, the population increase was correlated with total mortality in *A. clausi* ($r = -0.880$, $p < 0.001$) and *T. longicornis* ($r = -0.380$, $p < 0.001$) and not with birth rates, which implicated a stronger impact of mortality to population size. This was also suggested by Halsband-Lenk (Halsband-Lenk, 2001), who did not find a reflection of egg production rates in seasonal distribution patterns.

During times of high birth rates, also the highest total loss of individuals was found. This was a result of the high birth rates and the low population increase, from which total mortality was estimated. Otherwise, high mortality during intense breeding was already reported by earlier studies (Ianora and Buttino, 1990; Kiørboe and Nielsen, 1994). We could relate total mortality of all species to temperature, which was already predicted by Hirst and Kiørboe (Hirst and Kiørboe, 2002). Whether the increasing mortality with increasing temperature was due to physiological reasons, predation or due to a temperature effect of another mortality influencing factor is still unanswered. We found total mortality positively correlated with female copepod abundance (*A. clausi* and *T. longicornis*), abundance of the chaetognath *Sagitta* sp. (*T. longicornis*) and dinoflagellate biomass (*Centropages* spp.), which implicated first a cannibalistic, second a predatory, and third a nutritional effect of phytoplankton components to mortality. The latter may also explain the negative correlation with ciliate biomass (*Centropages* spp.). No explanation of the negative correlation of the abundance of fish larvae and total mortality of *T. longicornis* and *Centropages* spp. was found.

The stage specific mortality rates were very variable, which demonstrated the difficulties in sampling pelagic populations due to the effect of advection. In the present study, the mortality in the egg-nauplii stage was highest only in *Centropages* spp., although this was reported also for other species (e.g. Kiørboe et al., 1988; Ianora and Buttino, 1990; Peterson and Kimmerer, 1994; Ohman and Hirche 2001). In *A. clausi* and *T. longicornis* highest mortality appeared most of the time in the copepodite stages CI-CII and CIII, respectively. We found no evidence of stage specific temperature effects, which was suggested by Hirst et al. (Hirst et al. 2007) for the mortality rates of the developmental stages egg-NII of *Calanus helgolandicus*. Several studies gave highest mortality in the egg and young nauplii stages, which could account for up to 100 % of the loss (Ianora and Buttino, 1990; Peterson and Kimmerer, 1994). Kiørboe et al. (Kiørboe et al., 1988) found a high egg mortality of about 9.1 d^{-1} in *Acartia tonsa* from the Kattegat (western Baltic), which was about 15 times higher than that found in the present study. We observed no relationships of mortality in the egg-nauplii stage and environmental conditions, whereas mortality of copepodite stages was correlated with the abundance of *Sagitta* spp., fish larvae and female copepods. Especially fish as a visual oriented predator, could be more successful in feeding on better visible older stages. With respect to adult copepods as predators this result was a little bit unexpected, as the feeding efficiency on the own offspring declines with ascending developmental stage of the prey, due to larger size and/or higher escape capability (Landry 1978, Londsdale et al.1979, Daan et al. 1988).

Although concrete evidence of stage specific mortality factors is scarce and still controversial, the present results contribute to a better understanding of the seasonal cycles of the copepod community of the German Bight. The study stresses the importance of high frequency and long-term sampling strategies to detect small scale variations as well as seasonal patterns of highly variable habitats.

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TABLE AND FIGURE LEGENDS

Table I: Two-way ANOVA testing the dependence of instantaneous birth rates on season and species (*A. clausi*, *T. longicornis*, *Centropages* spp.).

Table II: *Acartia clausi*, *Temora longicornis*, *Centropages* spp.. Correlation coefficients (r) of ^{1}instantaneous birth rates and temperature, and ^{2}residuals of temperature-birth rate regressions and salinity and phytoplankton components at Helgoland Roads. ppc: total phytoplankton biomass, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Table III: Two-way ANOVA testing the dependence of total population mortality on season and species (*A. clausi*, *T. longicornis*, *Centropages* spp.).

Table IV: *Acartia clausi*, *Temora longicornis*, *Centropages* spp.. Correlation coefficients (r) of total mortality (3-point running mean), hydrographic conditions and predator abundance
at Helgoland Roads. ppc: total phytoplankton biomass, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Table V: *A. clausi*, *Temora longicornis*, *Centropages* spp.. Correlation coefficients (r) of stage specific mortality and predator abundance at Helgoland Roads. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Figure 1. *Acartia clausi*, *Temora longicornis*, *Centropages* spp.. Monthly mean instantaneous birth rates ± SD at Helgoland Roads from September 2003 to August 2005. n.d.: no data.

Figure 2. *Acartia clausi*, *Temora longicornis*, *Centropages* spp.. Monthly mean population increase (3-point running mean) ± SE at Helgoland Roads from September 2003 to August 2005.

Figure 3. *Acartia clausi*, *Temora longicornis*, *Centropages* spp.. Monthly mean total population mortality (3-point running mean) ± SD at Helgoland Roads from September 2003 to August 2005. n.d.: no data.

Figure 4. Monthly mean abundances of main potential predators, chaetognaths (*Sagitta* spp.), hydromedusae, ctenophores and fish larvae* at Helgoland Roads from September 2003 to August 2005. * data from Malzahn and Boerma (Malzahn and Boersma, 2007).

Figure 5. *Acartia clausi*, *Temora longicornis* and *Centropages* spp.. Monthly mean stage specific mortality ± SD at Helgoland Roads from September 2003 to August 2005. Note different scales.

Figure 6. *Acartia clausi*, *Temora longicornis* and *Centropages* spp.. Proportion of stage specific mortality at Helgoland Roads from September 2003 to August 2005.

Table I

source of variation	**df**	**SQ**	**MQ**	**F**	**p**
season	3	27.05	9.02	43.53	<0.001
species	2	50.38	25.19	121.61	<0.001
season * species	6	14.70	2.45	11.82	<0.001
residual	230	47.65	0.21		

Table II

	A. clausi	***T. longicornis***	***Centropages* spp.**
temperature^1	0.057	0.795***	0.579***
salinity^2	0.113	0.222*	-0.367**
dinoflagellates^2	0.380***	0.088	0.400***
flagellates^2	0.317**	0.413***	-0.415***
diatoms^2	0.218	0.328**	0.029
ciliates^2	0.386***	0.119	0.393***
ppc^2	0.265	0.332**	0.065

Table III

source of variation	**df**	**SQ**	**MQ**	**F**	**p**
season	3	13.85	4.62	28.34	<0.001
species	2	18.26	9.13	56.07	<0.001
season * species	6	9.82	1.64	10.05	<0.001
residual	202	32.90	0.16		

Table IV

	A. clausi	***T. longicornis***	***Centropages* spp.**
temperature	0.242*	0.805***	0.301*
salinity	-0.103	-0.115	0.173
dinoflagellates	0.140	-0.043	0.273*
flagellates	0.154	0.118	0.229
diatoms	0.041	0.076	0.067
ciliates	0.018	-0.025	-0.259*
ppc	0.056	0.073	0.094
Sagitta spp.	0.151	0.520***	-0.018
fish larvae	-0.191	-0.365**	-0.269*
hydromedusae and ctenophores	0.102	0.208	-0.011
copepod females	0.381**	0.422**	-0.001

Table V

	A. clausi				***T. longicornis***				***Centropages spp.***			
	egg-NVI	**CI-CII**	**CIII**	**CIV-adult**	**egg-NVI**	**CI-CII**	**CIII**	**CIV-adult**	**egg-NVI**	**CI-CII**	**CIII**	**CIV-adult**
Sagitta spp.	0.013	0.231	0.105	0.199	0.067	-0.140	0.404**	0.260	0.001	0.187	0.194	0.352
fish larvae	0.052	0.109	0.114	0.212	0.371	0.255	0.250	0.414**	0.829**	0.221	0.485**	0.650***
hydromedusae and ctenophores	-0.250	-0.361*	-0.271	-0.069	-0.036	0.066	-0.064	-0.099	0.029	-0.043	-0.077	-0.334
copepod females	0.150	0.152	0.013	0.345*	0.312	-0.304*	0.182	0.409**	-0.086	-0.034	0.138	0.105

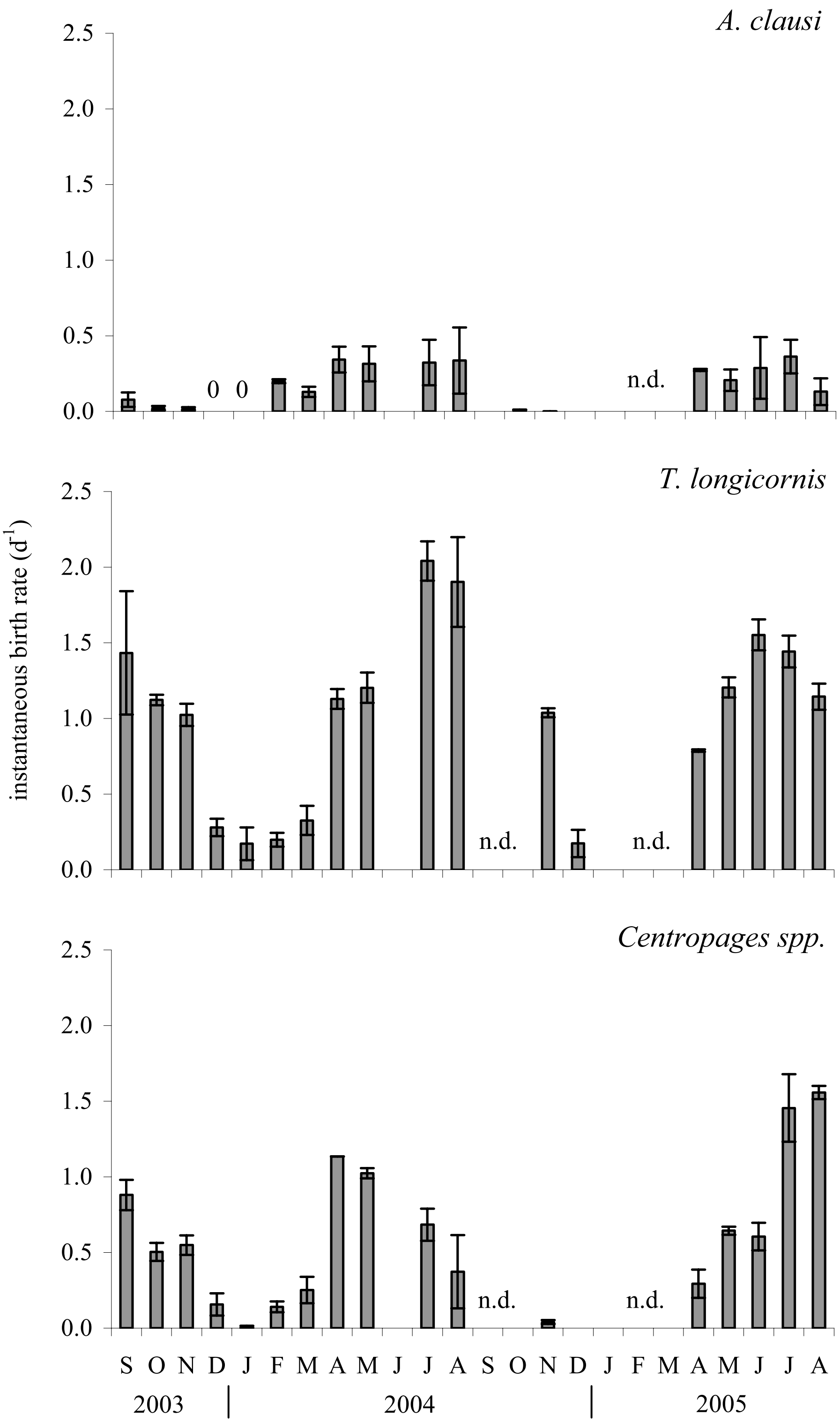
A. clausi
T. longicornis
Centropages spp.
instantaneous birth rate (d^{-1})
2.5
2.0
1.5
1.0
0.5
0.0
0 0
n.d.
n.d.
n.d.
n.d.
n.d.
S O N D J F M A M J J A S O N D J F M A M J J A
2003
2004
2005

Fig.1

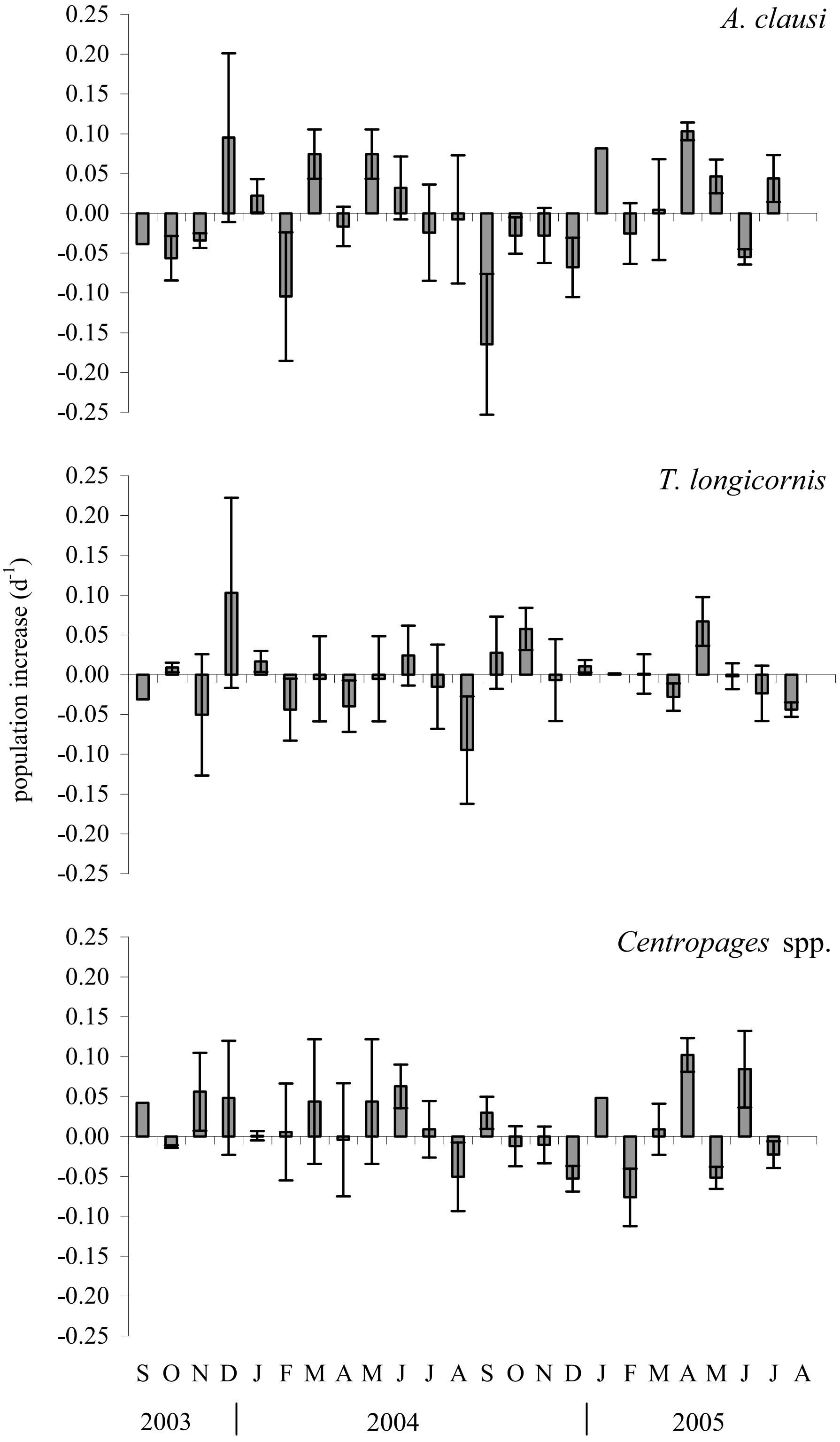
A. clausi
T. longicornis
Centropages spp.
population increase (d^{-1})
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
S O N D J F M A M J J A S O N D J F M A M J J A
2003
2004
2005

Fig.2

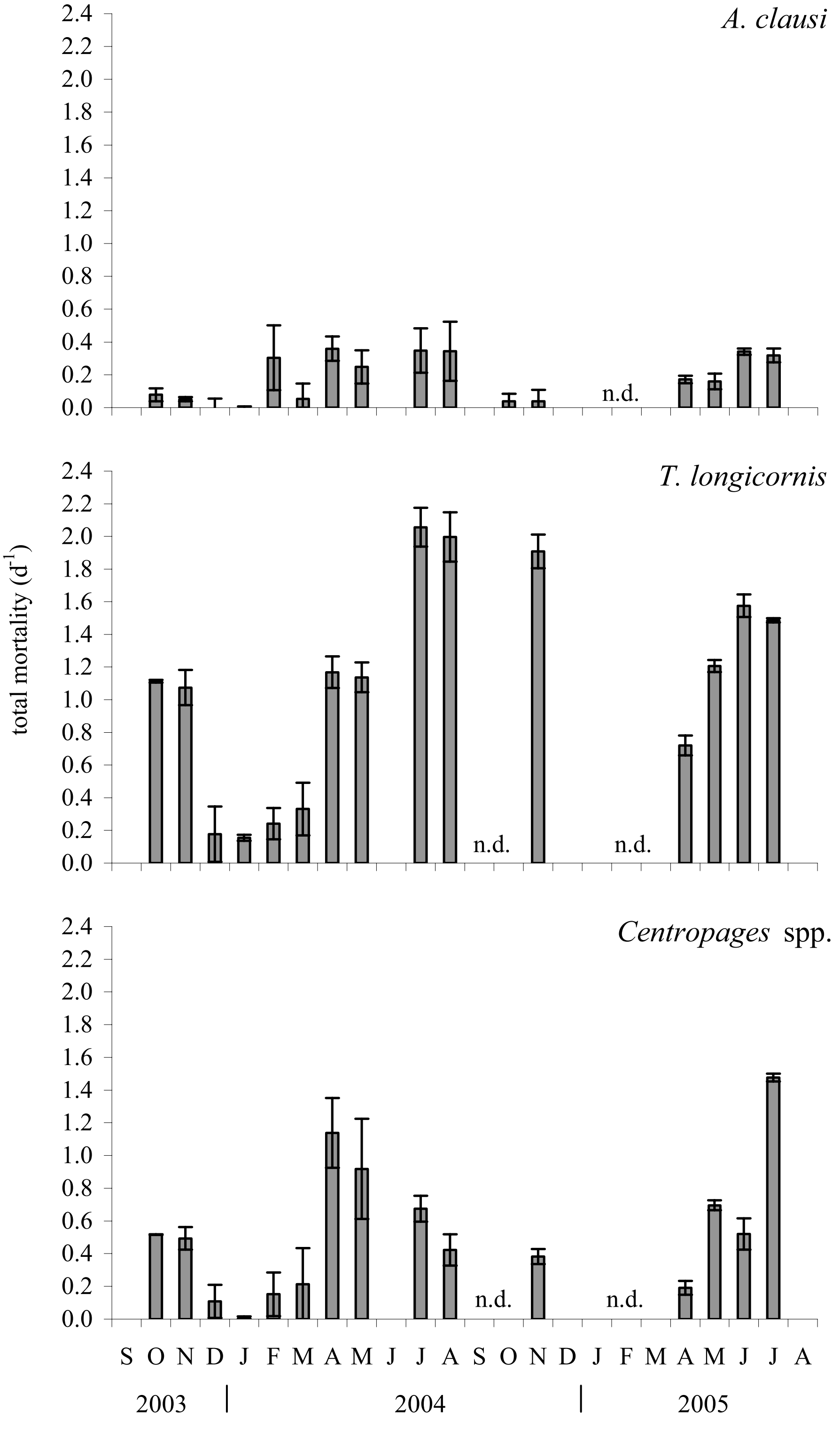
A. clausi
T. longicornis
Centropages spp.
total mortality (d^{-1})
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
n.d.
S O N D J F M A M J J A S O N D J F M A M J J A
2003
2004
2005

Fig.3

]

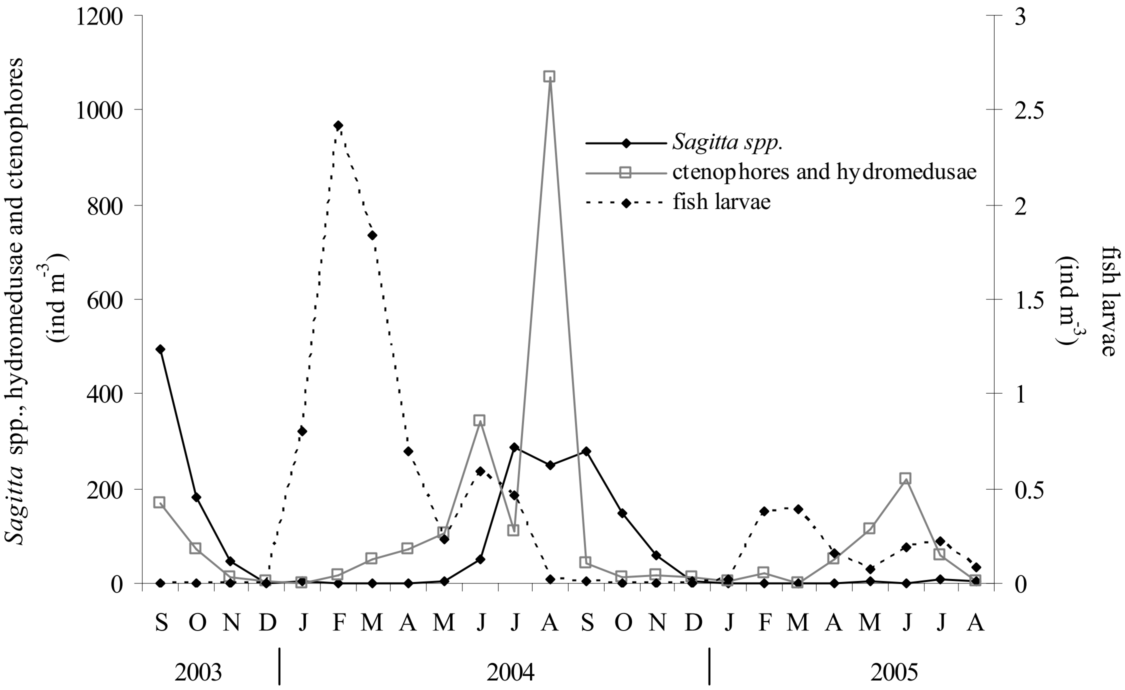
Sagitta spp., hydromedusae and ctenophores (ind m^{-3})
1200
1000
800
600
400
200
0
Sagitta spp.
ctenophores and hydromedusae
fish larvae
fish larvae (ind m^{-3})
3
2.5
2
1.5
1
0.5
0
S O N D J F M A M J J A S O N D J F M A M J J A
2003
2004
2005

Fig.4

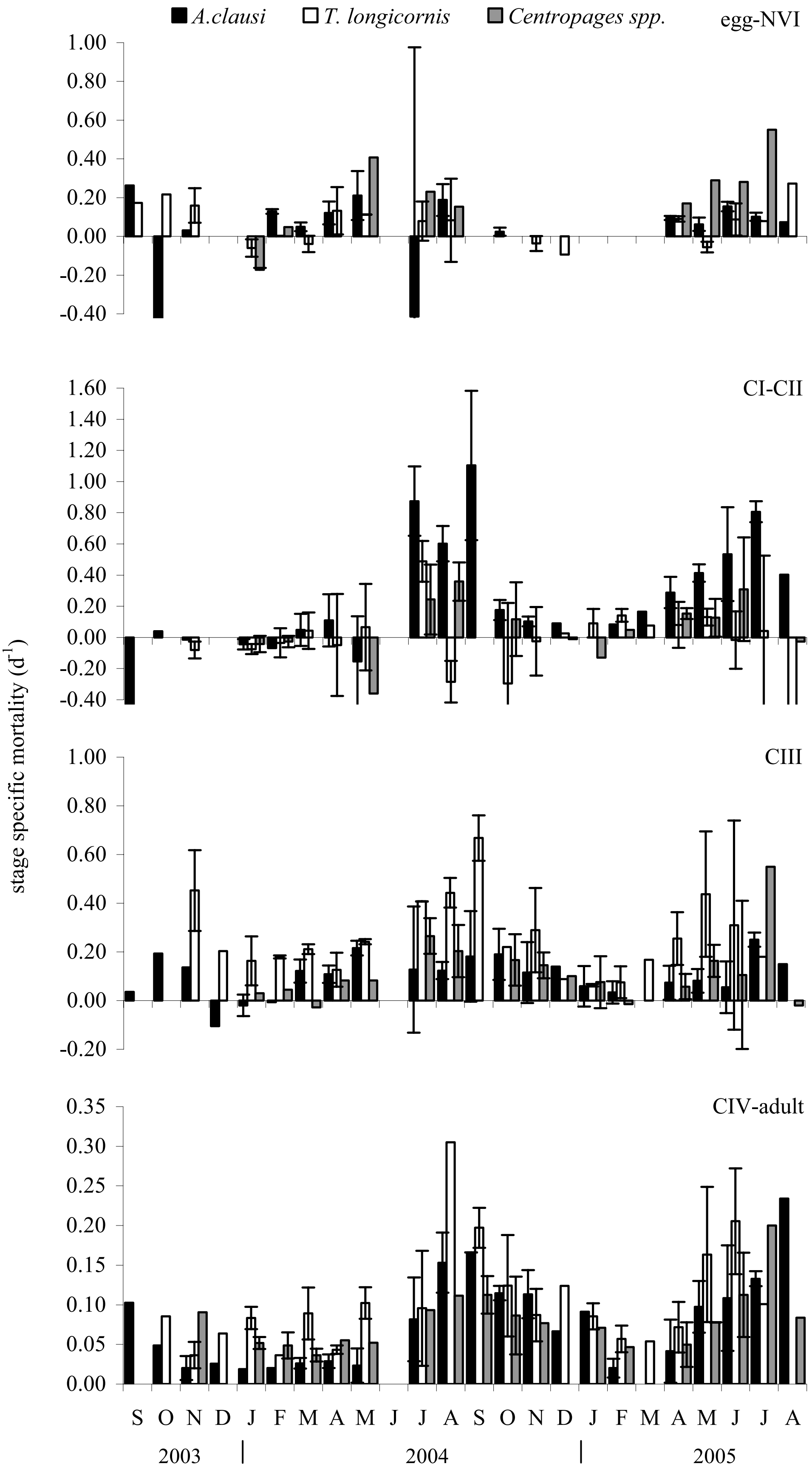
■ A.clausi
☐ T. longicornis
▨ Centropages spp.
egg-NVI
CI-CII
CIII
CIV-adult
stage specific mortality (d^{-1})
1.00
0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
1.00
0.80
0.60
0.40
0.20
0.00
-0.20
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
S O N D J F M A M J J A S O N D J F M A M J J A
2003
2004
2005

Fig.5

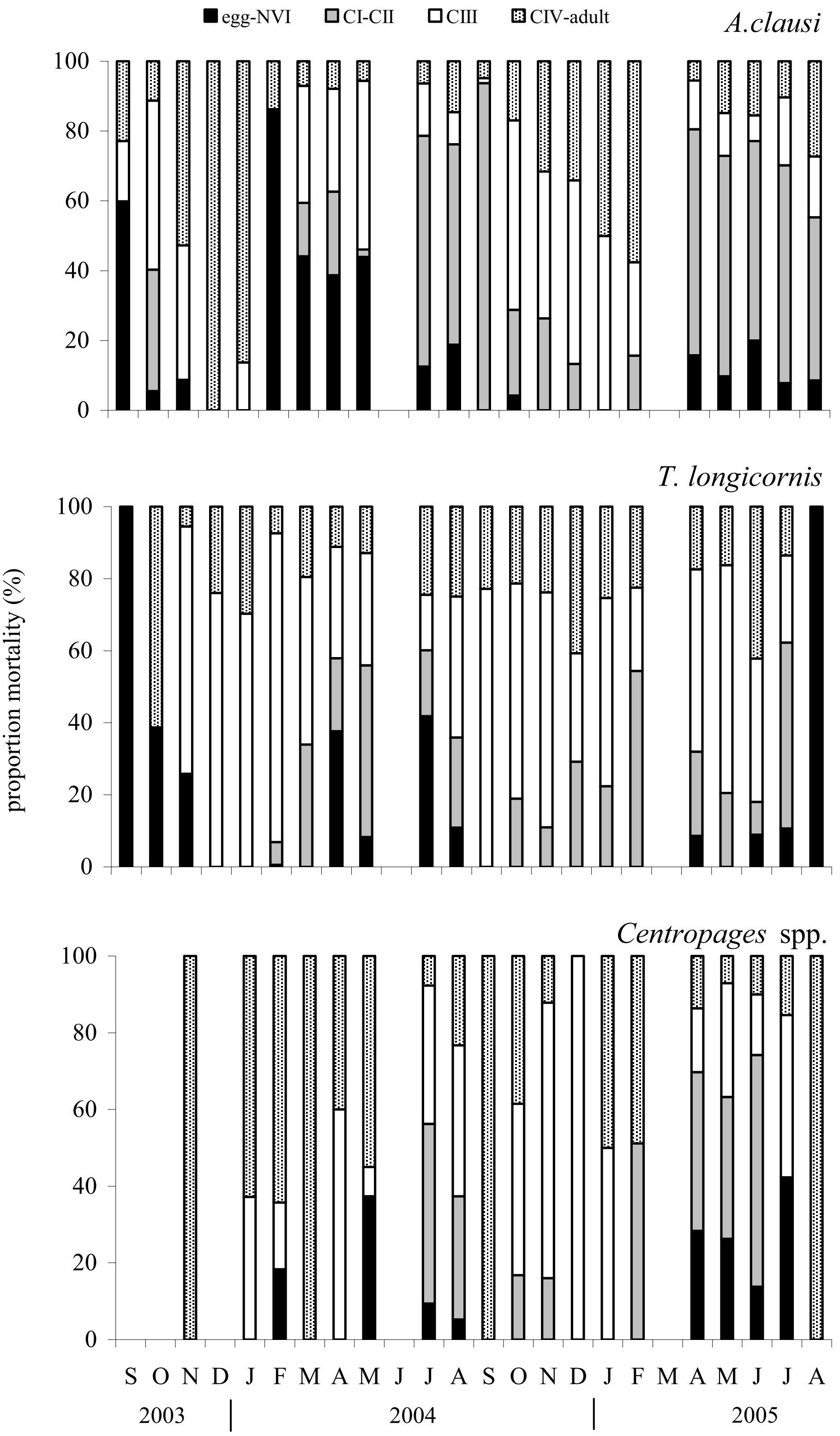
■egg-NVI
▨CI-CII
☐CIII
▨CIV-adult
A.clausi
T. longicornis
Centropages spp.
proportion mortality (%)
0
20
40
60
80
100
S O N D J F M A M J J A S O N D J F M A M J J A
2003
2004
2005

Fig.6

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ANNEX

Seasonal stage duration Acartia clausi

				egg	NI	NII	NIII	NIV	NV	NVI	CI	CII	CIII	CIV	CV
			proportion**	0,09	0,05	0,11	0,08	0,07	0,07	0,09	0,07	0,08	0,08	0,09	0,12
		temp °C	**generation time (d)***	**stage duration (d)**											
2003	**S**	**17,7**	15,7	1,38	0,80	1,76	1,29	1,09	1,07	1,36	1,14	1,18	1,25	1,41	1,93
	O	**13,7**	21,5	1,89	1,09	2,41	1,76	1,49	1,47	1,87	1,56	1,62	1,71	1,93	2,64
	N	**10,8**	28,0	2,47	1,43	3,14	2,30	1,95	1,92	2,44	2,03	2,12	2,24	2,52	3,45
	D	**8,3**	36,2	3,19	1,84	4,05	2,97	2,51	2,47	3,14	2,62	2,73	2,88	3,25	4,44
2004	**J**	**5,2**	52,3	4,61	2,67	5,87	4,30	3,64	3,58	4,55	3,80	3,95	4,17	4,71	6,43
	F	**4,7**	55,5	4,89	2,83	6,22	4,56	3,86	3,79	4,82	4,03	4,19	4,42	4,99	6,82
	M	**4,7**	55,5	4,89	2,83	6,22	4,56	3,86	3,79	4,82	4,03	4,19	4,42	4,99	6,82
	A	**7,0**	41,6	3,67	2,12	4,66	3,42	2,89	2,84	3,62	3,02	3,14	3,32	3,74	5,11
	M	**9,6**	31,5	2,78	1,61	3,53	2,59	2,19	2,15	2,74	2,29	2,38	2,51	2,83	3,87
	J	**13,5**	21,9	1,93	1,12	2,46	1,80	1,53	1,50	1,91	1,59	1,66	1,75	1,97	2,70
	J	**15,9**	18,0	1,59	0,92	2,02	1,48	1,26	1,23	1,57	1,31	1,36	1,44	1,62	2,22
	A	**18,1**	15,2	1,34	0,78	1,71	1,25	1,06	1,04	1,32	1,10	1,15	1,21	1,37	1,87
	S	**16,6**	17,1	1,51	0,87	1,92	1,40	1,19	1,17	1,49	1,24	1,29	1,36	1,54	2,10
	O	**13,6**	21,7	1,91	1,10	2,43	1,78	1,51	1,48	1,88	1,57	1,64	1,73	1,95	2,66
	N	**10,9**	27,6	2,44	1,41	3,10	2,27	1,92	1,89	2,40	2,00	2,09	2,20	2,48	3,40
	D	**8,3**	36,1	3,18	1,84	4,05	2,97	2,51	2,47	3,14	2,62	2,73	2,88	3,25	4,44
2005	**J**	**5,6**	49,6	4,37	2,53	5,56	4,07	3,45	3,39	4,31	3,60	3,75	3,96	4,46	6,10
	F	**4,0**	61,2	5,39	3,12	6,86	5,02	4,25	4,18	5,32	4,44	4,62	4,88	5,50	7,52
	M	**3,7**	64,6	5,69	3,29	7,24	5,31	4,49	4,41	5,61	4,69	4,88	5,15	5,81	7,94
	A	**6,1**	46,6	4,10	2,37	5,22	3,82	3,24	3,18	4,05	3,38	3,52	3,71	4,19	5,72
	M	**9,5**	31,8	2,80	1,62	3,56	2,61	2,21	2,17	2,76	2,30	2,40	2,53	2,86	3,91
	J	**13,4**	22,0	1,94	1,12	2,47	1,81	1,53	1,51	1,92	1,60	1,67	1,76	1,98	2,71
	J	**16,7**	16,9	1,49	0,86	1,90	1,39	1,18	1,16	1,47	1,23	1,28	1,35	1,52	2,08
	A	**17,2**	16,3	1,44	0,83	1,83	1,34	1,14	1,12	1,42	1,19	1,24	1,30	1,47	2,01

***McLaren 1978**
****Klein Breteler et al. 1994**

Seasonal stage duration Temora longicornis

				egg	**NI**	**NII**	**NIII**	**NIV**	**NV**	**NVI**	**CI**	**CII**	**CIII**	**CIV**	**CV**
			proportion**	0,11	0,03	0,07	0,06	0,06	0,09	0,08	0,07	0,08	0,07	0,11	0,15
		temp °C	**generation time (d)***	**stage duration (d)**											
2003	**S**	**17,7**	18,2	2,06	0,59	1,33	1,09	1,08	1,72	1,49	1,34	1,42	1,35	1,96	2,72
	O	**13,7**	24,9	2,83	0,81	1,82	1,50	1,49	2,36	2,05	1,84	1,95	1,86	2,70	3,73
	N	**10,8**	32,6	3,69	1,05	2,38	1,96	1,94	3,08	2,68	2,40	2,55	2,43	3,52	4,87
	D	**8,3**	42,1	4,77	1,36	3,08	2,53	2,51	3,98	3,46	3,11	3,30	3,13	4,55	6,29
2004	**J**	**5,2**	61,0	6,91	1,98	4,46	3,67	3,63	5,77	5,02	4,50	4,78	4,54	6,60	9,13
	F	**4,7**	64,7	7,33	2,10	4,73	3,90	3,86	6,12	5,32	4,78	5,07	4,82	7,00	9,68
	M	**4,7**	64,7	7,33	2,10	4,74	3,90	3,86	6,12	5,32	4,78	5,07	4,82	7,00	9,68
	A	**7,0**	48,4	5,49	1,57	3,54	2,92	2,88	4,58	3,98	3,57	3,79	3,61	5,24	7,24
	M	**9,6**	36,6	4,15	1,19	2,68	2,21	2,18	3,46	3,01	2,71	2,87	2,73	3,96	5,48
	J	**13,5**	25,5	2,89	0,82	1,86	1,53	1,52	2,41	2,09	1,88	2,00	1,90	2,75	3,81
	J	**15,9**	20,9	2,37	0,68	1,53	1,26	1,25	1,98	1,72	1,55	1,64	1,56	2,26	3,13
	A	**18,1**	17,6	2,00	0,57	1,29	1,06	1,05	1,67	1,45	1,30	1,38	1,31	1,91	2,64
	S	**16,6**	19,8	2,25	0,64	1,45	1,19	1,18	1,87	1,63	1,46	1,55	1,48	2,14	2,97
	O	**13,6**	25,2	2,85	0,81	1,84	1,52	1,50	2,38	2,07	1,86	1,97	1,87	2,72	3,76
	N	**10,9**	32,1	3,64	1,04	2,35	1,93	1,91	3,04	2,64	2,37	2,52	2,39	3,47	4,80
	D	**8,3**	42,0	4,76	1,36	3,07	2,53	2,50	3,97	3,46	3,10	3,29	3,13	4,54	6,29
2005	**J**	**5,6**	57,8	6,55	1,87	4,23	3,48	3,44	5,47	4,75	4,27	4,53	4,31	6,25	8,65
	F	**4,0**	71,4	8,09	2,31	5,22	4,30	4,25	6,75	5,87	5,27	5,59	5,32	7,72	10,68
	M	**3,7**	75,4	8,54	2,44	5,52	4,54	4,49	7,13	6,20	5,57	5,91	5,61	8,15	11,28
	A	**6,1**	54,2	6,15	1,76	3,97	3,27	3,23	5,13	4,46	4,00	4,25	4,04	5,87	8,11
	M	**9,5**	36,9	4,19	1,20	2,70	2,22	2,20	3,49	3,04	2,73	2,89	2,75	4,00	5,53
	J	**13,4**	25,6	2,90	0,83	1,87	1,54	1,53	2,42	2,11	1,89	2,01	1,91	2,77	3,83
	J	**16,7**	19,6	2,22	0,64	1,44	1,18	1,17	1,85	1,61	1,45	1,54	1,46	2,12	2,93
	A	**17,2**	19,0	2,15	0,61	1,39	1,14	1,13	1,79	1,56	1,40	1,49	1,41	2,05	2,84

***Klein Breteler and Gonzales 1986**

****Halsband, PhD Thesis**

Seasonal stage duration Centropages spp.

				egg	**NI**	**NII**	**NIII**	**NIV**	**NV**	**NVI**	**CI**	**CII**	**CIII**	**CIV**	**CV**
			proportion**	0,04	0,03	0,05	0,05	0,06	0,06	0,05	0,06	0,08	0,13	0,23	0,14
		temp °C	**generation time (d)***	**stage duration (d)**											
2003	**S**	**17,7**	17,4	0,77	0,60	0,83	0,93	1,08	1,09	0,96	1,11	1,34	2,30	4,00	2,40
	O	**13,7**	24,4	1,08	0,84	1,17	1,31	1,51	1,52	1,34	1,56	1,88	3,22	5,61	3,36
	N	**10,8**	33,0	1,46	1,14	1,58	1,77	2,05	2,06	1,82	2,11	2,54	4,36	7,60	4,55
	D	**8,3**	45,0	1,99	1,56	2,15	2,41	2,79	2,81	2,48	2,88	3,46	5,94	10,36	6,20
2004	**J**	**5,2**	74,1	3,27	2,57	3,54	3,97	4,59	4,62	4,07	4,74	5,70	9,78	17,04	10,20
	F	**4,7**	80,7	3,56	2,80	3,86	4,32	5,00	5,03	4,44	5,16	6,21	10,65	18,57	11,11
	M	**4,7**	80,7	3,56	2,80	3,86	4,32	5,00	5,03	4,44	5,16	6,21	10,66	18,57	11,11
	A	**7,0**	54,0	2,38	1,87	2,58	2,89	3,34	3,36	2,97	3,45	4,15	7,12	12,41	7,43
	M	**9,6**	38,0	1,68	1,32	1,82	2,03	2,35	2,37	2,09	2,43	2,92	5,02	8,74	5,23
	J	**13,5**	25,0	1,10	0,87	1,19	1,34	1,55	1,56	1,37	1,60	1,92	3,30	5,74	3,44
	J	**15,9**	20,2	0,89	0,70	0,97	1,08	1,25	1,26	1,11	1,29	1,55	2,67	4,65	2,78
	A	**18,1**	16,9	0,75	0,58	0,81	0,90	1,05	1,05	0,93	1,08	1,30	2,23	3,88	2,32
	S	**16,6**	19,1	0,84	0,66	0,91	1,02	1,18	1,19	1,05	1,22	1,47	2,52	4,39	2,62
	O	**13,6**	24,6	1,09	0,85	1,18	1,32	1,53	1,54	1,36	1,58	1,90	3,25	5,67	3,39
	N	**10,9**	32,5	1,43	1,13	1,55	1,74	2,01	2,03	1,79	2,08	2,50	4,29	7,47	4,47
	D	**8,3**	45,0	1,98	1,56	2,15	2,41	2,79	2,80	2,47	2,88	3,46	5,94	10,34	6,19
2005	**J**	**5,6**	68,6	3,03	2,38	3,28	3,67	4,25	4,28	3,77	4,39	5,28	9,06	15,79	9,45
	F	**4,0**	93,6	4,13	3,24	4,48	5,01	5,80	5,84	5,15	5,99	7,20	12,36	21,53	12,88
	M	**3,7**	101,9	4,50	3,53	4,87	5,46	6,32	6,36	5,60	6,52	7,84	13,46	23,45	14,03
	A	**6,1**	62,8	2,77	2,18	3,01	3,36	3,89	3,92	3,45	4,02	4,84	8,29	14,45	8,65
	M	**9,5**	38,4	1,69	1,33	1,84	2,05	2,38	2,39	2,11	2,45	2,95	5,07	8,83	5,28
	J	**13,4**	25,1	1,11	0,87	1,20	1,34	1,56	1,57	1,38	1,61	1,93	3,32	5,78	3,46
	J	**16,7**	18,9	0,83	0,65	0,90	1,01	1,17	1,18	1,04	1,21	1,45	2,49	4,34	2,60
	A	**17,2**	18,2	0,80	0,63	0,87	0,97	1,13	1,13	1,00	1,16	1,40	2,40	4,19	2,50

Liang et al. 1996, for *C. abdominalis

****Halsband, PhD Thesis**

Eidesstattliche Erklärung
(gem. § 6(5) Nr. 1-3 PromO)

Hiermit versichere ich, dass ich die vorliegende Arbeit

1. ohne unerlaubte, fremde Hilfe angefertigt habe
2. keine anderen, als die von mir im Text angegebenen Quellen und Hilfsmittel benutzt habe
3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe

Bremen

Anne Wesche