Die saisonalen Veränderungen der Copepodengemeinschaft in einem oligotrophen Meeresgebiet - dem nördlichen Golf von Aqaba (Rotes Meer)

Seasonal Dynamics of the Copepod Population in an Oligotrophic Environment - the Northern Gulf of Aqaba (Red Sea)

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Des Menschen wahres Haus ist nicht das Haus,
sondern der Weg,
und das Leben selbst ist eine Reise,
die zurückgelegt werden muß.
(Bruce Chatwin aus "What am I doing here?")

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Summary

The Gulf of Aqaba displays features of a typical subtropical ocean such as its oligotrophic condition during most of the year and a dominance of picoplankton as primary producers. In contrast to other subtropical areas, another characteristic of the Gulf is a distinct hydrographical and biological seasonality. While the seasonal variations in temperature were similar in 2002 and 2003, leading to vertical mixing in winter and stratification in summer, the seasonality in terms of chlorophyll *a* was rather different between the years. In 2002 a deep chlorophyll *a* maximum was found in autumn, in 2003 high chlorophyll *a* values occurred in spring (March) down to 300 m.

In 2002 and 2003, mesozooplankton samples were taken with a Nansen net equipped with 200 μm mesh size over a period of almost 2 years in varying intervals. The samples were sorted into major mesozooplankton taxa and 31 copepod taxa. Overall abundance ranged between 245 and 3065 ind. m^{-3}. Highest densities in 2002 were recorded in spring (March/April) and in autumn (October/November), while several peaks were revealed in 2003 with maximum abundance in early summer (June/July). Copepods were by far the most abundant taxon comprising on average 79% of the total mesozooplankton. Appendicularians ranked second in abundance (2.5%), closely followed by chaetognaths (2.4%). The other holoplankton taxa accounted for less than 4% throughout the investigation period. Meroplanktonic larvae, mainly gastropods and bivalve larvae, contributed 3 to 30% to total mesozooplankton abundance.

The deep vertical mixing in March 1999 resulted in an almost homogenuous distribution of the major holoplanktonic mesozooplankton taxa (Copepods, appendicularians, chaetognaths) and a bimodal distribution in the morning. The dominant meroplankton taxa (gastropods, bivalve larvae) were concentrated in the surface layer in the morning and displayed a bimodal distribution in the afternoon.

Within the copepods, the calanoids dominated, representing between 42 and 83%, followed by cyclopoids (8 - 46%) and poecilostomatoids (6 - 27%). Harpacticoids made up less than 0.1%. The diversity was low throughout the study period (Shannon Diversity H': 2.6-3.2). Calanoids accounted for most families (15), whereas poecilostomatoids featured three and cyclopoids only one family. The dominant calanoid copepods belonged to the families of Clausocalanidae (27%), Paracalanidae (20%), Acartiidae (5%) and Mecynoceridae (4%). Copepod taxa covaried with density, but not with chlorophyll, indicating only partial coupling between primary and secondary production. Positive correlation coefficients were established for taxa preferring higher temperatures and negative ones for copepods which occurred in higher numbers during the colder part of the year. In this connection a seasonal succession of dominant copepods was established.

Clausocalanids, which were the most abundant calanoids, were represented by four species in the northern Gulf of Aqaba: *Ctenocalanus vanus*, *Clausocalanus farrani*, *Clausocalanus furcatus* and *Clausocalanus minor*. This was the first record for *Clausocalanus minor* in the Gulf of Aqaba and the Red Sea. The seasonal changes in abundance, the reproductive activity and the feeding behaviour of this group was investigated. Only the females were distinguished by species. *Ctenocalanus vanus* was highly abundant during winter and spring, and scarce during summer and autumn. *Clausocalanus farrani* peaked in abundance in spring (2003 and 2003) and additionally in June 2003. The abundance of *Clausocalanus furcatus* showed no distinct seasonal change during 2002, whereas it peaked in January, July and November 2003. The copepodids and males of *Clausocalanus* spp. and *Ctenocalanus vanus* showed a similar annual course of abundance as the females. The vertical distribution of the clausocalanids (CI-CIII, CIV, CV, females, males) in October 1991, January, April and July 1992 showed that the majority of the individuals was situated in the upper 100 m (>65%), except for January. Then the specimens were homogenuously distributed down to 300 m depth.

To estimate periods of reproductive activity, gonad development was determined from preserved females. For *C. vanus*, the proportion of mature gonads and the number of oocytes was inversely related to the seasonal changes in sea surface temperature. *Clausocalanus farrani* had an almost constant low proportion of mature gonads and *Clausocalanus furcatus* had a high percentage of mature gonads. Endoparasitism in terms of the dinoflagellates *Blastodinium* sp. and *Syndinium* sp. occurred in the females of all three species with the highest level in *Clausocalanus farrani*. In addition, during autum 2002 and 2003, single females were incubated for 24 hrs to determine egg production rates. The egg production of *C. farrani* and *C. furcatus* varied between 0 and 3.3 eggs female^{-1} and between 1.8 to 9.2 eggs female^{-1}, respectively. Spawning was only rarely observed for *C. vanus* with higher values in spring 2002.

In spring (March/April) and autumn (September/October) 2002 twelve feeding experiments were carried out with females of the clausocalanid species (except *Clausocalanus minor*) as well as females of *Acartia negligens* and *Mecynocera clausi*, which were fed natural occurring particles (NOP) larger than 5 μm. The ambient chlorophyll a concentration at sampling depth (70 m) ranged between 0.15 - 1.00 μg chl a L^{-1} and NOP concentrations ranged between 1.78 - 14.0 $* 10^3$ particles L^{-1} during the sampling periods. The division of particles into five size classes (5 - 10, 10 - 20, 20 - 50, 50 - 100, >100 μm) revealed that most of the particles were found in the size classes below 50 μm (81 - 98%), while most of the natural occurring carbon (NOC) was concentrated in the size classes larger than 20 μm (70 - 95%). Ingestion rates were food density dependent rather than size dependent. For chlorophyll a they ranged between 0.3 and 84.2 ng chl a $ind.^{-1}$ d^{-1}, for NOP between 0.02 and 1.65 $* 10^3$ particles $ind.^{-1}$ d^{-1}, for NOC between 0.01 and 0.41 μg C $ind.^{-1}$ d^{-1} and for the body carbon (BC) uptake between 0.4 and 51.8% BC d^{-1}. The share of the size classes to the total ingestion resembled in most cases the size class composition of the natural particle community. No distinct difference in the feeding pattern could be observed between the copepod species studied.

In October 2003 the role of the microzooplankton in the food web of the Gulf of Aqaba was studied. The microzooplankton, was mainly composed of tintinnids and naked ciliates, but also Sarcodina and crustaceans were found. The autotrophic plankton was mainly represented by diatoms within the recognizable phytoplankton above 5 μm. The growth rates of the phytoplankton varied between 0.13 - 0.35 d^{-1} facing a grazing pressure due to the microzooplankton of 0.16 - 0.85 d^{-1}. The grazing pressure correspond with a loss of 60 to 100% of the potential production. Therefore, the microzooplankton, as in other subtropical areas, is mainly responsible for the loss of the primary production.

Zusammenfassung

Der Golf von Aqaba ist durch Oligotrophie sowie durch die Dominanz des Picoplanktons charakterisiert. Im Gegensatz zu anderen subtropischen Ökosystemen ist der Golf außerdem durch seine ausgeprägte hydrographische und biologische Saisonalität gekennzeichnet. Die saisonalen Veränderungen der Temperaturverteilung im nördlichen Golf von Aqaba führten zu einem regelmäßigen Wechsel zwischen vertikaler Durchmischung im Winter und Stratifizierung im Sommer. Die vertikale Verteilung der Chlorophyll a Konzentrationen hingegen zeigten Unterschiede zwischen 2002 und 2003. Ein ausgeprägtes Chlorophyll a Tiefenmaximum konnte nur im Herbst 2002 beobachtet werden, eine Frühjahrsblüte deutete sich nur im März 2003 an.

Innerhalb eines Untersuchungszeitraumes von 22 Monaten zwischen März 2002 und November 2003 wurden mit einem Nansennetz mit einer Maschenweite von 200 μm Mesozooplanktonproben genommen. Das Mesozooplankton wurde in 30 Großgruppen und zusätzlich 31 Copepodentaxa eingeteilt. Die Abundanz des Mesozooplankton variierte zwischen 245 und 3065 ind. m^{-3}. Die höchsten Dichten wurden im Frühjahr (März/April) und Herbst (Oktober/November) 2002 beobachtet, während 2003 mehrere Abundanzpeaks mit einem Maximum im Frühsommer (Juni/Juli) gefunden wurden. Die Copepoden stellten mit einem mittleren Anteil von 79% das häufigste Mesozooplanktontaxon dar. Darauf folgten die Appendicularien (2,5%) und die Chaetognathen (2,4%). Das Meroplankton, hauptsächlich vertreten durch Gastropoden und Bivalvier-Larven, steuerte einen beträchtlichen Anteil zu der Mesozooplanktonabundanz bei (3 - 30%). Die vertikale Durchmischung der Wassersäule am 5. März 1999 (400 m) fiel mit einer nahezu homogenen Verteilung der häufigsten Mesozooplanktongroßgruppen (Copepoden, Appendicularien, Chaetognathen) am Nachmittag und einer bimodalen Verteilung am Morgen zusammen. Die Meroplankton Taxa Gastropoden und Bivalvier-Larven dagegen waren morgens hautpsächlich in den oberflächennahen Wasserschichten und am Nachmittag bimodal verteilt.

Calanoide bildeten mit 42 bis 83% das dominante Taxon innerhalb der Copepoden, gefolgt von Cycplopoiden (8 - 46%) und Poecilostomatoiden (6 - 27%). Der Anteil der Harpacticoiden betrug weniger als 0,1%. Die Diversität der Copepoden blieb während des gesamten Untersuchungszeitraumes niedrig (Shannon-Diversität H': 2,6 - 3,2). Die Calanoiden stellten die meisten Familien (15), während die Poecilostomatoiden drei und die Cyclopoiden eine Familie beitrugen. Die dominanten calanoiden Copepoden verteilten sich auf die Familien Clausocalanidae (27%), Paracalanidae (20%), Acartiidae (5%) and Mecynoceridae (4%). Viele Copepodentaxa zeigten eine Affinität zur saisonalen Veränderung der Oberflächentemperatur, nicht aber zu den Chlorophyll *a* Veränderungen, was auf eine begrenzte Korrelation zwischen der Primär- und der Sekundärproduktion hindeutet. Positive Korrelationen wurden für die Taxa etabliert, die wärmere Temperaturen bevorzugten und negative für die Taxa, die während der kühleren Perioden hohe Abundanz zeigten. Auf diese Art konnte saisonale Sukkzession von dominanten Copepoden beobachtet werden.

Die Clausocalanidae, als häufige Copepodenfamilie, waren durch vier Arten im nördlichen Golf von Aqaba vertreten: *Ctenocalanus vanus*, *Clausocalanus farrani*, *C. furcatus* und *C. minor*. *C. minor* wurde zum ersten Mal im Golf von Aqaba beobachtet. Die saisonalen Veränderungen in der Abundanz, die Reproduktionsaktivität und das Freßverhalten dieser Gruppe wurde untersucht. Nur die Weibchen konnten auf Artniveau bestimmt werden. Die Weibchen von *Ctenocalanus vanus* und *Clausocalanus farrani* erreichten die höchste Abundanz im Frühjahr in beiden Jahren. *C. farrani* zeigte außerdem eine hohe Abundanz im Juni 2003. *C. furcatus* wies 2002 keine ausgeprägte Saisonalität auf, während es 2003 drei Abundanzpeaks aufwies (Januar, Juli, November). Die saisonale Verteilung der älteren Copepoditstadien und Männchen von *Clausocalanus* spp. und *Ctenocalanus vanus* zeigten einen ähnlichen Verlauf wie der der Weibchen. Männliche Individuen machten nur einen geringen Teil der Population der Clausocalaniden aus. Die Vertikalverteilung der Clausocalaniden im Oktober 1991, April und Juli 1992 zeigte, daß sich die Mehrheit der Individuen im den oberen 100 m der Wassersäule befinden (>65%). Im Januar 1992 dagegen waren die Clausocalaniden homogen in den oberen 300 m verteilt.

Um die Reproduktionsaktivität abzuschätzen, wurde die Gonadenentwicklung von fixierten Weibchen der Arten *Ctenocalanus vanus*, *Clausocalanus farrani* und *C. furcatus* bestimmt. Der Anteil reifer Gonaden war bei *C. vanus* invers mit der Wasseroberflächentemperatur korreliert. Dieser Zusammenhang wurde bei *Clausocalanus farrani* und *C. furcatus* nicht deutlich. *C. farrani* hatte einen gleichbleibenden geringeren Anteil an reifen Gonaden verglichen mit *C. furcatus.* Bei der mikroskopischen Untersuchung der Weibchen wurde der Befall mit Endoparasiten beobachtet, die den Gattungen *Blastodinium* und *Syndinium* angehören. Ihr Anteil war am höchsten bei *C. farrani.* Zusätzlich wurden im Frühjahr und Herbst 2002 sowie im Herbst 2003 Eiproduktionsexperimente mit einer Inkubationszeit von 24 Stunden durchgeführt. Die Eiproduktion von *C. farrani* und *C. furcatus* variierte zwischen 0 und 3,3 Eier pro Weibchen bzw. zwischen 1,8 und 9,2 Eiern pro Weibchen.

Das Freßverhalten dominanter calanoider Copepoden (*Ctenocalanus vanus*, *Clausocalanus farrani*, *C. furcatus*, *Acartia negligens* und *Mecynocera clausi*) wurde im Frühjahr und Herbst 2002 untersucht. Insgesamt wurden 12 Experimente mit natürlich vorkommenden Partikeln (NOP) >5 μm durchgeführt. Die natürliche Chlorophyll *a* Konzentration lag zwischen 0,15 und 1,0 μg L^{-1} in der Beprobungstiefe (70 m), die NOP Konzentrationen zwischen 1,78 und 14,0 $* 10^3$ Partikeln L^{-1}. Die Einteilung der Partikel in 5 Größenklassen (5 - 10, 10 - 20, 20 - 50, 50 - 100, >100 μm) erwies, dass die meisten Partikel kleiner als 50 μm waren (81 - 98%). Der aus der Größe der Partikel berechnete organische Kohlenstoff (NOC) hauptsächlich in den Partikeln größer als 20 μm gefunden wurde (70 - 95%). Die Ingestionsraten waren eher von der Nahrungskonzentration als von der Nahrungsgröße abhängig. Für Chlorophyll *a* variierten die Ingestionsraten zwischen 0,3 und 84,2 ng chl *a* ind.$^{-1}$ d^{-1}, für NOP zwischen 0,02 und 1,65 $* 10^3$ Partikel ind.$^{-1}$ d^{-1} und für NOC zwischen 0,01 und 0,41 μg C ind.$^{-1}$ d^{-1}. Die Kohlenstoffaufnahme des einzelnen Tieres lag zwischen 0,4 und 51,8% BC d^{-1}. Der Anteil der Größenklassen an der Ingestion spiegelte in den meisten Fällen die Zusammensetzung der natürlichen Partikelgemeinschaft wider. Zwischen den untersuchten Arten konnten keine Unterschiede im Freßverhalten gefunden werden.

Im Oktober 2003 wurde abschliessend die Bedeutung des Mikrozooplanktons im Nahrungsnetz des nördlichen Golfes untersucht. Die Hauptvertreter des Mikrozooplanktons waren Tintinniden und nackte Ciliaten, aber auch Sarcodina und Crustaceen wurden regelmäßig gefunden. Das autotrophe Plankton wurde im Bereich >5 μm hauptsächlich durch Diatomeen vertreten. Die Wachstumsraten des Phytoplanktons schwankten zwischen 0,13 und 0,35 d^{-1} und standen einem Fraßdruck von 0,16 bis 0,85 d^{-1} durch das Mikrozooplankton gegenüber. Der Fraßdruck ging einher mit einem Verlust der potentiellen Produktion von 60 bis 100%. Das bedeutet, dass das Mikrozooplankton, wie in anderen subtropischen Meeresgebieten, hauptsächlich für den Verlust der Primärproduktion verantwortlich ist.

1 Introduction

1.1 Seasonality in tropical oceans

The subtropical and tropical oceans (45°S to 45°N) occupy the major part of the world's oceans. Generally, they are characterised by thermal stratification. Wind-forced vertical mixing occurs only in the upper 50 - 100 m (e.g. Philander 1985), and the euphotic zone can be regarded as relatively stable, typified by small changes in physical and chemical parameters. Therefore, it seems possible to describe the principal environmental features as if they were in a steady state (Goldman et al. 1979, Hayward et al. 1983). Within such an environment, planktonic communities may be expected to demonstrate minimal seasonal variation, with standing stocks of organisms changing only by a factor of two or three over an annual cycle (e.g. Moore and Sander 1977, McGowan and Walker 1979, Webber and Roff 1995a). The seasonality is often unpredictable and less pronounced than in temperate waters. Annual fluctuations are generally related to shorter-term patterns of variability, for example rainfall, especially in coastal regions (Chisholm and Roff 1990).

The lack of seasonal vertical mixing in tropical environments usually causes a strong nutrient depletion the euphotic zone, where the regenerated production of nutrients is several times that of new production (e.g. Platt et al. 1983, Harrison 1993, Banse and English 1994). The subtropical gyres are zones of minimal production with low phytoplankton biomass and translucent water. Hence, the secondary production and fish production are also low.

Warm oligotrophic waters support a complex and diverse planktonic community with pico-sized (0.2 - 2 μm) phytoplankton providing most of the primary production (Platt et al. 1983, Li et al. 1983, 1992, Campbell and Vaulot 1993, Fogg 1995, Lindell and Post 1995). The dominant picoplankton typically forms a deep chlorophyll *a* maximum (DCM) between 50 and 100 m, where light and nutrients are in sufficient amounts to sustain photosynthesis (Lindell and Post 1995). These DCMs may represent areas of intense trophic activity (Ortner et al. 1981). The picoplankton is largely unavailable to direct utilization by mesozooplankton because of size constraints in the feeding mechanisms of the mesozooplankton (Conover 1982, Berggreen et al. 1988, Hansen et al. 1997) except for appendicularians and salps (Paffenhöfer 1975, Deibel and Turner 1985). Nonetheless, they are linked to larger zooplankton by the cascading effect of mesozooplankton grazing on consumers of intermediate size, mainly protozoan microzooplankton (Ciliates, Sarcodines) (e.g. Sherr and Sherr 1988, Gifford 1991, Calbet and Landry 2004).

Copepods are the dominant mesozooplankton group in most oceans (e.g. Verity and Smetacek 1996). In warm tropical oceans they comprise up to 75% of the total zooplankton abundance (e.g. Moore and Sander 1977) and are composed chiefly of smaller species (Hopcroft et al. 1998). Due to the absence of major seasonal cues, tropical systems generally lack a distinct seasonal variability in the plankton communities (Moore and Sander 1977, Webber and Roff 1995b).

Seasonal variations in zooplankton biomass, however, have been found in subtropical localities where the climatic changes are of sufficient magnitude to impose an annual cycle on the biological production. This applies particularly to coastal and upwelling regions, but also to the Gulf of Aqaba, Red Sea.

1.2 Trophic interactions in the planktonic community

In simple terms, the seasonal plankton cycle can be viewed as a ”food chain” with the different trophic levels following in succession: phytoplankton, herbivorous zooplankton, carnivorous zooplankton, and finally fish and/or squid. Ideally, each trophic level draws on the energy resources of the level immediately below, which means standing stocks increase in succession, reach a maximum and then decline. A more accurate description of the natural energy flow in the plankton community is provided by a ”food web” design with multidirectional interactions between the involved organisms.

Pelagic ecosystems in upwelling areas were traditionally considered as dominated by relatively simple and short food webs. One of the best known examples is the direct transfer of organic matter from phytoplankton to sardines and anchovies that form large populations and support intensive fisheries (Ryther 1969, Blaxter and Hunter 1982). However, it now appears that the food web in upwelling regions is more complex than previously thought (Moloney 1992, Bode et al. 2003). The same holds true for the Antarctic (Hopkins 1985).

Of high importance for the mesozooplankton in oligotrophic regions is the ”microbial loop” which describes the trophic interactions between dissolved organic matter (DOM), particulate organic matter (POM), bacteria, phytoplankton, heterotrophic flagellates and protozoan microzooplankton in the pelagic food web (Sherr and Sherr 1988). The mesozooplankton utilizes the food resources of the microbial food web by grazing on larger (>5 μm) phytoplankton and protozoans. The results of Calbet and Landry (1999) suggest strong trophic linkages at the base of the food web. Bacterial picoplankton is consumed by heterotrophic nanoflagellates smaller than 5 μm which are eaten in turn by larger heterotrophic nanoflagellates and ciliates.

Smaller-sized mesozooplankton, especially copepods, have long been overlooked with respect to their influence on the trophic structure of the pelagic system. They are probably important intermediates between the classical and the microbial food webs (Roff et al. 1995, Calbet et al. 2000). This role might be particularly important in oligotrophic systems, where pico-sized organisms predominate (Li et al. 1992).

Traditionally, small-sized copepods were considered to be herbivorous. However, this view had to be revised after increasing evidence of omnivory was found (for review see Kleppel 1993). Protozoans, especially ciliates, are known to be an important food source for small calanoids (Kleppel et al. 1988, Stoecker and Mc Dowell Capuzzo 1990, Gifford 1991, Calbet and Landry 1999, Levinsen et al. 2000, Broglio et al. 2004). Feeding experiments of calanoid copepods with naturally occurring particulate matter indicate that copepods are rather unselective and opportunistic in their feeding habits (e.g. Poulet 1973, 1974, 1976, Dagg and Grill 1980, Huntley 1981, Turner 1991). Also, it has been noted that the feeding behaviour can alter with the seasonal changes in natural particle concentrations (Poulet 1978, Dagg and Grill 1980, Kleppel et al. 1988). Hence, the copepods have to be able to adapt rapidly to the changing natural occurring particle (NOP) composition. It is now well established that protozoans, especially ciliates, are an important food source for small calanoids (e.g. Kleppel et al. 1988, Stoecker and McDowell Capuzzo 1990, Calbet and Landry 1999, Levinsen et al. 2000, Broglio et al. 2004).

1.3 The copepod community of the Gulf of Aqaba

The mesozooplankton community of the Gulf of Aqaba was originally recruited from the northern Indian Ocean. Due to the shallow sills at the southern entrance of the Red Sea (Strait of Bab-El-Mandab) and entrance to the Gulf of Aqaba (Straits of Tiran) mainly epipelagic species made their way up to the Gulf of Aqaba (for review see Halim 1969, Fenaux 1979, Echelman and Fishelson 1990a, 1990b, Richter and Abu-Hilal in press). So far, 48 calanoid copepod species have been discovered in the Gulf of Aqaba (Halim 1969, Almeida Prado-Por and Por 1981, Almeida Prado-Por 1983, 1985, Abd El-Rahman 1999, Al-Najjar 2000). In comparison, the calanoid community of the northern Indian Ocean includes more than 198 species (Madhupratap and Haridas 1986). The impoverishment can also be seen in other mesozooplankton taxa (Halim 1969, Fenaux 1979). For example, the species number of oncaeid copepods is reduced from 31 species in the southern Red Sea to 21 species in the Gulf of Aqaba (Böttger-Schnack et al. 2001).

Despite the importance of mesozooplankton within the pelagic food web, only limited information is available with regard to the Gulf of Aqaba. A few numerical taxonomical studies have been carried out (Halim 1969, Echelman and Fishelson 1990a, Abd El-Rahman 1999, Böttger-Schnack et al. 2001 and references therein), as well as some ecological studies on nearshore and surface distributions (Vaissiere and Seguin 1982, 1984, Almeida Prado-Por 1985, Echelman and Fishelson 1990a,b, Khalil and Abd El-Rahman 1997, Al-Najjar et al. 2003). The vertical distribution of mesozooplankton has been studied mainly in the northernmost part of the Gulf of Aqaba (Schmidt 1973, Almeida Prado-Por 1983, 1990, Farstey et al. 2002).

In subtropical oligotrophic marine environments, small sized copepods are often predominant (Deevey and Brooks, 1977, Webber and Roff, 1995a, Mazzocchi et al., 1997, Hopcroft et al., 1998, Calbet et al., 2001). This is also true for the Gulf of Aqaba (Almeida Prado-Por 1983, 1985, 1990) whereby the family of clausocalanids plays an important role.

1.4 Clausocalanidae

The clausocalanid copepods almost entirely epipelagic, apart from *Farrania* which is bathypelagic. The genera *Pseudocalanus* and *Drepanopus* have more neritic species, whereas most of the remaining species are oceanic (Boltovskoy 1999). Clausocalanids have a wide distribution in the world's oceans, but their abundance was often underestimated due to large mesh sizes (>300 μm) used, for example by Weikert and Trinkaus (1990) in the Mediterranean or by Madhupratap and Haridas (1986) in the Indian Ocean.

Table 1: Taxonomy of Clausocalanidae

- **Copepoda**
  - **Calanoida** Sars, 1902
    - **Clausocalanidae** Giesbrecht, 1892
      - *Clausocalanus* Giesbrecht, 1888
      - *Ctenocalanus* Giesbrecht, 1888
      - *Drepanopus* Brady, 1883
      - *Farrania* Sars, 1920
      - *Microcalanus* Sars, 1901
      - *Pseudocalanus* Boeck, 1873
      - *Spicipes* Grice and Hülsemann, 1965

In the Gulf of Aqaba, four clausocalanid species have been recorded: *Ctenocalanus vanus* Giesbrecht, 1888, *Clausocalanus farrani* Sewell, 1929, *Clausocalanus furcatus* Brady, 1883, and *Clausocalanus arcuicornis* Dana, 1849. *Ctenocalanus vanus* is a well-known copepod with a large geographical range, mainly found in epipelagic waters but also in considerably deeper waters down to around 500 m (Fragopoulu et al. 2001). It has been recorded from temperate to tropical waters e.g. off Brazil by Lopez et al. (1999), in the Sargasso Sea by Schulz (1986), in the Mediteranean by Hure and Scotto Di Carlo (1970), in the Benguela current by Peterson et al. (1990) and in Subantarctic waters by Heron and Bowman (1971). The genus *Clausocalanus* is one of the most dominant and wide spread taxa within the smaller sized calanoids (Frost and Fleminger 1968). It is found in high numbers, for example in the Caribbean (Webber and Roff 1995a), the Sargasso Sea (Schulz 1986) and the Mediterranean (Mazzocchi et al. 1997, Fragopoulu et al. 2001). All three species of *Clausocalanus* previously found in the Gulf of Aqaba are common in subtropical and tropical parts of the oceans. *C. furcatus* and *Clausocalanus arcuicornis* are distributed circumglobally, while *C. farrani* is restricted to the Indian and Pacific Oceans (Frost and Fleminger 1968). Despite their wide distribution, the ecology of *C. vanus* and *Clausocalanus* spp. has received little attention in comparison to its neritic and temperate counterpart *Pseudocalanus* (e.g. Poulet 1973, 1974, 1976, Ohman 1990, Dagg et al. 1998). Only few investigations have included data of feeding rates for *Clausocalanus* spp. and *C. vanus* (e.g. Kleppel et al. 1988, Peterson et al. 1990, Broglio et al. 2004). The most detailed studies on the biology were conducted on *C. furcatus* (Webber and Roff 1995a, b, Mazzocchi and Paffenhöfer 1998, 1999).

1.5 Aims of this study

The northern Gulf of Aqaba provides a unique setting to study the seasonality of marine planktonic communities. Earlier investigations revealed that the thermal seasonality and the oligotrophy in this deep and narrow basin had a strong influence on the primary producers. Studies on mesozooplankton mainly focused on the geographic or vertical distribution and on the composition of the community. The attempt of this study was to combine studies on the seasonality of the mesozooplankton community, especially for copepods, with the feeding and reproductive activities of dominant species in trying to answer the following questions:

- Does the pronounced thermal seasonality influence the annual cycle of the mesozooplankton community?
- Do the epipelagic copepods exhibit seasonal and annual variations of occurrence?
- What impact does the availability of food have on the observed zooplankton patterns?
- What is the role of microzooplankton in the Gulf of Aqaba food web?
- Do the dominant copepods (e.g. Clausocalanids) show feeding preferences?
- Do all copepods correspond in the same way to the seasonality?
- Is there a seasonality in the reproduction activity of the dominant clausocalanid species?

Summary

- Subtropical and tropical marine regions provide a relative stable environment for the plankton community.
- The mesozooplankton community of the Gulf of Aqaba represents an impoverished community of the Indian Ocean.
- Smaller-sized calanoid copepods such as clausocalanids, paracalanids as well as cyclopoid and poecilostomatoid copepods dominate the epipelagic waters of subtropical and tropical oceans.
- Primary producers are dominated by pico-sized plankton in subtropical, oligotrophic environments.
- The picoplankton is not directly available as food source for the mesozooplankton due to size constraints of the feeding mechanisms.
- The microbial food web is of high importance for the smaller-sized copepods. Microzooplankton is an important trophic link between the microbial loop and the grazing food chain.
- Only little is known about the biology of the dominant copepod species in the Gulf of Aqaba.

2 The Gulf of Aqaba

The Gulf of Aqaba is a narrow northeastern extension of the Red Sea and is located on a fault of the major East African riftvalley system (Figure 1). It is 165 km long and in average 15 km wide. The maximum depth is 1830 m, whilst the average depth is about 800 m. The Gulf is surrounded by sparsely inhabited desert regions, except for the highly industrialized north (port activity, tourism, phosphate loading). The narrow shelves of the Gulf of Aqaba are mainly covered by coral reefs which are accompanied by a diverse benthic community (Loya 1972, Schuhmacher 1977). The steep slopes result in a close proximity between offshore and coastal waters.

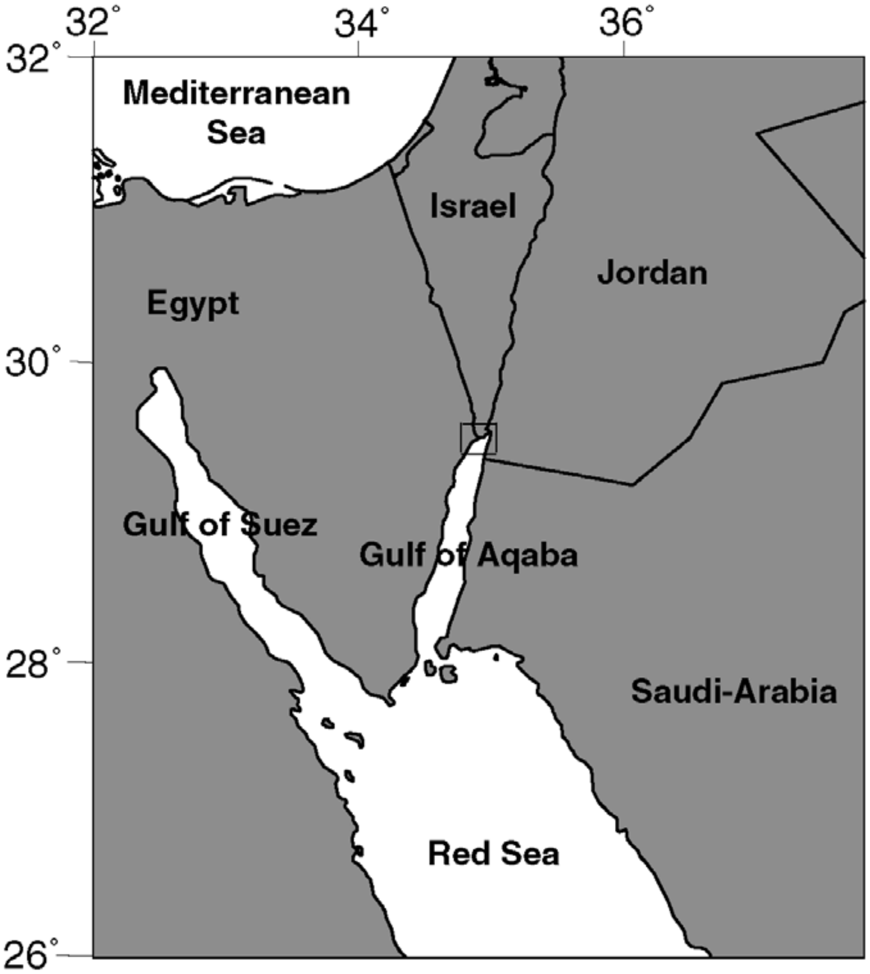

Figure 1: Overview of the Middle East with the study area (rectangle); Scale 1:3 900 000.

The climate is arid with a net evaporation of 0.5 - 1 cm day^{-1} (Assaf and Kessler 1976). The salinity of the Gulf of Aqaba is high (40 - 41). The sea-surface temperature ranges between 20 and 27°C with temperatures above 20°C even at great depths. In contrast to the Red Sea there is no oxygen minimum layer, the oxygen saturation varies between 3.75 - 6.0 ml L^{-1} (Klinker et al. 1978). The circulation in the Gulf of Aqaba is made up of a series of permanent gyres orientated along its main axis. Coastal currents on the eastern side run southwards during winter and northwards during summer at least in the upper 50 m (Berman et al. 2000). Tides are generally semi-diurnal with maximal sea level differences of 1 m (Monismith and Genin 2004).

Despite the main southward winds, the Gulf of Aqaba constantly receives nutrient depleted surface water from the Indian Ocean through the Gulf of Aden across two shallow sills, the Bab al Mandab (approx. 140 m deep) at the entrance of the Red Sea and 2000 km to the north at the entrance of the Gulf of Aqaba the Straits of Tiran (approx. 250 m deep). The inflow into the Gulf of Aqaba is counterbalanced by an efflux of denser deeper waters (Reiss and Hottinger 1984, Wolf-Vecht et al. 1992).

Unlike the Red Sea and other subtropical marine systems, the Gulf of Aqaba has a strong hydrographical and biological seasonality (Paldor and Anati 1979, Wolf-Vecht et al. 1992, Badran 2001). Throughout the summer thermal stratification dominates the water column with a shallow mixed surface layer due to wind mixing. In late autumn the sea surface temperature cools and creates a deep mixed layer (>250 m) which persists until spring (e.g. Klinker et al. 1978, Paldor and Anati 1979). The mixing depth is directly linked to variations in the net heat flux (Genin et al. 1995). The convective mixing in winter is probably the most important source of nutrient transport into the euphotic zone (Klinker et al. 1978). During summer stratification, the surface layer becomes depleted of nutrients (Reiss and Hottinger 1984, Lindell and Post 1995, Al-Qutob et al. 2002). Light penetration is high throughout the year which results in the passive entrainment of phytoplankton down to a depth of more than 300 m (Kimor and Golandsky 1977, Winter et al. 1980). The changes in the physical and chemical hydrography therefore induce a strong seasonality of phytoplankton (Genin et al. 1995, Lindell and Post 1995, Labiosa et al. 2003, Sokoletsky et al. 2004) and primary production (Levanon-Spanier et al. 1979). The trophic state of the Gulf of Aqaba exhibits rather meso-oligotrophic characteristics compared with other subtropical oceans at similar sea surface temperatures and light regimes (Sargasso Sea, Mediterranean Sea) despite its nutrient depleted seas in summer (Carlson et al. 1994, Labiosa et al. 2003). The phytoplankton of the Gulf of Aqaba is generally dominated by ultraphytoplankton (Li et al. 1992, Lindell and Post 1995): procaryotic and small eucaryotic phytoplankton (<8 μm) like in other oligotrophic seas (Sargasso Sea, Li et al. 1992). After the onset of stratification due to the warming of the air and sea surface temperatures in spring, usually a phytoplankton bloom develops. The magnitude of the bloom is strongly correlated with the mixing depth of the previous winter (Genin et al. 1995). In winter, eukaryotic phytoplankton (diatoms) dominate the water column (Reiss and Hottinger 1984, Kimor and Golandsky 1977) while in summer the procaryotes, *Synechococcus* and *Prochlorococcus* predominate.

3 Material and Methods

3.1 Mesozooplankton Sampling

3.1.1 Quantitative Sampling

52 mesozooplankton samples including 6 night samples were taken over a period of 22 months from February 26th, 2002 to December 2nd, 2003 from the upper 100 m of the water column at the tip of the Gulf of Aqaba (Fig. 2, Table 2). The sampling position (E 34°57.872; N 29°27.868) was situated off the Marine Science Station (MSS) in Aqaba (Jordan) (Fig. 2) with a total depth of 300 m.

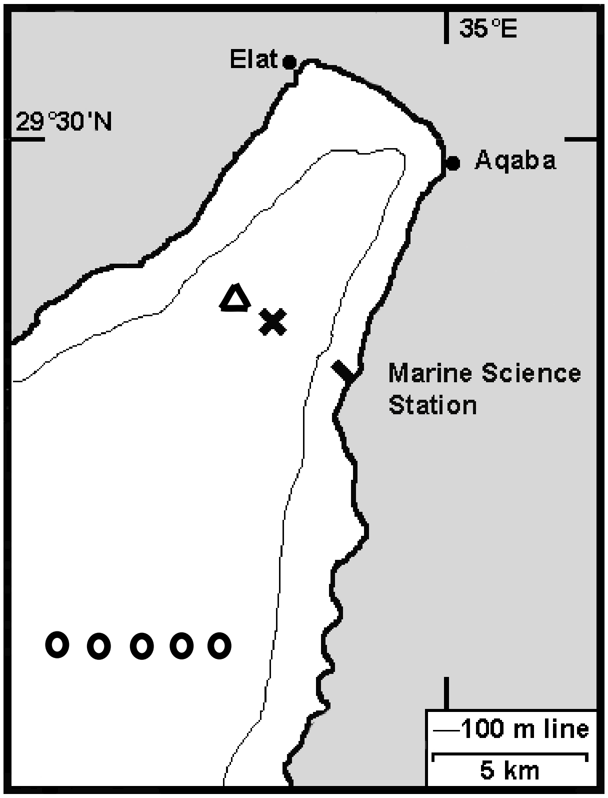

Figure 2: Northern Gulf of Aqaba with the sampling stations (X: sampling position in 2002/2003; Δ: sampling position of V. Farstey 1991/1992 (Station A); O: sampling positions onboard RV"Meteor" in March 1999)

The mesozooplankton was collected with a Nansen net (0.4 m^2 aperture) equipped with a 200 μm mesh size and a flowmeter. The net was towed vertically from 100 m to the surface with a constant speed of 1 m s^{-1}. The samples were collected between 9 a.m. and 3 p.m. on a monthly basis and more frequently during the height of the growing seasons in spring 2002, autumn 2002 and autumn 2003. For diurnal comparison, 6 night samples were taken between 1 and 2 a.m.. The samples were preserved in borax-buffered 4% formaldehyde seawater solution.

Table 2: Sampling dates of quantitative mesozooplankton sampling (N: date sampled also during night).

Monthly sampling	**Spring 2002**	**Autumn 2002**	**Autumn 2003**
17.04.2002 (N)	26.02.2002	11.09.2002	01.10.2003
06.06.2002 (N)	03.03.2002	18.09.2002	06.10.2003
25.07.2002 (N)	07.03.2003	30.09.2002	12.10.2003
17.09.2002 (N)	10.03.2002	14.10.2002	23.10.2003
05.11.2002 (N)	14.03.2002	21.10.2002	27.10.2003
06.01.2003 (N)	18.03.2002	03.11.2002	30.10.2003
12.03.2003	21.03.2002	07.11.2002	04.11.2003
21.04.2002	24.03.2002	12.11.2002	06.11.2003
19.05.2003	26.03.2002		02.12.2003
30.06.2003	28.03.2002		
22.07.2003	31.03.2002		
19.08.2003	03.04.2002		
	14.04.2002		
	16.04.2002		
	18.04.2002		
	21.04.2002		
	23.04.2002		

For further processing, the preserved samples were divided with a Folsom-Splitter. One quarter of each sample was counted. Rare taxa, which contributed less than 40 specimens in the quarter, were counted from the entire sample. The samples were sorted into and 31 copepod and 30 other taxa.

The specimens of the clausocalanid copepods were separated in more detail. The smaller clausocalanid copepodite stages (CI - CIII) were pooled as morphological characteristics were inconclusive for the identification of the species. Due to the large mesh size they were not sampled quantitatively and will be neglected. Copepodite stages IV and V and the male individuals were separated into the genera *Clausocalanus* and *Ctenocalanus*. Only the females were identified at species level.

3.1.2 Sampling during MET44/2

Vertically stratified mesozooplankton samples were collected on a cross-shore transect in the northern Gulf of Aqaba during the RV "Meteor" cruise MET 44/2 on March 6th in 1999 by S. Schiel (Alfred-Wegener-Institute, Bremerhaven) and W. Hagen (University of Bremen). Samples were taken during the daytime from west to east in the northern Gulf of Aqaba starting in the west in the early morning to late afternoon in the east (Fig. 2). A multiple opening-closing net system (0.5 m^2 aperture) equipped with nine nets of 150 μm mesh size was used to sample mesozooplankton in stratified vertical hauls taken from near the bottom to the surface in mostly 50 m steps. For each net, the filtered volume was measured by a flow meter (HYDROBIOS). Samples were preserved in borax-buffered 4% formaldehyde seawater solution. The subsequent processing is described in Cornils et al. (submitted).

3.1.3 Sampling in Elat during 1991 and 1992

Mesozooplankton samples were taken at a fixed station in the center of the northern Gulf of Aqaba (Station A; E 34°56', N 29°28') in 100 m steps over a total depth of 600 m (Fig. 2). A WP2 net was used equipped with a 100 μm mesh size (0.26 m^2 aperture). The sampling and preserving procedures were conducted by V. Farstey (Inter-University-Institute, Elat) and are described in Farstey et al. (2002). In the present study the clausocalanid copepods of the October 1991, January, April and July 1992 samples were counted from stemple pipette (Volume: 2.5 ml) subsamples of the upper 100 m. Below 100 m depth specimens were counted from the entire sample. The sample was diluted to 250 ml and subsamples were taken until at least 50 individuals of each stage were found. The specimens were identified as described in 3.1.1, except that the late copepodite stages IV and V and the male individuals of *Clausocalanus* were separated by species.

3.2 Sampling for Environmental Data

For logistical reasons the sampling for environmental data could not be obtained at the same time. The sampling of temperature and chlorophyll *a* was conducted within the framework of Jordan's National Monitoring Program and is described in Publication I. The temperature and salinity profiles were taken with a CTD. Water samples for chlorophyll *a* measurements were collected with 5 L Niskin bottles from the upper 400 m of the water column (0, 25, 50, 75, 100, 125, 150, 200, 300, 400 m). The water samples were filtered on cellulose acetate filter and frozen. Later, the samples were transferred to 10 ml of 90% acetone, homogenised and extracted for 24 h. Chlorophyll *a* measurements were done with a spectrofluorometer (SFM 25 of BIO-TEK KONTRON Instruments).

For the subsequent correlation, integrated values over the upper 100 m of the water column were used for temperature and chlorophyll *a*.

3.3 Experimental Design

3.3.1 Mesozooplankton Grazing

A total of 14 experiments were conducted in 2002 from February 26 to April 16 and September 11 to October 21 (Table 3). Natural occurring particles (NOP), were used as food source to obtain information about the natural feeding preferences of dominant calanoid copepod species.

Table 3: Sampling dates of grazing experiments

Spring 2002	**Autumn 2002**
26.02.2002	11.09.2002
03.03.2002	18.09.2002
07.03.2003	30.09.2002
10.03.2002	21.10.2002
21.03.2002	
26.03.2002	
31.03.2002	
01.04.2002	
11.04.2002	
16.04.2002	

Water samples were collected with 10 L Niskin water samplers at ca. 70 m depth near the deep autumn chlorophyll *a* maximum (Levanon-Spanier et al. 1979, Lindell and Post 1995). A CTD was run every time to determine the density stratification. Zooplankton was collected with a 200 μm Nansen net (see section 3.1.1), transferred to the laboratory and sorted immediately. Only females were selected for the experiments, since the males of the clausocalanids have reduced mouthparts (Frost and Fleminger 1968, Heron and Bowman 1971) and are therefore unlikely to feed. Females of abundant calanoid copepods (*Ctenocalanus vanus*, *Clausocalanus farrani*, *Clausocalanus furcatus*, *Acartia negligens*, *Mecynocera clausi*) were separated from the net sample, transferred to 250 ml beakers with 200 μm pre-screened seawater to remove larger zooplankton and kept there for 1 - 2 hours to adjust. Experiments with *Acartia negligens* were conducted only in spring, experiments with *Mecynocera clausi* only in autumn. Only free-swimming individuals with intact antennae were selected for the experiments. For each species, three experimental bottles and three control bottles (without copepods) were prepared. 2.7 L Nalgene bottles, previously rinsed with 10% HCl were filled with 200 μm screened sea water. Nutrients ($NO_3{}^-$, $PO_4{}^{3-}$, $SiO_3{}^{2-}$) and vitamins were added to prevent limitation of phytoplankton growth. 20 - 25 pre-adjusted copepod specimens of one species were placed in each experimental bottle, and all bottles were incubated for 8 to 24 hours (for the setup of each experiment see Publication II) and placed on a plankton wheel in the laboratory with dim light during the day and darkness at night time (March/April). High air temperatures and lack of temperature-controlled laboratory space led me to carry out the September/October experiments in a shaded watertank with a flowthrough system. Bottles of the latter experiments were turned every few hours in order to prevent settlement. The temperature during the experiments was maintained within 2°C of ambient conditions (March/April 21 - 22°C and September/October 24 - 25.5°C). The food concentration (particles, chlorophyll *a*) was measured at the start and the end of the incubation. Triplicates of 2 L subsamples were filtered onto GF/F filter paper and frozen for chlorophyll *a* measurements, subsamples of 500 ml were fixed with Lugol's iodine solution for NOP counts. Copepods were removed after the experiment, screened for mortality and transferred to pre-weighed tin caps for CN-measurements.

The GF/F filters for chlorophyll *a* analysis were transferred to 10 ml of 90% Acetone, homogenised and the chlorophyll extracted for 24 h. Chlorophyll *a* measurements were done with a SFM 25 of BIO-TEK KONTRON spectrofluorometer. The volume of the subsamples for NOP counts was reduced by sedimentation to 100 ml and transferred to an 100 ml Utermöhl sedimentation chamber (Utermöhl 1958). After 24 hours of particle settlement the sedimentation cylinder was removed and $\frac{1}{2}$ of the Utermöhl chamber was counted for all particles at a magnification of 400x using an inverted microscope (Zeiss Axiovert 35). The number of NOP was then calculated for 1 L. The identification of taxa was based on the publications of Massuti & Margalef (1950), Brandt & Apstein (1964), Drebes (1974), Pankow (1990) and Tomas (1993, 1995). Individual cells were identified and later grouped in five size classes: 5 - 10 μm, 10 - 20 μm, 20 - 50 μm, 50 - 100 μm and >100 μm (Publication II) according to Poulet (1978), Cowles (1979) and Uye and Kasahara (1983). The classification of size classes was made under the assumption that copepods in oligotrophic regions are rather non-selective feeders (Poulet 1974, 1976). First results of feeding experiments in the Gulf of Aqaba with small copepods (4.36 ± 1.02 μgC ind.$^{-1}$) showed higher clearance rates for particles larger than 10 μm (Sommer et al. 2002). Particles smaller than 5 μm have been neglected since they could not be counted quantitatively with inverted light microscopy and are consumed inefficiently by copepods. Boyd (1976) indicated that *Clausocalanus arcuicornis* retains only 50% of particles below 8 μm, but virtually all particles above 20 μm.

Carbon content of the individual cells was estimated according to Smetacek (1975) referring to similar genera of the same size. Although the calculated values are only a rough estimate of the actual carbon content, the carbon concentrations of the experiments can be compared, because they contain all the same factor of error being taken from one area and one publication. For each experiment, the growth rate, the grazing coefficient, the mean cell concentration, the filtration rate and the ingestion rate were calculated according to the equations of Frost (1972). The carbon content of the incubated copepod specimens was measured with a CHN-Analyser (EuroEA3000). The tin caps containing the copepods were dried for 24 h, weighed and then combusted in the CHN-Analyser. The results were used to calculate the percentage of body carbon uptake per day.

3.3.2 Microzooplankton Grazing

In October and November 2003 (Table 4) microzooplankton grazing experiments were conducted, so-called dilution experiments, according to Landry and Hassett (1982). 90 L natural seawater (sampling see section 3.3.1) from approximately 70 m depth, the presumed chlorophyll *a* maximum layer, was prefiltered through 200 μm mesh to remove larger zooplankton. 20 L were filtered through 0.2 μm cellulose-nitrate filter paper and used as dilution medium. Triplicate dilution treatments of 10, 30, 50, 70 and 100% natural sea water were prepared in 2.7 L experimental bottles (for description see section 3.3.1). Nutrients were added to each bottle to promote the growth of the phytoplankton (see section 3.3.1). In most cases two bottles were filled with undiluted natural seawater without nutrients to provide a control for the effects of nutrient enrichment on phytoplankton growth. Three subsamples of each dilution were taken to measure initial and final concentrations, respectively: 1 L samples for chlorophyll *a* analysis and 1L for microscopical cell counts (fixation and treatment see chapter 3.3.1). The experimental bottle were incubated for 24 h at a similar temperature and light regime as under natural conditions in 70 m depth. Samples for bacterial counts were obtained only from the last two experiments.

Dilution experiments were introduced by Landry and Hassett (1982) to estimate the grazing pressure of the microzooplankton on the phytoplankton. The experiments are based on two assumptions: Firstly, the growth of phytoplankton is not limited and independent of the dilution of sea water. Secondly, the microzooplankton has a constant clearance rate. Consequently the ingestion rate depends on the plankton density, or rather the dilution factor. Therefore, the gross growth rate of the phytoplankton remains unchanged, if the natural sea water is diluted with particle-free sea water (first assumption). The grazing pressure decreases due to the diminished encounter rate (second assumption) despite constant clearance rates, which are dependent on the dilution. Consequently, the net growth rate (k) of the phytoplankton (measurable through chlorophyll a content (N)) increases with growing dilution. A simple exponential growth model ($N_t = N_0 \cdot e^{k \cdot t}$) is used to determine the growth rates of different dilutions in the experiments over the incubation period (t). For each experiment, the phytoplankton growth rate under nutrient-enriched conditions (μ) and the phytoplankton mortality due to microzooplankton grazing (m) were obtained by linear regression of apparent growth rate (k) against dilution factor (D, fraction of un-filtered seawater) from the nutrient-enriched dilution treatments. Consequently, m was calculated from ($m = \mu - k \cdot D$).

Table 4: Sampling dates of microzooplankton dilution experiments

Autumn 2003
06.10.2003
12.10.2003
23.10.2003
27.10.2003
30.10.2003
04.11.2003
06.11.2003
02.12.2003

The ratio between grazing pressure and growth rate (μ/m) is an important factor of the balance for the experiments. Actually, it is more figurative to put these ratios in relation to the chlorophyll *a* standing stock, and to look at the potential and actual growth (ΔN_p and ΔN_r) and the relative mortalities (M) deriving from the following equations:

potential (gross) phytoplankton production: $\Delta N_p = N_0 \cdot e^{\mu \cdot t} - N_0$

actual (net) phytoplankton production: $\Delta N_r = N_t - N_0$

impact of grazing mortality on initial standing stock: $M_N = \Delta N_p - \Delta N_r / N_0$

impact of grazing mortality on gross production: $M_{\Delta N} = \Delta N_p - \Delta N_r / \Delta N_p$

In this concept the phytoplankton appears as chlorophyll *a* content and the zooplankton as grazing pressure. Information about the plankton community is not included in this concept, it will be obtained by microscopical and taxonomical analysis.

3.3.3 Egg production

Egg production experiments were carried out during periods of high frequent sampling (March/April, October/November 2002, and October/November 2003) with *Clausocalanus farrani*, *Clausocalanus furcatus* and *Ctenocalanus vanus*. Additional samples were taken with the Nansen net (200 μm mesh size) and transported to the laboratory immediately after capture. Of each species, 30 - 90 actively swimming, healthy looking females were sorted using a stereomicrosope (Nikon) and individually placed in multiwells (5 ml) filled with 150 μm pre-screened sea water. After an incubation period of 24 hrs at 23 - 27°C, the multiwells were checked for the number of eggs released, nauplii and mortality of the females (Publication III). The mortality rate was quite high during the experiments. However, during periods of high egg production 90% of the dead females spawned before death. The reproductive activity was expressed as percentages of spawning females and as eggs female^{-1} d^{-1}.

Except for *Clausocalanus lividus* and *C. mastigophorus* all *Clausocalanus* species are considered to carry egg sacks (Saiz and Calbet 1999, Peralba and Mazzocchi 2004). The egg sacks of *C. furcatus* are supposed to be fragile and indistinguishable, and the eggs are easily released from it due to disturbance (Mazzocchi and Paffenhöfer 1998). The egg of *C. furcatus* were released from the sacks quickly after spawning, while the egg sacks of *C. farrani* sometimes remained attached to the females until hatching. Then, the determination of the number of eggs was impossible. *C. vanus* is a free spawning species.

Table 5: Dates of egg production experiments; Cfa: *Clausocalanus farrani*, Cfu: *Clausocalanus furcatus*, Ctv: *Ctenocalanus vanus*

Spring 2002	**Autumn 2002**	**Autumn 2003**
03.03.2002 (Cfa, Ctv)	21.10.2002 (Cfa, Cfu)	01.10.2003 (Cfa, Cfu, Ctv)
07.03.2003 (Cfa)	23.10.2002 (Cfa, Cfu)	06.10.2003 (Cfa, Cfu, Ctv)
10.03.2002 (Cfa, Ctv)	03.11.2002 (Cfa, Cfu, Ctv)	12.10.2003 (Cfa, Cfu, Ctv)
21.03.2002 (Ctv)	07.11.2002 (Cfa, Cfu, Ctv)	23.10.2003 (Cfa, Cfu, Ctv)
26.03.2002 (Cfu)	12.11.2002 (Cfa, Cfu, Ctv)	27.10.2003 (Cfa, Cfu, Ctv)
		30.10.2003 (Cfa, Cfu, Ctv)
		04.11.2003 (Cfa, Cfu, Ctv)
		06.11.2003 (Cfa, Cfu, Ctv)

3.3.4 Gonad maturation stages

Gonad maturity was established from 40 - 50 preserved females of each species using a stereomicroscope (Leica M16). As the female gonads of both *Ctenocalanus* and *Clausocalanus* are similar to those of *Pseudocalanus*, the gonad development stage (GS) was subdivided according to the classification of system of Niehoff (2003). GS1 characterises females with empty diverticula. GS2 describes the females carrying small opaque oocytes in the diverticula. In GS3, the oocytes in the diverticula are large and their nuclei are clearly visible. Similar to GS3 in *Pseudocalanus* (Niehoff 2003), the oocytes in the GS3 of *C. vanus* were brownish coloured, whereas the oocytes of *Clausocalanus* spp. remained opaque throughout the development. Prior to spawning, the nucleus is not visible anymore, and the mature oocytes form a single ventral band in the diverticula (GS4). Females in GS3 and GS4 are considered as mature, i.e. ready to spawn, as here final oocyte development processes take place (Niehoff 2003). In addition to the determination of gonad maturity stages, developing oocytes in the diverticula of *C. vanus* were counted. Due to the lacking pigmentation, single oocytes in the diverticula of *Clausocalanus* spp. were impossible to identify correctly and hence, the oocytes were not counted. In all females, prosome length was measured.

3.4 Data Analysis

3.4.1 Primer

Cluster analysis was performed in order to explore similarities between the sampled stations and taxa. The analysis was performed with the PRIMER5 (Plymouth Routines in Multivariate Ecological Research) program developed at the Plymouth Marine Laboratory. Abundance (ind. m^{-3}) was double square root-transformed to reduce the weight of dominant taxa. Hierarchical agglomerative clustering was applied to differentiate the mesozooplankton communities using the Bray-Curtis Index. The complete linkage method was used to obtain strong separations of the groupings. Distinct station groups were identified in a dendrogram. The similarity matrix with the transformed data was also used to create MDS Plots, sorted by the factors year and month. The rank of species was also calculated with special features of the primer program. Diversity was calculated with the Shannon Index (Heip and Engels 1974) with the logarithms to the base of 2.

3.4.2 Statistics

The similarities between stations were statistically tested with the ANOSIM permutation test of the PRIMER5 program. A one-way ANOSIM (analysis of similarity) was conducted to reveal differences between the regional and temporal mesozooplankton composition at the sampling stations. The ANOSIM test is a multivariate randomisation procedure broadly analogous to ANOVA. The output statistic, R, takes a value of 0 if there is no separation of community structure attributable to a factor, and 1 if perfect separation occurs (Clarke and Gorley, 2001). For single taxa the ANOVA posthoc test after Fisher was used to reveal possible differences in regional and temporal distribution. Correlation between temperature and chlorophyll *a* and the abundance of copepods was calculated with the non-parameteric Kendall Correlation, which is based on ranks, using the statistical software Statview 4.5. With the number of samples $n<40$ the sum of ranks (S) will be used as significance criterium.

Summary

- The Gulf of Aqaba provides a unique subtropical environment with high salinity (40 - 41) and pronounced seasonality in the physical and chemical oceanography.
- Sea surface cooling creates a deep vertical mixed layer during winter, while sea surface warming in late spring leads to thermal stratification during summer.
- The sampling took place over an almost two-year period on a fixed station in the northern Gulf of Aqaba.
- Vertical distribution was studied on samples taken in 1991/1992 and 1999.
- Feeding of dominant copepod species was investigated through incubation experiments (8 - 24 h) with natural food particles.
- Feeding of microzooplankton was investigated through dilution experiments over 24 hrs.
- Egg production and gonad maturation were analysed for the *Ctenocalanus vanus*, *Clausocalanus farrani* and *Clausocalanus furcatus*.
- Multivariate statistical analysis was used to discover similarities between samplings, mesozooplankton taxa and environmental parameters.

4 Results and Discussion

The following section summarizes and discusses the published and some unpublished results of this study. A more detailed discussion can be found in the attached publications. The first section will focus on the methodological constraints, the second will concentrate on the seasonal distribution of holo- and meroplankton, with particular emphysis on the copepods and the third part will discuss the annual cycles and biology of the predominant clausocalanids in the Gulf of Aqaba.

4.1 Comparison with other subtropical systems

The Gulf of Aqaba, the adjacent Red Sea and the Eastern Mediterranean are semi-enlosed basins separated from other water bodies by shallow sills, while the Arabian Sea is an open sea in the northern Indian Ocean. The shallow sills allow only little exchange with adjacent waters and bring about a partial isolation of the deeper water layers in terms of floristic and faunistic characteristics (Halim 1969, Scotto Di Carlo et al. 1984, Weikert and Trinkaus 1987). While the surface water inflow from the Gulf of Aden into Red Sea is influenced by the seasonally reversed monsoons, the Gulf of Aqaba experiences a constant inflow of low-salinity surface water from the Red Sea. The water of the Eastern Mediterranean has its origin from the surface waters of the Western Mediterranean (Azov 1991).

A comparison between the Gulf of Aqaba, the Red Sea and the Arabian Sea raises two important conclusions: (i) the plankton of these regions is dominated by tropical indo-pacific species and (ii) the diversity decreases from the Arabian Sea northwards to the Gulf of Aqaba. The Eastern Mediterranean Sea is dominated by species of atlantic origin with a diversity ranging between the Red Sea and the Gulf of Aqaba (Table 6).

The assessment of the relative productivity of the fours regions under discussion is particularly difficult as the few relevant published results are based on different seasons and years. The productivity of the northern Gulf of Aqaba was quoted to be considerably higher than the remaining Gulf (Klinker et al. 1978, Labiosa et al. 2003) and as the Red Sea, due to deep vertical mixing (new production of nutrients). The average primary production in the Eastern Mediterranean is considerably lower than in both other areas (Table 6). The Arabian Sea is quoted as the most productive area of the Indian ocean.

Table 6: Characteristics of the Gulf of Aqaba, the Red Sea, the Eastern Mediterranean and the Arabian Sea (SST: Sea Surface Temperature, PP: Primary Production. MeZP: Mesozooplankton).

characteristics	Gulf of Aqaba	Red Sea	Eastern Med.	Arabian Sea
Latitude	N28 - 29.30°	N14 - 28°	N32 - 46°	N15 - 25°N
Climate	arid	arid	arid	arid
Insolation	high	high	high	high
Evaporation	high	high	high	high
Wind	N	SW-NE reversed		SW-NE reversed
Sills (m)	250 (Straits of Tiran)	130 (Hanish Sill)	<365 - 430 (Straits of Sicily)	
SST (°C)	20.5 - 27.3[1]	21.5 - 27.7[2]	13 - 26[3]	17 - 30[4]
Temp. >400 m	>20.5	>21.5	>13	?
Salinity	40.2 - 40.7	39.7 - 40.7	38.2 - 39	35.6 - 36.8
Deep Vertical Mixing	>250 m			
O_2 (ml L^{-1})	3.75 - 6.1[5]	0.5 - 4[6]	4.9 - 6[3]	0.1 - 5[7]
Chl *a* (mg m^{-3})	0.02 - 0.5[8,9]	0.07 - 0.55[10]	0.1 - 1[11]	0.2 - 0.8[7]
PP (mgC m^{-2} d^{-1})	200 - 900[8]	300 - 600[12]	82 - 165[13]	600 - 1200[7]
Picoplankton	>90% of PP[14]	90% of PP[10,12]	>90% of PP[3]	>60% of PP[15]
MeZP (ind. m^{-3})	161 - 2594[16]	200[17]	100 - 6000[18]	?
Copepds (%)	>75.5[16]	>50[17]	>72[18,19]	>75[20]
Number of Copepod species	77 [21,22]	158[23]	140[24]	>270[23]
Dominant Taxa	*Clausocalanus* spp. *Paracalanus* spp. *Ctenocalanus vanus* *Calocalanus* spp. *Oithona* spp.[24,25]	due to large meshsize used (300μm) only large species[17,23]	*Clausocalanus* spp. *Paracalanus* spp. *Temora stylifera* *Acartia clausi* *Oithona* spp.[18,26,27]	*Clausocalanus* spp. *Paracalanus* spp. *Acrocalanus* spp. *Cosmocalanus* spp. *Oithona* spp.[20,28]

1: Paldor and Anati 1979, 2: Morcos 1970, 3: Yacobi et al. 1995, 4: Shalapyonok et al. 2001, 5: Klinker et al. 1976, 6: Weikert 1980, 7: Jochem 1995, 8: Levanon-Spanier et al. 1979, 9: Labiosa et al. 2003, 10: Pillen 1989, 11: Siokou-Frangou 1996, 12: Lenz et al. 1988, 13: Azov 1991, 14: Lindell and Post 1995, 15: Blackford and Burkill 2002, 16: Publication I, 17: Weikert 1982, 18: Christou 1998, 19: Siokou-Frangou et al. 1997, 20: Madhupratap and Haridas 1990, 21: Abd El-Rahman 1999, 22: Böttger-Schnack et al. 2001, 23: Halim 1969, 24: Almeida Prado-Por 1983, 25: Publication I, 26: Fragopoulu and Lykakis 1990, 27: Siokou-Frangou 1996, 28: Smith et al. 1998

From the Arabian Sea to the northern Red Sea a reduction in density of dinoflagellates and diatoms (Sukhanova 1969) as well as zooplankton (Delalo 1966) could be observed. The northern Gulf of Aqaba, however, is an exception in the northwards trend of reduction. Phyto- and Zooplankton densities are much higher in the northern Gulf than in the southern parts and the northern Red Sea (Levanon-Spanier et al. 1979, Cornils et al. submitted).

The immigration of plankton to the Red Sea, the Gulf of Aqaba and the Eastern Mediterranean is restricted due to several problems: (i) shallow sills, (ii) high temperatures at great depths, and (iii) high salinities. Thus, mainly epipelagic plankton species are able to migrate into these basins. Some of the planktonic organisms are not able to survive the increasing salinity from the Arabian Sea to the Gulf of Aqaba, and thus the northbound migration is restricted in the Red Sea. This explains the reduction of the number of plankton species from the Indian Ocean to the Red Sea or the Gulf of Aqaba (Halim 1969, Sukhanova 1969, Table 6).

The Eastern Mediterranean is inhabited by plankton species of Atlantic origin, having reached this basin after passing the Straits of Gibraltar and Sicily. There is also a possibility of immigration of Red Sea plankton through the Suez Canal. The circulation pattern and the high salinities in the channel favour the northward migration of Red Sea species rather than that of Mediterranean species in the opposite direction (Halim 1990). About 10 copepod species could be recognized as Indo-Pacific immigrants to the Levantine basin.

The shallow sills and the restriction to the inflow of warm surface waters result in high temperatures at great depths (Table 6) in the Gulf of Aqaba (>20.5°C), the Red Sea (>21.5°C) and in the Eastern Mediterranean (>13°C), which restricts the inhabitation of deep-sea species. The high temperature, therefore, results in a strong decline of plankton abundance between the epipelagic and deeper water layers (Weikert 1982, Weikert and Trinkaus 1990, Farstey et al. 2002).

The mesozooplankton of the Gulf of Aqaba, the Red Sea, the Eastern Mediterranean and the Arabian Sea is dominated by small-sized copepods, belonging to the clausocalanids, paracalanids and oithonids (e.g. Almeida Prado-Por 1983, Siokou-Frangou 1996, Smith et al. 1998, Publication I). For example, the lowest diversity of copepods is found in the Gulf of Aqaba (77 species, Table 6), the species number of the Eastern Mediterranean (158) and the Red Sea (140) are similar and most species are found in the Arabian Sea (>270) (Table 6).

Despite the seclusion from other water bodies, the number of endemic species in the Red Sea and the Gulf of Aqaba is low. One reason might be the geological history of the basins with rapid changes in temperature and salinity, and recolonizazion after last glacial period from the Indian Ocean (Weikert 1987).

SUMMARY

- True deep-sea species are absent from the Gulf of Aqaba, the Red Sea and the Mediterranean due to the shallow sills, the high temperatures and salinities.
- The northern Gulf of Aqaba is an exception from the general northward decrease in productivity and mesozooplankton density. It has, however, the lowest diversity.

4.2 Seasonal abundance development of mesozooplankton

4.2.1 The environment

The environmental parameters **temperature** and **salinity** showed a fairly regular annual cycle for 2002 and 2003 as known from earlier publications (Klinker et al. 1976, Paldor and Anati 1979, Reiss and Hottinger 1984). During winter and early spring deep vertical mixing occurred with a mixing layer down to 300 m, while in summer the water column was stratified due to higher sea surface temperatures with a mixed surface layer of around 50 m (Publication I). The annual sea surface temperature varied between 21.3°C in February and 26.7°C in August. The salinity ranged from 40.21 to 40.61 and its annual profile showed lowest values in early summer between 50 and 150 m.

The phytoplankton community in the Gulf of Aqaba is dominated by ultraplankton (<8 μm), which is known to create a deep **chlorophyll *a*** maximum (Lindell and Post 1995). In autumn of both years, a deep chlorophyll *a* maximum was found between 50 and 100 m (0.67/0.57 μg L^{-1}, Publication I). During winter (December - February) the chlorophyll *a* was homogenuously distributed throughout the mixed water column. After the onset of stratification in March 2003 higher chlorophyll *a* concentrations were found within the upper 75 m persisting until May (0.42 - 0.50 μg L^{-1}), which indicate a phytoplankton bloom, caused by microplankton (diatoms, Kimor and Golandsky 1977, Al-Najjar et al. subm.). The year-to-year variations of chlorophyll *a* concentrations are probably related to the interannual variations in the winter mixing intensity in the Gulf of Aqaba both in terms of depth and persistence (e.g. Genin et al. 1995, Badran and Foster 1998), even so no significant correlation between temperature and chlorophyll *a* was found (Kendall Correlation).

The composition of the **protist community** was investigated only during spring and autumn (Publication II, A. Cornils and N. Schaaf, unpublished data). Smaller particles (5 - 20 μm), consisting mainly of dinoflagellates and flagellates, dominated the community of natural particles (35 - 80%). The size classes larger than 20 μm were composed mostly of ciliates and diatoms. Comparing spring and autumn 2002, it becomes clear that in autumn the percentage of dinoflagellates and ciliates in the NOP concentrations increased, while the importance of small flagellates and diatoms decreased (Publication II). For the contribution of the microzooplankton to the protist community see section 4.3.1.

SUMMARY

- Deep vertical mixing (0 - 300 m) occurred in winter between January and March.
- Deep chlorophyll *a* maxima were found in autumn of both years (October - December). Indications for a spring bloom were observed only in 2003 (March - May).
- The natural plankton community (5 - 200 μm) was dominated by small sized particles (<20 μm), consisting mainly of dinoflagellates and other flagellates.

4.2.2 The mesozooplankton community

The variability of mesozooplankton abundance in the two years might be influenced (i) by the seasonal variability of the environmental parameters (temperature, salinity), (ii) by the availability of the possible food sources (e.g. phyto- and microzooplankton), and (iii) by the taxa composition of the mesozooplankton.

The temperature is the main factor of the governing seasonality in the Gulf of Aqaba (Reiss and Hottinger 1984). It has a direct influence on the annual distribution of the mesozooplankton community, which can be seen especially for the copepod community (see section 4.2.3, Publication I). During the period of low temperatures and deep vertical mixing high abundance of the mesozooplankton was found in both years (Publication I). In 2002, high densities were found also in autumn, while in 2003 the high abundance was also observed in summer. The differences in the annual cycle between the two years indicate variability in the seasonal occurrence of the mesozooplankton in the northern Gulf of Aqaba. Although no significant relationships were found between the environmental parameters temperature and chlorophyll *a*, the differences between 2002 and 2003 mesozooplankton could be explained with the overall changes in the annual cycle of chlorophyll *a* distribution (see 4.2.1). The deep chlorophyll *a* maximum found in autumn 2002 may have caused the mesozooplankton abundance maximum in late autumn. The spring bloom in 2003 (March to May) may be responsible for the abundance maximum of some mesozooplankton groups in summer 2003. The comparison of the results of previous investigations in the Gulf of Aqaba with this work reveals marked interannual differences in the annual cycle of mesozooplankton abundance in the Gulf of Aqaba: A summer maximum was reported by Farstey et al. (2002) and Al-Najjar (2000), a maximum in early spring by Almeida Prado-Por (1983) and Al-Najjar (2000); high densities in winter by Echelman and Fishelson (1990a,b) and Khalil and Abd El-Rahman (1997). Interannual variation in the seasonal cycle of mesozooplankton abundance was also found in other subtropical areas, for example in the Sargasso Sea (Deevey and Brooks 1977) and the NW Mediterranean (Calbet et al. 2001), whereas in the Saronikos Gulf in the Eastern Mediterranean the annual cycle seemed fairly repetitive (Siokou-Frangou 1996).

Holoplankton Copepods are the most successful group of mesozooplankton of the world's oceans (Longhurst 1985b). In subtropical, epipelagic waters they amount for at least 70% of the mesozooplankton community (e.g. Deevey 1971, Madhupratap and Haridas 1990, Mazzocchi and Ribera d'Alcala 1995). In the northern Gulf of Aqaba, copepods were predominant during the entire period with 58 to 92% (mean 79%) of the total mesozooplankton abundance (Publication I). These data correspond with recent results from the northern Gulf (Al-Najjar 2000) and from the entire Gulf of Aqaba (mean 89%, Cornils et al. submitted).
Appendicularians and chaetognaths were the other abundant mesozooplankton taxa contributing 0.03 - 16.5% and 1.1 - 5.5% to the total mesozooplankton abundance. The proportion of appendicularians and chaetognaths corresponded with those known from other subtropical regions (7.7% and 3.3% Sargasso Sea, Deevey 1971), but were higher than those known from March 1999 along the whole Gulf of Aqaba (1.8 and 2.0%, Cornils et al. submitted). Longhurst (1985b) stated that chaetognaths have the most consistent frequency of relative abundance in the world's ocean, ranging between 2 and 10% . The ostracods were probably underestimated in our study because their vertical maxima are often found below the thermocline (Longhurst 1985a, Cornils et al. submitted). Cladocerans which are a typical summer form (e.g. Komarovsky 1958, Calbet et al. 2001), were represented by one species, *Evadne tergestina*, occurring only during summer 2003 (June, July).

Meroplankton Coastal currents, semidiurnal tides and winds transport meroplankton to the offshore waters. Belgrano and Dewarumez (1995) revealed a strong correlation between the tidal currents and the distribution of meroplankton larvae. Therefore, many meroplanktonic larvae seem to be introduced to the open Gulf of Aqaba. During the whole investigation period in 2002 and 2003 a considerable part of the mesozooplankton community was comprised of meroplankton (3 - 30%, Publication I). Gastropods (1.2 - 25.3%), bivalve larvae (0.1 - 14.2%), polychaete larve (0 - 6.7%) and echinoderm larvae (0 - 8.5%) were the main contributors. The taxa gastropods also included some pteropods. Other important meroplankton were polychaete and echinoderm larvae.

Approximately 70% of the benthic species release eggs or embryos into the water column and the resulting larvae become part of the planktonic community (Thorson 1950, Bhaud 1993). Depending on the species, these meroplanktonic larvae may spend from a few minutes to several months in the plankton before they settle onto a substrate and metamorphose into the adult form. Especially for sessile species this ensures a wide distribution and a good ability for exploitation of new territories (Thorson 1950).

In contrast to continuous presences of meroplankton in other tropical and subtropical regions, the seasonal cycles of the major meroplankton taxa in the Gulf of Aqaba showed considerable changes (Publication I). The presence of meroplankton is linked to the reproductive patterns of the adults and those are probably also influenced by the pronounced seasonality of the hydrography and chlorophyll *a*. In 2002 all major taxa (gastropods, bivalve larvae, polychaete larvae and echinoderm larvae) reached higher densities in spring (March), gastropods and polychaete larvae also showed another peak of abundance in autmn (September, October). In 2003, the seasonal occurrence differed between the taxa: the abundance of gastropods did not changed considerably, bivalve larvae reached high densities in winter (January), echinoderm larvae in summer (July) and polychaete larvae in autumn (October). At higher latitudes, the larvae of benthic invertebrates and fish appear seasonally because reproduction in the adults is linked to higher temperatures and elevated phytoplankton production (Bhaud 1993). Jaklin (2003) suggested that the pattern of spawning is variable within one species as a result of the timing and magnitude of the phytoplankton bloom in the North Sea.

The influence of vertical mixing The influence of the deep vertical mixing in the Gulf of Aqaba has been described by Farstey et al. 2002. The vertical distribution of the mesozooplankton has a strong relationship with the mixing depth in the Gulf of Aqaba (Böttger-Schnack et al. 2001, Farstey et al. 2002, Cornils et al. subm.) and elsewhere (Banse 1965, Longhurst 1985b).

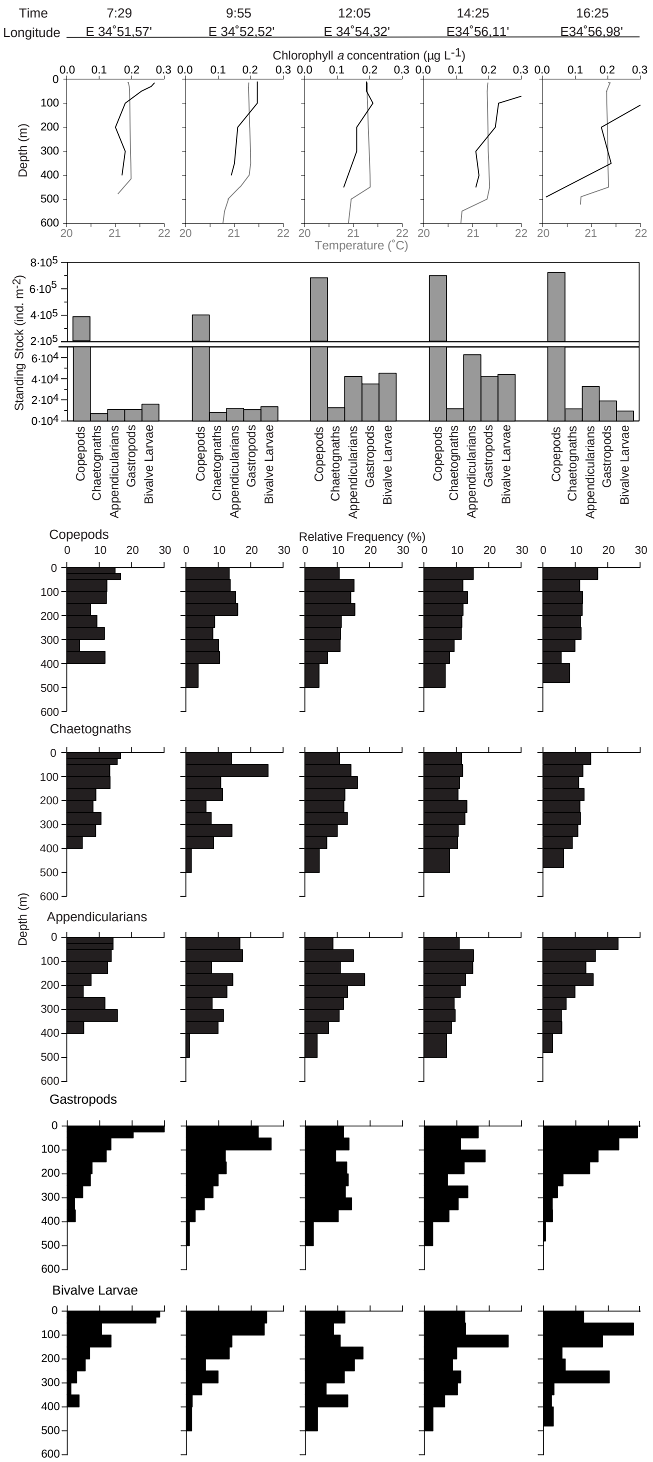

Figure 3: Vertical distribution of the temperature, chlorophyll *a* concentration. Standing stock and vertical distribution of major mesozooplankton groups in the northern Gulf of Aqaba on a cross-shore transect during MET44/2 on March 5th in 1999.

During thermal stratification in summer the mesozooplankton is usually restricted to the upper water layers, while during deep vertical mixing in winter it is homogenuously distributed (Klinker et al. 1978, Farstey et al. 2002). A cross-shore transect, taken during the deep vertical mixing period in March 1999, however, revealed, that during this period there are also small-scale differences in the vertical distributions (Fig. 3). The water column at all five stations was thermally mixed to at least 400 m with a homogenuous vertical distribution of chlorophyll *a*. The major mesozooplankton taxa were the same as those in the seasonal investigations (Publikation I): copepods, chaetognaths, appendicularians, gastropods and bivalve larvae. The highest standing stocks were found for copepods (3.8 - 7.2 $* 10^5$ ind. m^{-2}), the lowest for chaetognaths (0.7 - 1.3 $* 10^4$ ind. m^{-2}). The standing stocks of appendicularians, gastropods and bivalve larvae were rather similar (1.0 - 6.3 $* 10^4$ ind. m^{-2}). The lowest standing stocks occurred in the western station in the morning for all five taxa, while the highest were found between 12:25 and 2:25 p.m.. For appendicularians, gastropods and bivalve larvae, the standing stocks decreased again in late afternoon at the easternmost station while the standing stocks of copepods and chaetognaths remained high. The vertical distribution at the westernmost stations (between 7:29 and 9:55 a.m.) showed a bimodal vertical distribution pattern for copepods, chaetognaths, and appendicularians with highest densities in the upper 50 m and between 300 and 400 m. At the stations sampled during midday (12:05) the majority was found between 100 and 200 m. In the afternoon (2:25 and 4:25 p.m.) copepods and chaetognaths were relatively equal distributed within the water column while highest densities of appendicularians were found at the surface (4:25 p.m.). The meroplankton, represented here by gastropods and bivalve larvae showed a different pattern in their vertical distribution. They were concentrated in the surface layers in the morning and displayed a bimodal vertical distribution or surface maxima in the afternoon.

The difference between the western (7:29 and 9:55 a.m.) and the eastern stations (12:05 a.m., 2:25, 4:25 p.m.) could be either explained by the daily migration patterns of the zooplankton or by the influences of the local circulation patterns investigated on the same transect by Manasreh (2002). The vertical pattern of density suggests upwelling at the eastern coast and downwelling at the western coast (Manasreh 2002).

At other stations in the Gulf of Aqaba taken also during March 1999 appendicularians and calanoid copepods were found in high numbers in the mixed surface layers, whereas chaetognaths were rather homogenuously vertically distributed (Cornils et al. subm.).

SUMMARY

- The vertical distribution as well as the seasonal cycle of the mesozooplankton is driven by the thermal structure of the water column.
- Interannual differences, however, seem to be caused by variations in the chlorophyll *a* distribution.
- Meroplankton contributes a considerable proportion to the total mesozooplankton abundance (3 - 30%).

4.2.3 Copepods

A two years study is not sufficient to define year to year trends in number and composition, but it might provide basic information about the patterns within a copepod community. Throughout the investigation period calanoid copepods dominated the upper 100 m (mean: 62%), followed by cyclopoids (23%) and poecilostomatoids (12%, Publication I). The diversity remained low throughout the investigation period (Shannon index H' = 2.603 - 3.238, Publication I). The copepod community was dominated by the following taxa: *Calocalanus* spp., *Paracalanus* spp., *Mecynocera clausi*, *Clausocalanus* spp., *Ctenocalanus vanus*, *Acartia negligens*, *Oithona* spp., oncaeids and corycaeids which coincided with earlier publications (Almeida Prado-Por 1983, Abd El-Rahman 1999, Al-Najjar 2000).

Although there are interannual differences in the total copepod community, most taxa show a rather distinct annual cycle (Publication I), and the copepod taxa could be divided by their seasonal maximum: (i) taxa occurring in highest densities in spring (*Clausocalanus* spp., *Paracalanus* spp., *Ctenocalanus vanus*, *Acrocalanus* spp.), (ii) taxa reaching their abundance maximum in autumn (*Calocalanus* spp., *Mecynocera clausi*, *Acartia negligens*, *Lucicutia* spp., *Candacia* spp., *Centropages* spp., and (iii) taxa with highest abundance in winter (Calanidae, *Parvocalanus crassirostris*, corycaeids). Beside the autumn peak in autumn and winter, *Acartia negligens* and the Calanidae reached also high densities during both summers, whereas *Clausocalanus* spp., *Acrocalanus* spp., *Candacia* spp., *Oithona* spp., and the oncaeids occurred in high summer densities only in 2003 (Publication I). The summer maximum of *Clausocalanus* spp. is caused mainly by *C. furcatus* as can be seen in Publication III. Compared to the annual fluctuations observed in the eastern Mediterranean Sea, the seasonal variability of copepod abundance in the Gulf of Aqaba was quite low (Publication I, Mazzocchi and Ribera D'Alcala 1995, Christou 1998).

A positive correlation was found between the annual temperature cycle and most taxa with high abundance in autumn during periods of higher temperatures (Publication I). An inverse significant relationship was found for *Ctenocalanus vanus* and *Parvocalanus crassirostris* which occurred mainly in spring during times of low temperatures. During this work, no significant correlations could be established between the chlorophyll *a* distribution and the abundance of the copepod taxa. It has to be taken into account, however, that there might be a staggered response of the copepod taxa to the annual cycle of phytoplankton, which will be further discussed in section 4.3.2. In the eastern Mediterranean the annual cycle is characterised by two abundance maxima, one in late winter or early spring and a second in autumn corresponding to the chlorophyll *a* seasonal cycle (Siokou-Frangou 1996). Studies including several years showed that the annual cycle of copepods changed with the interannual differences of chlorophyll *a* (Sargasso Sea: Deevey and Brooks 1977, Eastern Mediterranean: Christou 1998).

SUMMARY

- Typical for subtropical oceans, the copepod community were dominated by small sized families: Paracalanidae, Mecynoceridae, Clausocalanidae, Acartiidae and Oithonidae. Together they accounted for more than 80% of the calanoids.
- Most copepod taxa are either positively (abundance maximum in autumn) or negatively (abundance maximum in spring) correlated to the sea surface temperature.
- Additional summer maxima might be explained by the seasonal variations in phyto- and microzooplankton.

4.2.4 Clausocalanid Copepods

In the Gulf of Aqaba four clausocalanid species were found: *Ctenocalanus vanus*, *Clausocalanus farrani*, *Clausocalanus furcatus* and *Clausocalanus minor*. The first three species have been known from the Gulf of Aqaba from previous publications (Almeida Prado-Por 1983, Abd El-Rahman 1999, Al-Najjar 2000), while this is the first record for *C. minor* Sewell, 1929, in the Gulf (Publication III). The females of *C. minor* were found at low densities (Table 7), except for January 2003, when the abundance reached 8.6 ind m^{-3}. All previous publications described *Clausocalanus arcuicornis* instead of *C. minor* in the Gulf of Aqaba, which could not be found during this work. *C. arcuicornis* was also lacking from vertical stratified samples in the entire Gulf of Aqaba and the northern Red Sea in February/March 1999 (S. Schiel, unpublished data) and from the here presented data from 1991/1992 (Table 7). *C. arcuicornis* and *C. minor* are of similar size, distinguishable only by their genital segment (Frost and Fleminger 1968). Hence, the similarity might have caused a misinterpretation of species. As *C. farrani*, *C. minor* is restricted to the Indian and Pacific Ocean (Frost and Fleminger 1968), but quantitative records are scarce (Madhupratap and Haridas 1986, Smith et al. 1998). in contrast, *C. furcatus* has a worldwide distribution (e.g. Mazzocchi and Ribera D'Alcala 1995, Webber and Roff 1995a).

In the Gulf of Aqaba, the genus *Clausocalanus* contributed on average 23.7% to the total copepod community (6.6 - 52%) while *Ctenocalanus vanus* had an average share of 10.4% (0.8 - 46%) (Publication I and III). The average abundance was higher in 2003 than in (Table 7). Compared with the samples taken in 1991/1992 with 100 μm mesh size the older copepodite stages (CIV, CV) and the adults showed a similar abundance, while the densities of small copepodite stages (CI-CIII) were considerably higher during the sampling for vertical distribution in 1991/1992 due to the smaller mesh size used (Table 7). Compared to the results of Almeida Prado-Por (1983), the abundance of *Clausocalanus furcatus*, *Clausocalanus farrani* and *Ctenocalanus vanus* were about two orders of magnitudes higher (Table 7), although the same mesh size was used. Abundance data from other regions (Caribbean, Mediterranean) exist only for *Clausocalanus furcatus*, where the densities were similar to those found during this study (e.g. Webber and Roff 1995a, Peralba and Mazzocchi 2004).

The seasonal cycle of clausocalanid abundance has already been discussed in section 4.2.3. Seasonal data of clausocalanids are rather scarce. Deevey (1971) described the annual cycles

Table 7: Abundance data (ind. m^{-3}) of the clausocalanids in the upper 100 m in 2002, 2003 and 1992, taken with a mesh size of 200 μm (2002, 2003) and 100 μm (1992)), averages and standard deviation (±).

Taxa	Stage	year					
		2002		2003		1991/1992	
	copepodite IV	13.5	± 22.8	43.5	± 67.1	36.7	± 74.1
Clausocalanus	copepodite V	37.7	± 29.8	87.0	± 87.7	59.9	± 91.1
	male	6.2	± 7.2	18.3	± 24.1	18.0	± 46.6
C. furcatus	female	15.5	± 15.1	37.2	± 47.2	39.2	± 46.0
C. farrani	female	22.7	± 21.7	43.0	± 36.0	45.5	± 137.2
C. minor	female	0.2	± 0.1	1.2	± 2.5	0.8	± 1.2
	copepodite IV	8.8	± 20.4	13.2	± 45.8	35.2	± 84.9
Ctenocalanus	copepodite V	13.0	± 25.4	26.8	± 43.6	38.8	± 168.1
vanus	female	18.6	± 43.2	37.5	± 42.7	45.5	± 191.8
	male	0.2	± 0.3	1.6	± 2.4	2.8	± 12.3
clausocalanids	copepodite I-III	7.1	± 16.7	11.1	± 73.4	341.4	± 772.1

for the clausocalanids in the Sargasso Sea. While *Ctenocalanus vanus* had an repeatable annual cycle of abundance, the densities of *Clausocalanus furcatus*, *C. arcuicornis* and *C. paululus* varied greatly between the years. *C. furcatus* was abundant mainly during autumn, *C. paululus* had a higher abundance between November and April and *C. arcuicornis* did not show any real seasonality. Annual studies in the Mediterranean revealed that abundance of *C. furcatus* was highest during summer, different from all other *Clausocalanus* species (Mazzocchi and Ribera D'Alcala 1995, Peralba and Mazzocchi 2004) which corresponds with the peak of *C. furcatus* females in summer 2003 in the Gulf of Aqaba (Publication III). In the Mediterranean the annual cycle of *Ctenocalanus vanus* reveals the same picture as found in the Gulf of Aqaba (Siokou-Frangou 1996, Christou 1998). The different seasonal cycles of the *Clausocalanus* species may be a strategy to avoid competition. However, Peralba and Mazzocchi (2004) showed that the eight species of *Clausocalanus* in the Mediterranean Sea coexist over most of the year, but differed in the numerical development and vertical occurrence. An explanation for differences between *Clausocalanus* and *Ctenocalanus* might be the latitudinal distribution of the three species. Whereas *Clausocalanus farrani* and *C. furcatus* are restricted to subtropcial and tropical waters (Frost and Fleminger 1968), *Ctenocalanus vanus* has a broader range reaching temperate waters.

The development from the copepodite stages to adults could not be observed. This might be either a result from the broad monthly sampling strategy and the 200 μm mesh size, but also from the possible continuous breeding as observed in the Mediterranean (Gaudy 1972, Shmeleva and Kovalev 1974) and the short development time from egg to adult (under laboratory conditions 23 days, Mazzocchi and Paffenhöfer 1998).

Clausocalanids are mainly present in epipelagic waters as reported in many publications (e.g. Frost and Fleminger 1968). In the Gulf of Aqaba, the three dominant clausocalanid species co-occurred over the whole investigation period with varying densities (Publication III). Vertical profiles of the relative abundance of clausocalanids in the Gulf of Aqaba from October 1991, January, April and July 1992 showed that the majority of the clausocalanids are situated within the upper 100 m (>65%), except for January 1992, when high densities were found within the upper 300 m (Fig. 4). This applies to the copepodite stages as well as to the adults, except for the males of *Ctenocalanus vanus*, which occurred at high densities below 100 m in October, January and July. In January 1992, the vertical distribution of the two *Clausocalanus* species were similar, whereas the stages of *Ctenocalanus vanus* showed a bimodal distribution with high densities between 0 and 100 m and 200 and 300 m. In April 1992 the bimodality was still slightly visible: 6% of *C. vanus* individuals were situated below 400 m. The vertical distribution was concurrent with the findings of Almeida Prado-Por (1983) who also found a bimodal distribution for *C. vanus* as well as for *Clausocalanus furcatus* and *C. farrani* in January 1975. The higher densities of the clausocalanids in water layers below 100 m coincided with the deep vertical mixing (Almeida Prado-Por 1983, Farstey et al. 2002).

This is the first record of the vertical distribution for the copepodite stages I-III, IV and V of *Clausocalanus* spp. and *Ctenocalanus vanus*. For *Clausocalanus farrani*, the vertical distribution has so far only been studied within the Gulf of Aqaba, while the vertical profiles of *C. furcatus* and *Ctenocalanus vanus* and other *Clausocalanus* species have been studied in the Eastern Mediterranean with 100 μm mesh size (e.g. Pancucci-Papadopoulou et al. 1992, Siokou-Frangou et al 1997, Peralba and Mazzocchi 2004) and show that most of the clausocalanid species are favouring the upper 100 m during most of the year.

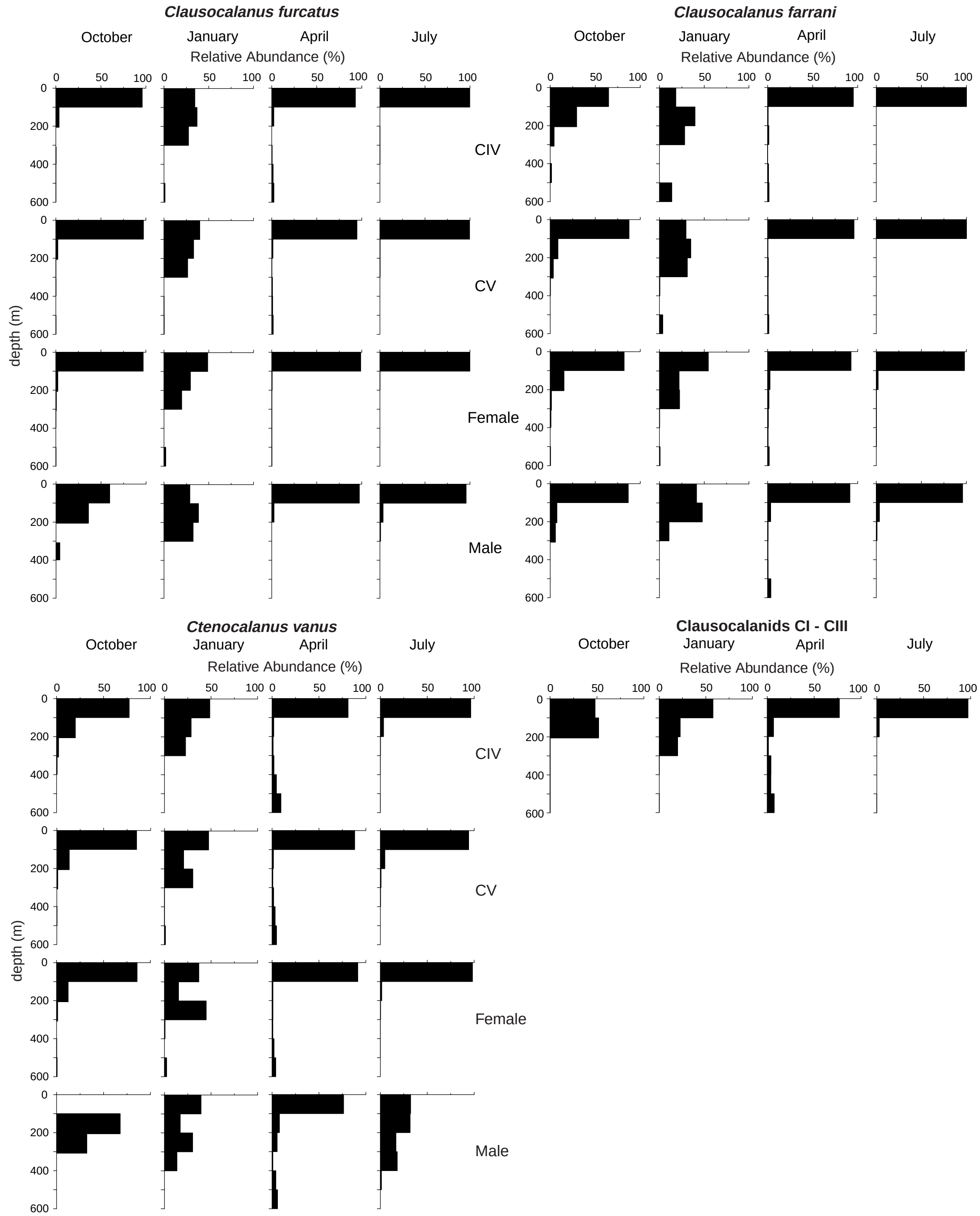

Figure 4: Vertical distribution of the late copepodite stages and adults of *Clausocalanus furcatus*, *C. farrani*, *Ctenocalanus vanus* and the combined younger copepodite stages in the northern Gulf of Aqaba between October 1991 and July 1992

However, within the upper 100 m differences in the vertical occurrence were observed. *Clausocalanus furcatus* has the smallest vertical range between the surface and 100 m (e.g. Scotto di Carlo et al. 1984) and occurs mainly in the upper 50 m (e.g. Fragopoulou et al. 2001). All other species of *Clausocalanus* and *Ctenocalanus vanus* undergo seasonal vertical migration and occur below 50 m depth during the hot summer months with high temperatures and insolation (e.g. Fragopoulu and Lykakis 1992, Peralba and Mazzocchi 2004). Seasonal vertical migration can also be seen for *Ctenocalanus citer* in the Antarctic (Schnack-Schiel and Mizdalski 1994). The copepodite stages in total of *Clausocalanus furcatus* and *Ctenocalanus vanus* show the same vertical pattern as the adults (Fragopoulou et al. 2001).

SUMMARY

- The clausocalanid copepods were represented by four species: *Ctenocalanus vanus*, *Clausocalanus farrani*, *C. furcatus* and *C. minor*. This is the first record of *C. minor* in the Gulf of Aqaba.
- The vertical distribution of all clausocalanids confirm that these copepods reside mainly in the upper 100 m, except during the winter period of deep vertical mixing.

4.3 Trophic Interactions and Life Cycles

The eucaryotic phytoplankton in the Gulf of Aqaba generally develops a bloom during spring, a summer minimum and sometimes also an autumn bloom (Kimor and Golandsky 1977, Levanon-Spanier et al. 1979, Lindell and Post 1995). The ultraplankton (<8 μm) dominates the water column throughout most of the year (Lindell and Post 1995, Al-Najjar 2000) and is known to create a deep chlorophyll *a* maximum. In spring microplankton, mainly diatoms, show higher concentrations than during the remaining year (Kimor and Golandsky 1977). The increase of the microplankton abundance is often followed by increased microzooplankton abundance (Kimor and Golandsky-Baras 1981) which is an important food source for copepods (Batten et al. 2001, Sommer et al. 2002, Publication II).

4.3.1 The importance of the microzooplankton

In autumn 2003, the microzooplankton comprised 1 - 2% of the abundance and around 40 - 68% of the plankton biomass (2 - 200 μm) in the northern Gulf of Aqaba. It was mainly composed of tintinnids and naked ciliates, but Sarcodina and crustaceans were also found. In the Gulf of Aqaba the importance of tintinnids was already recognized by Komarovsky (1959), who described zoogeographic and taxonomic aspects. Kimor and Golandsky (1977) showed that the tintinnids reach maximal abundance of more than 150,000 ind. m^{-3} during spring, parallel to the annual maximum of the phytoplankton abundance. Recent investigations of microzooplankton grazing in the Gulf of Aqaba showed that microzooplankton grazing rates were high, but declined with algal size (Sommer et al. 2002). This indicates that smaller algae are the main food source for the microzooplankton. Sommer et al. (2002) also showed that the grazing rates of microzooplankton were about two orders of magnitude higher than those of the mesozooplankton, and therefore, the impact on the investigated community, especially for the ingestion of the smaller size classes should not be neglected in further investigations. All these results suggest that ciliates play an important role in the microbial food web, because they show the highest growth, filtration and ingestion rates of the protozoa (e.g. Gifford 1991, Hansen et al. 1997).

The autotrophic plankton, reaching chlorophyll *a* concentrations between 0.34 and 0.62 μg L^{-1}, was mainly represented by diatoms within the recognizable plankton above 5 μm. Lindell

Table 8: Initial chlorophyll *a* concentrations, growth rates (μ), mortality (m) and the correlation coefficient (r^2) of regression analysis. If m>0, then m/μ and the relative grazing effects (M) were calculated (Cornils and Schaaf, in prep.).

Experiment	Initial chlorophyll *a*	μ	m	r^2	m/μ	M_N	$M_{\Delta N}$
	(μg L^{-1})	(d$^-$1)	(d$^-$1)		(%)	(%d$^-$1)	(%)
06.10.03	0.40	0.13	0.85	0.21	654	65	470
12.10.03	0.62	0.35	0.19	0.26	54	25	59
23.10.03	0.42	0.21	-0.11	0.27	-	-	-
27.10.03	0.37	0.30	0.24	0.47	80	29	82
30.10.03	0.49	-0.62	-0.57	0.82	-	-	-
04.11.03	0.34	0.17	-0.08	0.17	-	-	-
06.11.03	0.36	0.33	0.26	0.55	79	32	81
02.12.03	0.51	0.16	0.16	0.71	100	17	100

and Post (1995), however, showed that the eucaryotic phytoplankton community of the Gulf of Aqaba is dominated by small flagellates. The growth rates (μ) of the phytoplankton in terms of chlorophyll *a* varied between 0.13 - 0.35 d^{-1} and the grazing pressure (m) of the microzooplankton in dilution experiments was about 0.16 to 0.85 d^{-1} (Table 8, Fig. 5). This equals a loss of 60 - 100% of potential production or 20 - 30% of the daily chlorophyll *a* standing stock. Through bacterivory about 90 - 95% of the bacterial production was removed (N. Schaaf, unpubl. data). Calbet and Landry (2004) compared numerous dilution experiments and established for the quotient μ:m a global average of 67%, and in reference to the tropical and subtropical region they suggested an average of 75%. Therefore, the microzooplankton of the Gulf of Aqaba, as in other subtropical and tropical regions, is mainly responsible for the loss of the primary production. However, the question remains whether such high microzooplankton grazing rates occur in the presence of mesozooplankton. Under natural conditions the cascading effect of the predatory and omnivorous mesozooplankton on lower trophic levels leads to a reduction of the grazing pressure on the phytoplankton. Other causes of phytoplankton mortality are losses due to sedimentation or viral lysis (Sommer 1998).

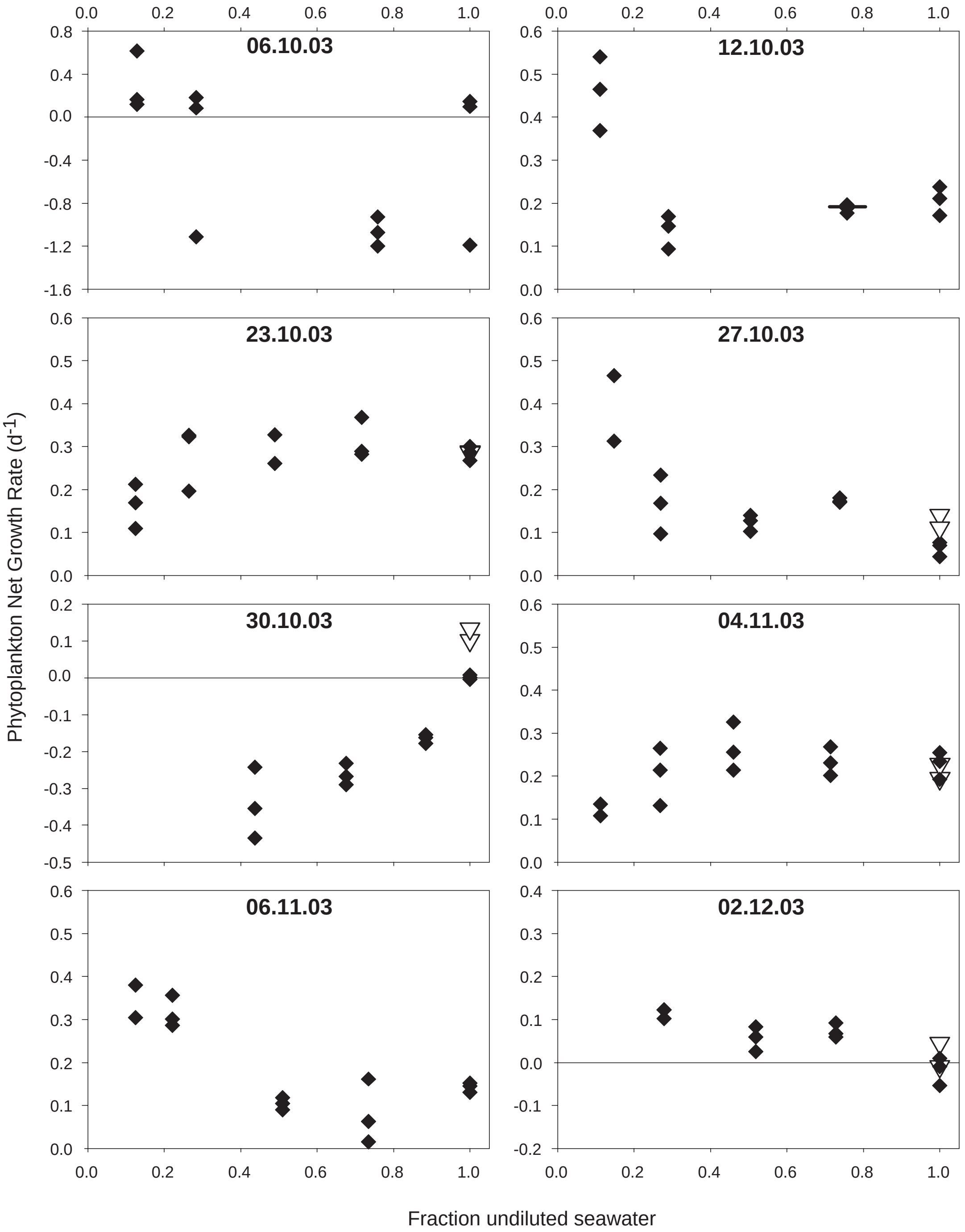

Figure 5: Phytoplankton growth rates (k) on the base of chlorophyll *a* concentrations in dependance of the fraction of undiluted seawater. ◇: nutrient enriched approaches; ∇: tests without nutrients (Cornils and Schaaf, in prep.)

Cascading effects may have also effected grazing experiments in this study. For example, microzooplankton grazing in the experimental controls (no copepods) may have led to an underestimation of copepod grazing rates in the treatment, especially on small size classes (5 - 10 μm). During the incubation experiments with calanoid copepods (Publication II) on March 31st and April 16th we found low densities of ciliates in the controls coinciding with the lack of ingestion of small flagellates. This might be an indication for the missing impact of microzooplankton in the treatments. This pattern, however, was only detectable for *Ctenocalanus vanus* and not for the *Clausocalanus* species.

Three of eight dilution experiments (23.10., 30.10. and 04.11.) were found with a negative grazing pressure which contradicts the concept (Table 8). The growth rates displayed in Fig. 5 are shown in relation to the dilution. The negative grazing pressure can be either caused by methodological shortcomings or hardly detectable complexity of microbial food webs of oligotrophical systems. Tests including the influences of nutrient enrichment (blank triangles) showed only little difference from the variance of growth rates with nutrient enrichment. Therefore, the correction of the growth rates was neglected.

The taxonomic composition of the plankton community smaller than 200 μm revealed three or four trophic layers: bacteria, autotrophic and heterotrophic flagellates, larger protists and metazoens. The differences in the composition of the samples suggest succession within the investigation period, which resembled the transition between summer stratification and vertical mixing in winter.

The analysis of the growth rates showed differences between the taxa discovered by inverted microscopy (Fig. 6). The growth rates were calculated from the abundance. Rare taxa, for which the growth rates could only be calculated in two experiments, were excluded from the figure. The dinoflagellates showed predominantly a decrease in abundance, especially the smaller specimens (<20 μm). Within the diatoms only the pennate taxa (20 - 100 μm) decreased while the centric diatoms did not show a clear tendency, but in part considerable dispersion with positive and negative growth rates. The growth rates of flagellates were positive in the last three experiments, while negative in the first experiments. Ciliates showed a decrease in growth rates, while sarcodines clearly increased.

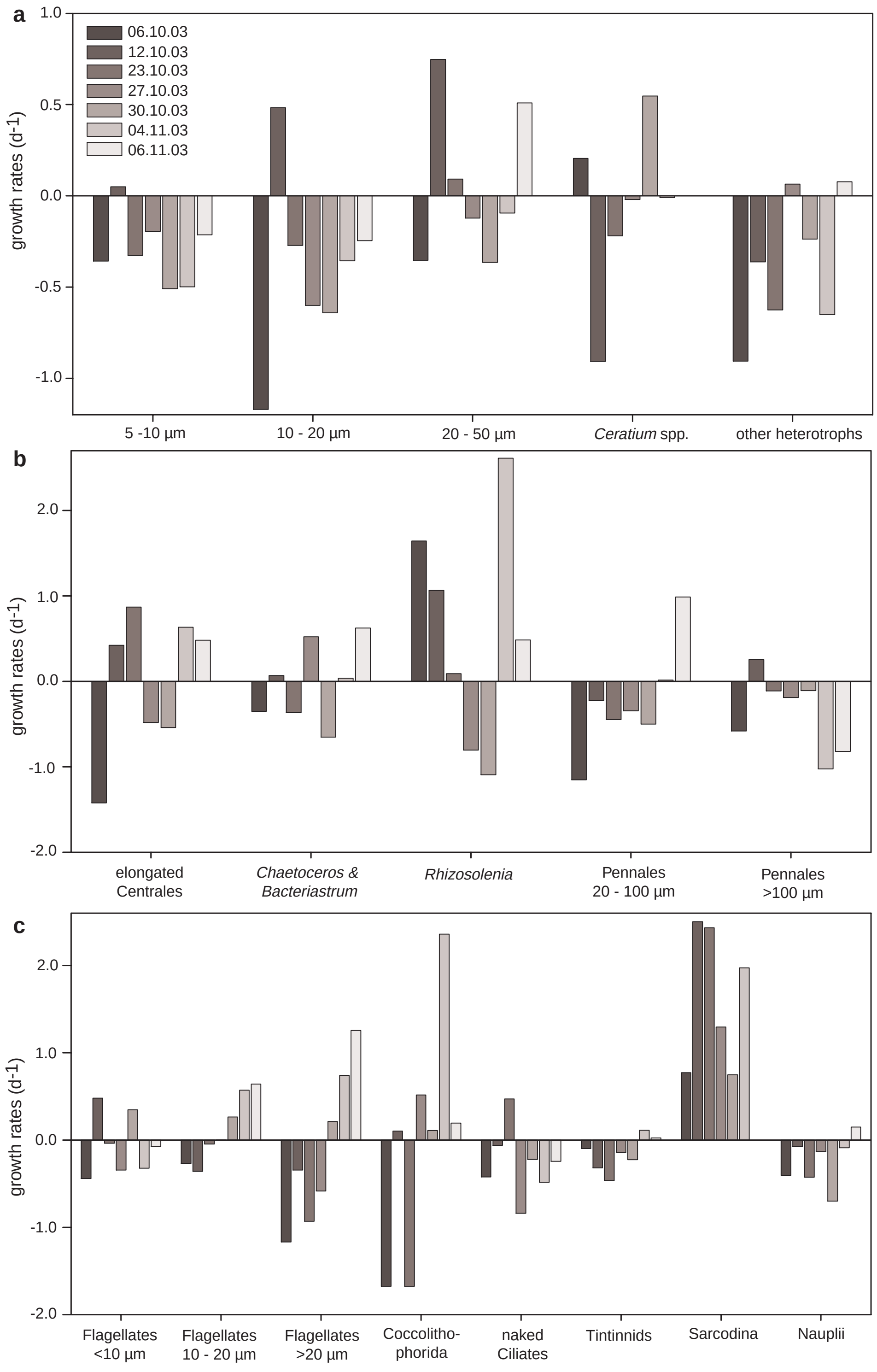

Figure 6: Growth rates (k) of (a) dinoglagellates, (b) diatoms (c) other microzooplankton taxa.

The comparison between the growth rates of ciliates and sarcodina implies that inspite of the high turnover rates, ciliates might also be exposed to a higher grazing pressure of possibly sarcodina or crustacean nauplii. The growth rates of nauplii also decreased. However, it is questionable whether nauplii have microzooplankton predators.

SUMMARY

- The grazing pressure of the microzooplankton equals a loss of 65 - 100% of the potential production. Hence, the microzooplankton is responsible for the major loss of the primary production.
- Under natural conditions (including the mesozooplankton) cascading effects might lead to a decrease of the grazing pressure on the phytoplankton.

4.3.2 The feeding pattern of calanoid copepods

The results of this work represent one of the few studies available to date on the feeding behaviour of clausocalanids (Publication II), *Acartia negligens* and *Mecynocera clausi* (Figs. 8, 7) from subtropical regions. Historically, small calanoid copepods were thought to be mainly herbivorous. Recent investigations in many marine regions, however, have shown that the microzooplankton is an important food source for copepods, especially in oligotrophic regions where the primary producers are dominated by ultraplankton. Poulet (1974, 1978) found that copepods prefer to feed on growing rather than senescent particles, and are able to switch between size classes. Hence, they seem to be able to quickly adjust to changes in their food supply.

During this work copepods fed predominantly on smaller sized food items between 5 and 20 μm (mainly flagellates and dinoflagellates) in terms of abundances, which were also the main representatives of the natural particle community (Fig. 7, Publication II, Sommer 2000, Al-Najjar et al. submitted). This corresponds with the findings of Kleppel (1993). The author found that the diet of calanoids reflects the natural protist community.

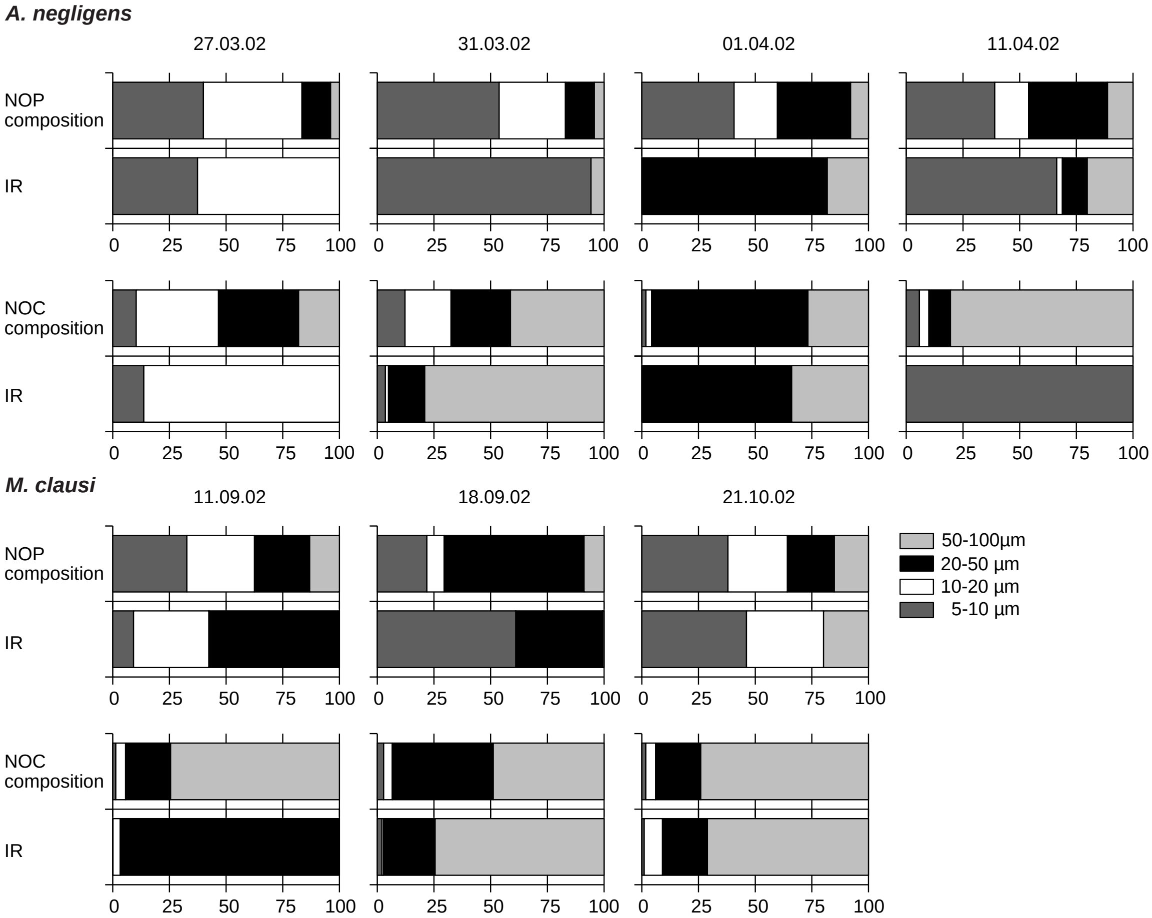

Figure 7: Food selectivity in *Acartia negligens* and *Mecynocera clausi* as determined from NOP and NOC composition of the diet relative to the NOP and NOC composition of available food.

Feeding of small copepods in oligotrophic regions takes place probably predominantly on naked cells including flagellates, small naked dinoflagellates and ciliates.

Gut content analysis of *Clausocalanus* spp. in the vicinity of the Great Meteor Seamount in the subtropical North Atlantic showed that the guts were filled with a high percentage of unidentifiable particles, and as shown by histological studies, the animals have been in a good nutritional condition, which indicates the feeding mainly on naked cells (Fischer 2004). Combined with the findings of Kleppel et al. (1988) that the gut pigments of *Clausocalanus* spp. consisted mainly of carotenoids of heterotrophic organisms followed by carotenoids of dinoflagellates.

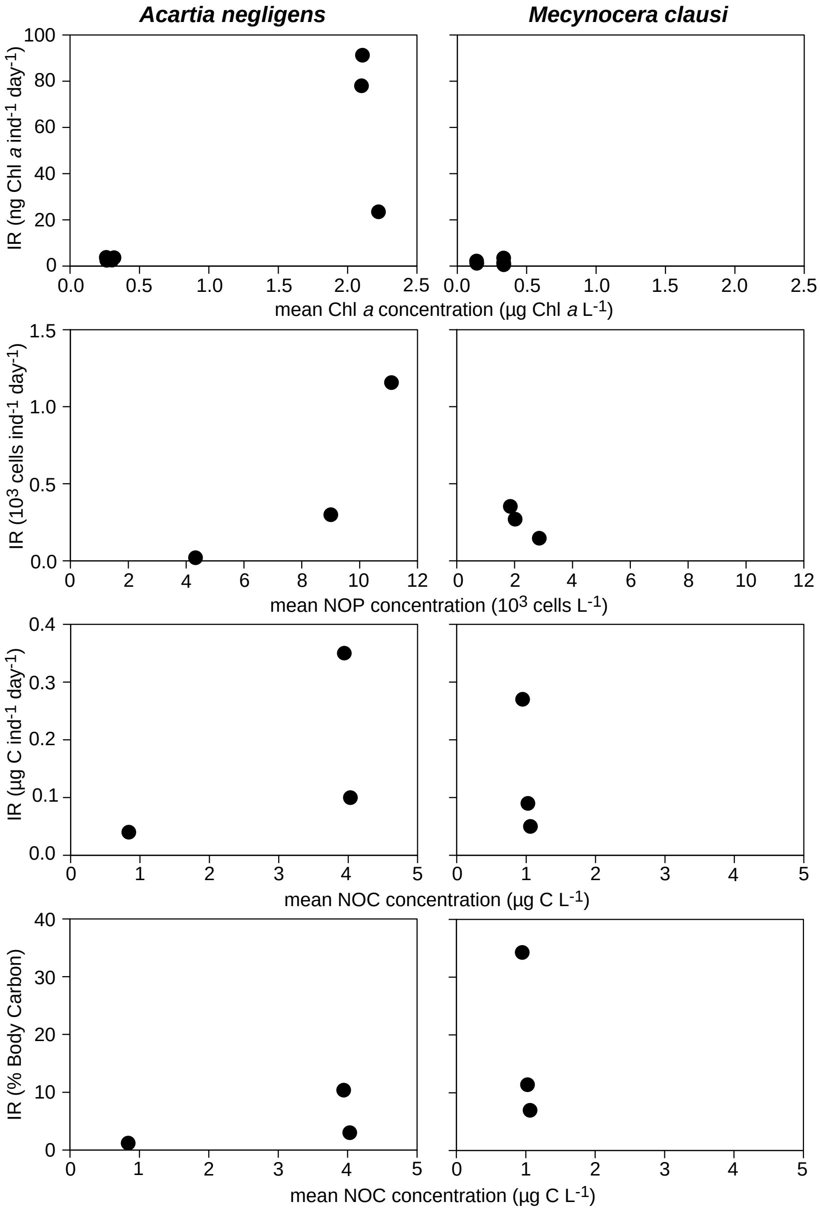

Figure 8: *in situ* Ingestion rates (IR) of the females of *Acartia negligens* and *Mecynocera clausi* to mean cell concentration for chlorophyll *a* (a), NOP (b), NOC (C) and % body carbon (d).

The size class composition of the natural particles changed not greatly, which resulted in similar feeding patterns between spring and autumn. The total ingestion rates for chlorophyll *a*, naturally occurring particle (NOP), naturally occurring carbon (NOC) and proportion of body carbon (%BC) were not significantly related to the mean food concentrations, however, a tendency could be seen (Publication II, Fig. 8). Non-selectivity and omnivory of copepods are a good feeding strategy in subtropical waters as the copepods have short life spans (Gaudy 1972, Shmeleva and Kovalev 1974). Selective feeding would inhibit the development of a continuous population in these environments of limited food supply. Non-selectivity under conditions of low food concentration has been reported from different region worldwide (e.g. Poulet 1976, 1978, Cowles 1979, Huntley 1981) as well as omnivory (Paffenhöfer and Knowles 1980). Poulet (1976) claimed that the copepod *Pseudocalanus minutus* was feeding on the dominant food type at high food concentrations, whereas they fed on a broader size range at low food concentrations, which could also be found in this work (Publication II, Fig. 8). Omnivory has been shown in several publications with positive selection for microzooplankton (e.g. ciliates (Kleppel et al. 1998, Batten et al. 2001, Halvorsen et al. 2001, Broglio et al. 2004). However, preferential feeding of microzooplankton could not be found during this investigation (Publication II). Non-living particles may also play an important role as food source in regions with low living particle concentrations. The carbon-chlorophyll ratio in faecal pellets of *Clausocalanus arcuicornis* from Onagawa Bay (Japan) suggests that non-phytoplankton particles, presumably detritus, constitute a dominant fraction of particulate materials in their diet (Ayukai 1990).

Comparisons with the few data available on feeding rates of *Clausocalanus* spp. and *Ctenocalanus* spp. reveals that the ingestion rates of the present study correspond well with published results with natural occurring particles as well as with algal monocultures (Publication II). The low rates for *Clausocalanus furcatus* found during this study (carbon uptake of less than 4.5% BC d^{-1} (Table 9) are corroborated by similar findings of Mazzocchi and Paffenhöfer (1998) under laboratory conditions with dinoflagellates as food source (Publication II). Low body carbon ratios were found despite the high swimming activity of the copepods (Mazzocchi and Paffenhöfer 1999), suggesting that continuous movement might be energetically better than 'stop-and-go' movement. Broglio et al. (2004) found ingestion rates for *Clausocalanus* spp. between 10 - 40% BC d^{-1} in the NW Mediterranean feeding on natural particles, which are in the range of *Clausocalanus farrani* in this study (1.1 - 51.8 % BC; Table 9, Publication III). Under natural conditions, the daily ratio can vary over a wide range, which has also been shown for other small calanoid species such as *Centropages typicus* (4 - 70%, Dagg and Grill 1980). Smaller copepods should exhibit higher growth rates than larger species under food-limited conditions (Hopcroft et al. 1998).

Cyclopoid copepods in tropical and subtropical ecosystems compare favorably with small co-occurring calanoids in terms of ingestion and growth rates (Calbet et al. 2000). Thus, their system function and impact should be re-examined in light of their high biomass-specific rates. In the Gulf of Aqaba cyclopoid copepods contribute 23% to the total copepod community (Publication I) and might be important food competitors of the dominant calanoid copepods. It has also been shown that small genera such as the cyclopoid *Oithona* is able to feed sufficiently on nanoplankton (Calbet et al. 2000).

Table 9: The *in situ* ingestion rates as carbon uptake (% Body Carbon) for the investigated females.

Experiment	*C. farrani*	*C. furcatus*	*C. vanus*	*A. negligens*	*M. clausi*
26.02.02	2.60		1.66		
03.03.02	51.80		1.03		
07.03.02	26.20		12.81		
10.03.02	14.00				
21.03.02			3.42		
26.03.02		0.94			
31.03.02	1.11	3.33	0.67	1.19	
01.04.02			8.91	3.01	
11.04.02				10.37	
16.04.02			1.26		
11.09.02			11.38		
18.09.02					9.18
30.09.02		4.49	7.04		
21.10.02					34.28

SUMMARY

- The ingestion rates of the dominant calanoids were food density dependent rather than size dependent. The share of the size classes to the total ingestion resembled in most cases the size class composition of the natural particle community. Hence, the copepods were able to use the low food concentrations of the natural plankton community (<200 μm) sufficiently and are adapted to the oligotrophic conditions of the Gulf of Aqaba.

4.3.3 Trophic status of other mesozooplankton

Feeding experiments in the Gulf of Aqaba showed that the dominant mesozooplankton taxa fed on different size spectra (Sommer et al. 2002). Tunicates, ostracods and cladocerans mainly fed on bacteria and small eukaryotic cells (<10 μm) whereas calanoid copepods fed efficiently on particles larger than 10 μm. Therefore, the seasonal distribution of phytoplankton might have an influence on the distribution of the mesozooplankton taxa and also on the interannual variation. Assuming that the deep chlorophyll *a* maximum in autumn 2002 consisted predominantly of ultraplankton, this might explain the high abundance of appendicularians and salps during autumn (Publication I).

The carnivorous mesozooplankton taxa (Cnidarian, chaetognaths) feed mainly on copepods (e.g. Kehayias et al. 1996, Purcell 1997) and hence, had an influence on their occurrence.

4.3.4 Reproductive activities of clausocalanid copepods

The structure of the female gonads of *Ctenocalanus vanus* and *Clausocalanus* spp. is similar to those of *Pseudocalanus* (Niehoff 2003) and *Ctenocalanus citer* (Niehoff et al. 2002) indicating that the morphology of gonads does not vary much within the Clausocalanidae. A major difference between the oocytes of *Clausocalanus* and *Ctenocalanus* was their colouring. The oocytes of *Ctenocalanus vanus* darkened with progressing development as shown previously for *Pseudocalanus* (Corkett and McLaren 1978, Niehoff 2003) and many other calanoid copepod taxa (e.g. *Calanus*, Runge 1985). In contrast, *Clausocalanus farrani* and *C. furcatus* did not show any colouring during maturation, which made it difficult to distinguish between GS3 and GS4 and to count the oocytes.

The relationship between the sea surface temperature and the mature gonads was only significant for *Ctenocalanus vanus*. These results indicate that the reproductive period of *C. vanus* is adapted rather to moderate than to high temperatures. For *Clausocalanus furcatus* and *C. farrani* breeding seemed to be independent to the seasonal temperature changes. The chlorophyll a concentrations (food source) were below 1 μg L^{-1} during the entire investigation period (Publication III). The reproduction of the clausocalanids seemed to be independent of food concentrations, as no relationship between the chlorophyll *a* concentrations and the percentage of mature gonads could be established. In *Pseudocalanus* laboratory studies have shown that reproduction is closely related to food supply (Corkett and McLaren 1978, Jonasdottir 1989, Niehoff 2003). In field studies, however, the reproductive activity of clausocalanoid species (*Pseudocalanus* in the North Sea, Halsband and Hirche, *Ctenocalanus citer* in the Bellingshausen Sea, Niehoff et al. 2002) did not show any correlation to chlorophyll *a* concentration which was used as a proxy for food availability indicating that reproduction was not food limited. Halsband and Hirche (2001) have shown in their study that egg production of *Pseudocalanus* was correlated to prosome length which in turn was dependend on temperature. The same seems to be true for *Ctenocalanus vanus* in our study which did not react to changes in feeding conditions but reproduction was related to prosome length and hence temperature. It is interesting, that though the prosome length of the *Clausocalanus* spp. changed with temperature as did the length of *Ctenocalanus vanus*, the reproductive activity however did not. In contrast to our results, Webber and Roff (1995a) did not find considerable changes in the prosome length, concurrent with the lacking of seasonal changes in temperature.

During the 24 hrs of observation only one spawning event occurred in *Clausocalanus farrani*, *C. furcatus* and *Ctenocalanus vanus*. The spawning interval of *Clausocalanus furcatus* is approximately one to two days (Mazzocchi and Paffenhöfer 1998), becoming longer at the end of the reproduction period, assuming a life span of less than 23 days. The high fluctuation between the percentages of spawning females and females with mature gonads during the experimental seasons (Publication III) imply that the female do not spawn all simultaneously. Since all females were taken from the natural environment their life history remained unknown. The egg development time at more than 25°C fluctuates between 8 -

31 hrs (Bjoernberg 1972). In contrast to the findings of Mazzocchi and Paffenhöfer (1998), during this investigation hatching occurred not only within the egg sack, but also on isolated eggs. Nauplii of stage one were found after 24 hrs of female incubation for *Clausocalanus farrani* and *C. furcatus*.

The egg production rates of *Clausocalanus furcatus* (1.8 - 9.2 eggs females^{-1} d^{-1}) and *C. farrani* (0 - 3.3 eggs female^{-1} d^{-1}) obtained in the Gulf of Aqaba during this work were similar to those observed in the Caribbean for *C. furcatus* (4.5 eggs female^{-1} d^{-1}, Webber and Roff 1995b), but considerably lower than the egg production of a free spawning representative of *Clausocalanus*, *C. lividus* (2.2 - 35 eggs female^{-1} d^{-1}, Calbet et al. 2002). The egg production of clausocalanids, especially in those producing egg sacks, seems to be low compared to e.g. the large *Calanus* species (>50 eggs female^{-1} d^{-1}, e.g. Runge 1985, Niehoff and Hirche 2000).

SUMMARY

- The mature gonads of *Ctenocalanus vanus* and *Clausocalanus* spp. differed in their colouring.
- The reproductive period of *Ctenocalanus vanus* was adapted rather to moderate than high temperatures, while the reproductive period of *Clausocalanus farrani* as well as *C. furcatus* was not related to temperature.

4.3.5 Influences of endoparasitism

While conducting the egg production experiments and distinguishing the gonad maturation stages of *Clausocalanus farrani*, *C. furcatus* and *Ctenocalanus vanus* females, infestations of endoparasites in some females were observed (Publication III). Two types of parasites were detected: 1. A parasite infested in the gut of the female, identified as *Blastodinium* sp.; 2. Abnormalities in the P5 of the females indicating an infestation of *Syndinium* sp.. *Clausocalanus* spp. and *Ctenocalanus vanus* are known to be infested by three types of dinoflagellate parasites: the endoparasites *Blastodinium* and *Syndinium*, and the ectoparasite *Ellobiopsis* (Ho and Perkins 1985, Shields 1994). *Ellobiopsis* is an external parasites, which penetrates the cuticle to gain its nutrition. Females infested with *Ellobiopsis* were not found in the clausocalanids of the Gulf of Aqaba, but has been observed for *Rhincalanus nasutus* by V. Farstey (personal communication).

The percentage of infestations of endoparasites was highest in the females of *Clausocalanus farrani* (11.9% SD 7.6) with highest densities in summer 2002 and winter 2002/2003 (15 - 55%). The proportion of parasitized females of *C. furcatus* (6.1% SD 3.8) and *Ctenocalanus vanus* (5.1% SD 3.4) never exceeded 10%. Endoparasites of *Clausocalanus furcatus* were mainly found between August and October, highest proportions for *Ctenocalanus vanus* occurred in summer of both years and January 2003 (Publication III).

In the Gulf of Aqaba, the infestation of *Blastodinium* spp. was also observed in other copepod taxa (e.g. *Oithona* spp., *Acartia negligens*, *Calocalanus* spp., *Mecynocera clausi*, *Paracalanus* spp.), but not quantified. In the Mediterranean, the frequency of infection of paracalanid copepods has been documented as high as 37% in the Gulf of Naples (Ianora et al. 1987).

Blastodinium spp. almost completely occupies the alimentary tract and can deform its lining. They are filled with photosynthetically active chloroplasts, but it remains unclear, whether the host benefits from this activity (Shields 1994). Previous publications suggest a seasonality in the prevalence of *Blastodinium* infections, with high infections in summer and fall (Chatton 1920, Ianora et al. 1990). In general, the parasites have a low prevalence in their host populations (Shields 1994). However, communities with more than 10% parasitised hosts have been reported from the North Sea, the Mediterranean Sea and the Pacific Ocean (Chatton 1920, Vane 1952, Pasternak et al. 1984). Pasternak et al. (1984) suggest that the parasites are more abundant in nutrient-poor temperate and tropical waters, hence, the higher diversity and prevalence in hosts from these regimes. *Blastodinium* spp. was the predominant parasite of *C. vanus*, with the exception of three females in March 2003 which were found with abnormalities of the P5, but mature oocytes in the diverticula, which contradicts the common opinion that intersexual females are castrated (Ianora et al. 1988). Fleminger (1985) suggests that the intersex condition might also result from the timing of maturation in copepods. Females with abnormalities at the P5 were considered to be infested by *Syndinium* sp. which supposedly causes sterility and would diminish the reproductive success (Ianora et al 1990). The gonads of the parasitized females of *Clausocalanus farrani* and *C. furcatus* were never found to be mature, showing only a maturation stage of GS1.

During the egg production experiments it could be observed that tiny "balls" were ejected through the anus of alive females of *C. farrani* and *C. furcatus*. Spawning was never observed in these females (Publication III).

Syndinium spp. are osmotrophic parasites residing in the hemal sinuses or soft tissues of the hosts. The infections with *Syndinium* are considerably more pathogenic to their copepod host than *Blastodinium*. The parasite invades the dorsal nerve ganglion, fills the hemal sinuses, insinuates itself in the muscles and in an advanced stages the muscles and other organs degenerate and lyse, and the body of the host dilates or swells and becomes opaque (Ianora et al. 1990). Host castration via the destruction of the gonads is noticeable in the stage IV and V copepodids and adult females (Chatton 1920, Ianora 1990). Male copepods are rarely infected, presumably because they are short lived and have reduced feeding capacities compared to females. Individuals with infestations of either *Syndinium* or *Blastodinium* can mate, but it remains unclear if they survive long enough to produce eggs (Sewell 1951).

SUMMARY

- The clausocalanids of the Gulf of Aqaba were infected by two types of dinoflagellate endoparasites (*Blastodinium* sp. and *Syndinium* sp.).
- The females of *Clausocalanus farrani* had the highest proportion of endoparasites (5 - 55%).

4.4 Critical assessment of methods

Sampling The northern part of the Gulf of Aqaba where the study was carried out, is relatively urbanized including two important harbours and industries compared to the central and southern Gulf which is mainly surrounded by uninhabited deserts. Hence, the pelagic community in the north might be exposed to conditions (e.g. higher nutrient input) not representative for the whole Gulf of Aqaba.

The mesozooplankton sampling of this study was carried out year round in the upper 100 m, and only a few deeper samples from 1991/1992 and 1999 (see section 3.1.2 and 3.1.3) have been available. However, during most of the year the mesozooplankton in the northern Gulf of Aqaba is concentrated in the upper 100 m (Almeida Prado-Por 1983, Farstey et al. 2002), this applies also to the Red Sea proper (e.g. Weikert 1982). Only during periods of deep vertical mixing in the northern Gulf of Aqaba periods the mesozooplankton is distributed homogenuously over the entire mixed water column (Farstey et al. 2002, Cornils et al. submitted) and therefore represent also all taxa in the upper 100 m. In summer a deep chlorophyll *a* maximum evolves in the northern Gulf of Aqaba (Levanon-Spanier et al. 1979, Lindell and Post 1995, Badran 2001) between 50 and 100 m. In the Pacific it has been assumed that this layer may represent an area of "intense trophic activity" (Ortner et al. 1981), although it has not been proven that zooplankton congregate at or just above the subsurface chlorophyll *a* maximum (Longhurst and Herman 1981).

As most species in the Gulf of Aqaba are epipelagic, it can be assumed that the upper 100 m reflect the seasonal cycle of densities of the mesozooplankton in the Gulf of Aqaba as a whole. Furthermore, Almeida Prado-Por (1990) showed that the diurnal migration of the abundant calanoids copepods does not exceed 100 m, except for the few mesopelagic species (*Pleuromamma indica, Temeropia mayumbiensis, Rhincalanus nasutus*).

The mesozooplankton samples for abundance were taken with 200 μm mesh size. Recently, investigations have shown that mesozooplankton samples taken with 63 μm mesh had a tenfold higher abundance than those taken with 200 μm mesh size (Paffenhöfer and Mazzocchi 2003). Due to the 200 μm mesh size used in this study younger copepodite stages, nauplii and small meroplankton were not sampled quantitatively. However, 80% of the mesozooplankton biomass taken with 100 μm mesh size in the northern Gulf of Aqaba was concentrated in the size fractions above 250 μm (Publication I). Therefore, the results of this work represent the majority of the mesozooplankton biomass in the northern Gulf of Aqaba.

The towing speed during the sampling was with 1 m s^{-1} rather fast. This might have caused avoidance in some taxa, because of the pressure in front of the net, which can result in a further underestimation of the community. The actual flow through the net was measured by a flowmeter installed in the net, which also corrects the influences of boat drift.

Experiments Experiments are susceptible to a series of errors (e.g. Harris et al. 1999). The incubation experiments were conducted under different conditions. The first series in spring 2002 was incubated in the laboratory on a plankton wheel while the second series in autumn 2002 were incubated in a water tank. Another possible source of error was the duration of the experiments, which varied between 8 and 24 hours. Gut content analysis of clausocalanids revealed a diel variation of feeding with high values at midnight and dawn (Mayzaud et al. 1984, Kleppel et al. 1988, Landry et al. 1994, Atkinson et al. 1996, Halvorsen et al. 2001, Fischer 2004). However, statistical tests (ANOVA posthoc test) between the incubations on the plankton wheel and in the water tank as well as between long (24h) and short (8-12h) experiments revealed no significant differences (Publication II). Therefore, it can be assumed that the methodological difference had no influence on the ingestion rates.

In principle, the importance of microzooplankton grazing can be investigated with the concept of dilution series by Landry and Hassett (1982) which includes taxonomical as well as trophic aspects of the plankton community reaching from procaryotes to metazoans and from auto- to heterotroph organisms. A series of possible errors during our incubation experiments has to be taken into consideration. The incubations of the dilutions were conducted under different conditions. The first three experiments were conducted in a light shaded water tank with a light intensity of 12% (compared to sea-surface) and the others in a water tank in the laboratory with 2% of light intensity which was similar to the natural conditions at the sampling depth of 70 m. A significant difference between the results of the different experiments could not be observed. Additional incubations were carried out to test the influence of the supplied nutrients on the phytoplankton growth rates and the activity in terms of chlorophyll *a* of filtered seawater, which showed no significant influences of the supplied nutrients.

The carbon content estimates for the incubated sea water of mesozooplankton as well as microzooplankton were made according to Smetacek (1975) referring to similar genera of the same size. Although the derived natural occurring carbon (NOC) is only a rough estimate of the real carbon content, the NOC concentrations of the experiments can be compared since the concentrations were all calculated from one area (Kiel Bight) and publication. Therefore, they are considered to have the same magnitude of error.

5 Conclusions and future perspectives

The Gulf of Aqaba, a semi-enclosed marine system, provides a unique environment for the plankton. The results of this work show that the vertical distribution as well as the seasonal abundance cycle of the mesozooplankton is closely related to the major environmental parameter, the temperature. This was especially evident for the abundance of the copepod taxa which were either positive or invers related to temperature. The microzooplankton was responsible for the main loss of the primary production. However, these estimation were made without the grazing pressure of the mesozooplankton. The latter might decrease the grazing pressure on the phytoplankton.

In the Gulf of Aqaba, the diversity of copepods is low compared to the Red Sea or the Eastern Mediterranean. The predominant genera, however, were the same as in other subtropical regions.

The comparison between the species of the predominant clausocalanids revealed differences in the relative frequency throughout the year. Differences were also observed in the reproductive activity of the clausocalanids. While the reproductive period of *Ctenocalanus vanus* was adapted rather to moderate than high temperatures, that of *Clausocalanus farrani* and *C. furcatus* was not related to temperature.

The food spectrum of the females of dominant calanoid copepod species (*Clausocalanus* spp., *Ctenocalanus vanus*, *Acartia negligens* and *Mecynocera clausi*) resembled the composition of the natural occuring particle. Hence, they seem to be able to use the low natural food concentrations sufficiently and are well adapted to oligotrophic conditions.

These results imply that the observed interannual variations in abundance might be caused by the annual differences in the chlorophyll *a* distributions (primary production) and the microzooplankton.

The conclusion of the results of this work raise a series of further questions:

- The meroplankton larvae contribute a considerable proportion to the mesozooplankton in the offshore waters of the Gulf of Aqaba. Further research should be done concerning the transport of these larvae and their destiny. Are they transported to the coastal areas again by the currents or will they be lost due to sedimentation?

- Investigations on cyclopoid copepods in comparison with calanoid copepods should be conducted to measure their impact on the food web.
- The dominant copepod species are all of similar size and feeding type. Fine scale vertical distribution could give further evidence on possible vertical partitioning between species and stages.
- The copepod community in the Gulf of Aqaba has its origin in the Indian Ocean. Although the Gulf of Aqaba is nearly separated from the Red Sea and in consequence from the Indian Ocean by the shallow sill, hardly any endemic zooplankton species have been recorded. Is there any evidence for genetical separation between the populations from the Gulf of Aqaba to the Red Sea and the Indian Ocean?
- The high salinity is also a restricting factor of species immigration to the Gulf of Aqaba. Are there physiological constraints?

6 Publications

Below the publication resulting from this thesis are listed with the explanation of my contribution

Publication I

A. Cornils, S.B. Schnack-Schiel, M. Badran, M. Rasheed, R. Manasreh, T. Al-Najjar, C. Richter

The seasonal cycle of mesozooplankton in the northern Gulf of Aqaba (Red Sea)

Manuscript

Sampling of mesozooplankton was done by myself and the sixth author. I sorted and identified all samples by myself. Temperatur, salinity and chlorophyll *a* data were provided by the third, fourth and fifth author. I developed the scientific concept, did the interpretation and statistical analysis of the data. I wrote the manuscript. The manuscript was improved by conceptional contributions of the second and last author.

Publication II

A. Cornils, S.B. Schnack-Schiel,T. Al-Najjar, C. Richter

Feeding of Clausocalanids (Calanoida, Copepoda) on natural occurring particles in the northern Gulf of Aqaba (Red Sea)

submitted to: Marine Biology

Sampling was done by the third author and myself. I conducted the experiments, interpreted the data and wrote the manuscript. The manuscript was revised by the second and fourth author.

Publication III

A. Cornils, B. Niehoff, C. Richter, T. Al-Najjar, S.B. Schnack-Schiel

Seasonality of the abundance and reproduction of the clausocalanid copepods of the northern Gulf of Aqaba (Red Sea)

Manuscript

Sampling was done by myself and the fourth author, experiments were carried out by myself. I sorted and identified the samples. The concept of the manuscript was developed by myself and the second author. The design of the experimental work was developed by the second author. I wrote the manuscript including improving suggestions of the second author.

further publications written during my thesis

B. Niehoff, S.B. Schnack-Schiel, M. Brichta, **A. Cornils**, R. Alheit

Reproductive activity of two dominant Antarctic copepod species, *Metridia gerlachei* and *Ctenocalanus citer*, in late autumn in the eastern Bellingshausen Sea .

published in: Polar Biology (2002) 25: 583 - 590 .

I helped with the sampling and sorting of the incubated females.

U. Sommer, U.G. Berninger, R. Böttger-Schnack, **A. Cornils**, W. Hagen, T. Hansen, . Al-Najjar, A.F. Post, S.B. Schnack-Schiel, H. Stibor, D. Stübing, S. Wickham

Grazing during early spring in the Gulf of Aqaba and the northern Red Sea

published in: Marine Ecology Progress Series (2001) 239: 251 - 261.

I sorted and identified the mesozooplankton for abundance used for this publication.

A. Cornils, S.B. Schnack-Schiel, W. Hagen, M. Dowidar, N. Stambler, O. Plähn, C. Richter

Spatial and temporal distribution of mesozooplankton in the Gulf of Aqaba and the northern Red Sea in February/March 1999

accepted in: Journal of Plankton Research

Sampling was conducted by the second, third, fourth and last author. Hydrographic data were provided by the sixth author, chlorophyll *a* by the fifth author. The samples were sorted and identified by myself and students. The concept of the study was developed by the second author and myself. My diploma thesis includes parts of this study. I wrote the manuscript.

6.1 Publication I

Manuscript

THE SEASONAL CYCLE OF MESOZOOPLANKTON IN THE NORTHERN GULF OF AQABA (RED SEA)

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Abstract

Mesozooplankton in the upper 100 m of the northern Gulf of Aqaba was collected by vertical hauls over a period of 22 months between February 2002 and December 2003. Overall, abundance ranged between 245 and 3065 ind. m^{-3}. Highest densities in 2002 were recorded in spring (March/April) and in autumn (October/November), while several peaks were revealed in 2003 with maximum abundance in early summer (June/July). Copepods dominated the mesozooplankton community during the whole sampling period (mean 79%). Other taxa were gastropods and bivalve larvae, appendicularians and chaetognaths. Within the copepods, calanoids were predominant throughout the sampling period (on average 62%). Cyclopoid and poecilostomatoid copepods ranked second and third, whereas harpacticoids occurred only in low abundance. Within the calanoid copepods, small-sized taxa were abundant, belonging to the families of Clausocalanidae, Paracalanidae, Calocalanidae, Acartiidae and Mecynoceridae. They accounted together between 78 and 98% of the calanoids. Most taxa with high densities during the time of deep vertical mixing showed a positive significant correlation to the annual cycle of temperature.

Keywords: Mesozooplankton, Calanoida, annual cycle, Gulf of Aqaba, epipelagic

Introduction

Unlike the Red Sea and other subtropical marine systems, the Gulf of Aqaba features a strong hydrographical and biological seasonality (Reiss and Hottinger 1984, Wolf-Vecht et al. 1992, Badran 2001). Thermal stratification dominates the water column with a shallow mixed surface layer due to wind mixing throughout the summer. In late autumn, cooling of the sea surface temperature deepens the mixed layer, which reaches its maximum depth (>250 m depth) in early spring (e.g. Klinker et al. 1978, Paldor and Anati 1979, Manasreh et al. 2004). The mixing depth is directly linked to variations in the net heat flux (Genin et al. 1995). The convective mixing in winter is probably the most important source of nutrient transport into the euphotic zone (Klinker et al. 1978, Badran and Foster 1998). During summer stratification, the surface layer becomes depleted of nutrients (Reiss and Hottinger 1984, Lindell and Post 1995, Badran 2001). Light penetration is high throughout the year which results in the formation of a vernal chlorophyll maximum of phytoplankton down to a depth of more than 300 m (Kimor and Golandsky 1977, Winter et al. 1980).

The changes in the physical and chemical hydrography therefore induce a strong seasonality of chlorophyll *a* concentration (Genin et al. 1995, Lindell and Post 1995, Labiosa et al. 2003, Sokoletsky et al. 2004) and primary production (Levanon- Spanier et al. 1979). The trophic state of the Gulf of Aqaba exhibits rather meso-oligotrophic characteristics compared with other subtropical oceans at similar water temperatures and light regime (Sargasso Sea, Mediterranean Sea) despite its nutrient depleted seas in summer (Carlson et al. 1994, Labiosa et al. 2003). Compared to other oligotrophic seas the phytoplankton of the Gulf of Aqaba is generally dominated by ultraphytoplankton (Li 1995, Lindell and Post 1995), particularly cyanobacteria and prochlorophytes, and small (<8 μm) eukaryotic phytoplankton. After the onset of stratification due to the warming of the air and sea surface temperatures in spring, usually a phytoplankton bloom dominated by diatoms develops (Kimor and Golandsky 1977). The magnitude of the bloom is strongly correlated with the mixing depth of the previous winter (Genin et al. 1995) and often dominated by *Synechococcus* (Lindell and Post 1995). In winter, eukaryotic phytoplankton dominates the water column (Kimor and Golandsky 1977, Reiss and Hottinger 1984) while in summer prochlorophytes are predominant.

In most subtropical and tropical parts of the world's oceans copepods are the predominant taxa of the mesozooplankton, where they comprise about 75% of the total community (e.g.

Deevey and Brooks 1977, Webber and Roff 1995a). Subtropical and tropical regions are also known to be inhabited by a diverse assemblage of species (Deevey and Brooks 1977, Madhupratap and Haridas 1986). In comparison to its adjacent seas, the Eastern Mediterranean and the Red Sea, the diversity in the Gulf of Aqaba is low. In the eastern Mediterranean around 100 copepod species were found (e.g. Lakkis 1986, Siokou-Frangou et al. 1997), while in the southern and central Red Sea about 158 species were described (Halim 1969). In contrast in the northern Red Sea and the Gulf of Aqaba only 73 copepod species (Almeida Prado-Por 1985, 1990, Abd El-Rahman 1999, Abd El-Rahman 1999, Böttger-Schnack et al. 2001) have been discovered. Reasons for the impoverishment from the Indian Ocean to the Gulf of Aqaba are the seclusion of the Red Sea and the Gulf due to shallow sills and the resulting high salinity in the evaporative basins.

In subtropical oligotrophic marine environments, small sized copepods are often predominant (Deevey and Brooks 1977, Webber and Roff 1995a, Mazzocchi et al. 1997, Hopcroft et al. 1998, Calbet et al. 2001). The dominance of small sized species might be explained by the higher proportion of small phytoplankton and protistan diet on which the copepods are known to feed rather unselectively (e.g. Poulet 1976, 1978, Cowles 1979, Huntley 1981). Many of the species in the subtropical oceans also have short life cycles and can produce four to five generations each year (Raymont 1983).

Despite its importance in the pelagic food web, the information on the mesozooplankton of the Gulf of Aqaba is still fragmentary. This study is the first attempt to study the seasonal variation in the mesozooplankton and, especially the copepod community of the northern Gulf of Aqaba. Previous studies focused either on the vertical distribution (Schmidt 1973, Almeida Prado-Por 1983, 1990, Cornils et al. in press) or on the geographical distribution along the Gulf of Aqaba (Almeida Prado-Por 1985, Echelman and Fishelson 1990). But most investigations described the taxonomic structure (Halim 1969, Almeida Prado-Por and Por 1981, Echelman and Fishelson 1990, Abd El-Rahman 1999, Al-Najjar 2000, Böttger-Schnack et al. 2001). The annual cycle and succession of abundant copepod taxa will be investigated as well as their possible response to the annual cycle of environmental parameters.

Study Side

The Gulf of Aqaba is the north-eastern extension of the Red Sea, separated by the narrow and shallow Straits of Tiran (<260 m sill depth). The semi-enclosed basin is a deep (max. depth <1800 m) and narrow basin (180 km long, 14 - 26 km wide) surrounded by desert mountains with little input of fresh water or nutrients. The climate is arid with a net evaporation of 0.5 - 1 cm day^{-1} (Assaf and Kessler 1976). The circulation in the Gulf of Aqaba is characterised by a series of permanent gyres orientated along its main axis (Berman et al. 2000). Coastal currents on the eastern side run southwards during winter and northwards during summer at least in the upper 50 m. The reversal of the currents occurs due to the hydrographic changes (Berman et al. 2000). Tides are generally semi-diurnal with maximal sea level differences of 1 m (Monismith and Genin 2004). Despite the mainly northern winds, there is continuous inflow of low-salinity surface water from the Red Sea, while a deeper countercurrent returns to the Red Sea (Klinker et al. 1978, Plähn et al. 2002). The salinity of the Gulf of Aqaba is high (40 - 41). The sea surface temperature ranges between 20 and 27°C with temperatures above 20°C even in deep waters. In contrast to the Red Sea, there is no oxygen minimum layer, the oxygen saturation varies between 3.75 - 6.0 ml L^{-1}.

Methods

The mesozooplankton sampling was conducted at N 29°27.868, E 34°57.872 near the tip of the Gulf of Aqaba (Fig. 9) off the Marine Science Station in Aqaba (Jordan). A total of 46 samples were collected over a period of 22 months from late February 2002 until early December 2003 during the daytime between 9 a.m. and 3 p.m.. Replicate samples could not be obtained due to logistical reasons. Samples were taken on a monthly basis with additional sampling in spring 2002 (March/April, 17 samples), autumn 2002 (September - November, 10 samples) and autumn 2003 (October - December, 9 samples). Sampling in May, August and December 2002 and February and September 2003 had to be omitted due to bad weather conditions. Vertical hauls were carried out with a Nansen net (0.4 m^2 aperture, 200 μm mesh size) between 100 m and the surface. The filtered volume was expressed by means of a flowmeter; the towing speed was 1 m s^{-1}. The samples were preserved in 4% borax-buffered formaldehyde seawater solution. For further processing the samples were divided with a Folsom-Splitter. The copepods were counted from a 0.25 aliquot of each sample. Rare taxa (i.e. groups with less than 40 specimens per subsample) were counted from the entire sample. Copepod naupliar stages were not further considered as they were not sampled quantitatively due to the relatively large mesh size (200 μm). The taxa gastropods included mainly larvae stages of benthic species but also a few pelagic pteropods. Mean abundances are given as geometric means.

Environmental parameters such as temperature, salinity and chlorophyll *a* were collected on a monthly basis within the framework of Jordan's National Monitoring. The temperature and salinity profiles were taken of the upper 400 m. Water samples for chlorophyll *a* measurements were collected with 5 L Niskin bottles from the upper 400 m of the water column (0, 25, 50, 75, 100, 125, 150, 200, 300, 400 m). Samples were filtered on cellulose acetate filter paper, transferred to light-shaded glass tubes with 10 ml of 90% acetone, homogenised and extracted for 24 h. Chlorophyll a measurements were done with a spectrofluorometer (SFM 25 of BIO-TEK KONTRON Instruments).

Multdimensional Scaling (MDS) was performed in order to explore similarities between the sampled seasons. The analysis was performed with the PRIMER5 (Plymouth Routines in Multivariate Ecological Research) program developed at Plymouth Marine Laboratory. The number of samples was reduced by using the geometrical mean for all month with frequent sampling. A similarity matrix using fourth root-transformation and the Bray-Curtis index was established. From this matrix one MDS Plot was produced sorted by the factors year and month. The rank of species was also calculated with special features of the PRIMER5 program. Diversity was calculated with the Shannon Index (Heip and Engels 1974).

Correlation between temperature and chlorophyll *a* and the abundance of copepods was analysed using the non-parametric Kendall Correlation test. With the number of samples $n<40$ the sum of ranks (S) was used as the significance criterion.

Results

Environmental parameters

The annual cycle of temperature in the upper 400 m of the northern Gulf of Aqaba reveals deep vertical mixing in winter (January - April 2002, February - April 2003) and stratification with a mixed surface layer during the remaining months (Fig. 10). The sea surface temperature varied between 21.3°C in February 2002 and 26.7°C in August 2003. In both years, sea surface temperature was highest in August. At the depth of 400 m, the temperature hardly changed during the sampling period (21.02 - 21.54°C). The salinity ranged from 40.21 to 40.61 at the sea surface and from 40.35 - 40.53 at 400 m. The annual profile of salinity in Fig. 10 showed lowest values in early summer between 0 and 150 m. The chlorophyll *a* profiles varied slightly between 2002 and 2003. A deep chlorophyll *a* maximum was noticed between 50 - 100 m in summer for both years, which was more pronounced in 2002. Vertical mixing occurred during winter with chlorophyll *a* concentrations greater than 0.1 μg L^{-1} down to 300 m (December - February). After the start of stratification in March 2003 a bloom developed within the upper 75 m persisting until May. This maximum in the upper layers was not visible in 2002.

Mesozooplankton

Copepods were by far the most abundant taxon of the total mesozooplankton contributing between 58 and 92% of the total specimens throughout the year (mean 79%, Table 10).

Appendicularians ranked second in abundance (0.03 - 16.5%) followed by chaetognaths (1.1 - 5.5%). A considerable part of the community was comprised of meroplanktonic larvae (3 - 30%), mainly gastropod (1.2 - 25.3%) and bivalve larvae (0.1 - 14.2%).

The total concentrations of mesozooplankton varied greatly between months but also between the two years studied (Fig. 11). In 2002, the abundance of the mesozooplankton was relatively low (237 - 2491 ind. m^{-3}) and showed a maximum in spring (March) and autumn (October/November) coinciding with the strengthening and decay of the thermal stratification. In 2003, the abundance was generally higher (943 - 3065 ind. m^{-3}) with two peaks, one in April and and one in June. During the periods of frequent sampling the samples showed a high fluctuation, especially evident in March and April 2002 (Fig. 11).

The seasonal pattern of the abundant holoplankton (copepods, appendicularians, chaetognaths) was significantly different between the taxa. Due to the high abundance of the copepods, their distribution pattern reflected that of the total mesozooplankton (Figs. 10, 11) with highest densities in spring 2003 and lowest in spring/summer 2002. Appendicularians, which ranked second in abundance, occurred in both years in higher numbers in summer and autumn, more pronounced in 2002 than in 2003 (Fig. 3). Chaetognaths showed great differences in their seasonal cycles with peak abundances in autumn (October/November) in 2002 and in spring (April-June) in 2003 (Fig. 11).

In 2002, the two abundant meroplankton taxa (gastropods and bivalves) occurred in peak abundance in winter and autumn. In 2003, no clear seasonal pattern was obvious (Fig. 11).

Copepods

Due to the overwhelming numerical dominance of copepods throughout the year (between 58 and 92% of the total mesozooplankton abundance, Table 10), they are considered separately. The calanoids contributed the largest fraction (62%) followed by cyclopoids and poecilostomatoids (23 and 12%, respectively, Table 11). Within the calanoids, 15 families and 22 genera were identified, only the family Scolecitrichidae could not further separated.

Six calanoid genera dominated, contributing 69% of the total copepod community: *Clausocalanus* (24%), *Paracalanus* (13%), *Calocalanus* (13%), *Ctenocalanus* (10%), *Acartia* (5%) and *Mecynocera* (4%). All other genera accounted for less than <1% (Table 11). The six dominant genera occurred regularly throughout the investigation period, however, in different dominance, which is most pronounced in *Acartia*, *Ctenocalanus* and *Mecynocera* (Fig. 12).

In both years, the calanoids could be roughly separated according to the time of their maximal occurrence but the peak differed between years for most genera. In 2002, *Clausocalanus*, *Ctenocalanus*, *Paracalanus*, *Acrocalanus*, *Parvocalanus* and *Centropages* occurred in high densities in winter/early spring and autumn, and hence, during the period of deep vertical mixing (Fig. 13, significant for *Ctenocalanus*, *Paracalanus*, *Parvocalanus*; paired t-test, $p<0.03$). In 2003, this seasonal pattern was less clear, and *Clausocalanus* and *Acrocalanus* also showed high abundances in summer. In contrast, *Calocalanus*, *Mecynocera*, *Acartia*, *Lucicutia* and *Candacia* occurred in higher numbers from late spring to autumn and hence, during the time of thermal stratification (Fig. 6, paired t-test, $p<0.03$). The abundance of most genera was significantly higher in 2003 than in 2002 (Table xx).

The remaining calanoid copepods with a mean share of less than 0.2% could also be grouped according to their appearances during the study period. *Calanopia*, *Rhincalanus*, *Euchaeta*, *Nannocalanus*, *Undinula* and *Pontellina* occurred mainly during the vertical mixing period in winter and early spring. *Temoropia*, *Pleuromamma*, *Mesocalanus* and the Scolecitrichidae had their highest densities in summer and autumn during the stratification period. *Pontella*, and *Haloptilus* occurred only sporadically in the samples.

Positive significant correlation (Kendall correlation) for calanoid taxa with temperature was found only for taxa with high abundance in autumn; *Calocalanus* ($S = 60$; $p<0.03$), *Mecynocera* ($S = 94$; $p<0.005$), *Acartia* ($S = 76$; $p<0.005$) and *Lucicutia* ($S = 64$; $p<0.01$). Inverse significant relationships were found for *Ctenocalanus* ($S = -74$; $p<0.005$) and *Parvocalanus* ($S = -50$; $p<0.05$) which occurred mainly in spring during times of low temperatures. Low positive correlation was also found between salinity and abundance for *Paracalanus* ($S = 42$, $p<0.1$), *Acartia* ($S = 52$; $p<0.05$) and *Centropages* ($S = 64$; $p<0.05$), and an inverse relationship for *Ctenocalanus* ($S = -38$; $p<0.1$). However, no significant correlations were revealed between the abundance of calanoid genera and the chlorophyll *a* concentration.

The non-calanoid copepods were sorted into five taxa (Table 11). The cyclopoids were represented by the genus *Oithona*. The poecilostomatoids were separated into three taxa: the oncaeids (mainly *Oncaea*), corycaeids (mainly *Farranula* spp.) and sapphirinids (mainly *Sapphirina*). Oncaeids and corycaeids had a share of 4.6 and 5.6%, respectively, of the total copepod abundance. The sapphirinids occurred only in low abundance contributing less than 0.1% to the total copepod community. Harpacticoids were found in low densities (7 ind. m^{-3}) with a share of less than 0.1%. As in the calanoids, the abundance differed greatly between the two years studied (Fig. 17). In 2002, all taxa seem to occur in higher numbers during the deep vertical mixing period while in 2003, the taxa were found also in high densities during the time of the stratification of the water column. Only the corycaeids were significantly correlated to the temperature distribution ($S = 62$, $p<0.03$), but not to salinity.

Calculations of similarities between the sampling months of all copepods revealed that the samples of August to December were grouped very closely together while summer months June and July varied greatly between the years (Fig. 16). This difference is probably due to the high abundance found for some taxa in late June 2003, which does not coincide with the results of 2002. Due to the high numbers of many taxa in January 2003, this month is closely related to June and July 2003. Spring months were partly grouped (February to May).

The diversity remained low throughout the investigation period (Shannon index H' = 2.603

- 3.238). The calculation of taxa rank for the total copepod community showed that the copepod community in both years was dominated by a combination of 10 taxa, which added up to more than 95% (Fig. **??**).

Discussion

The investigation period included 22 months, which was clearly too short to detect interannual variability in the seasonal pattern of dominant mesozooplankton taxa. However, the remarkable difference observed between the two years studied, can be discussed in comparison with earlier investigations in the northern Gulf of Aqaba, which also revealed a great variation of the time of maximal mesozooplankton abundance. Farstey et al. (2002) studied the mesozooplankton in the whole water column (down to 400 m) in northern Gulf of Aqaba in 1991 and 1992 and found also great interannual variations in the abundance of the mesozooplankton.

Other studies reported peak abundance of mesozooplankton in summer (Al-Najjar 2000, Farstey et al. 2002), in early spring (Al-Najjar 2000, Almeida Prado-Por 1983), and for the surface mesozooplankton also in winter (Echelman and Fishelson 1990a, 1990b, Khalil and Abd El-Rahman 1997). Such great differences are also known from other subtropical areas (e.g. Sargasso Sea: Deevey and Brooks 1977, NW Mediterranean: Calbet et al. 2001) whereas in the Saronikos Gulf in the Eastern Mediterranean the annual cycle seemed to be repeatable (Siokou-Frangou 1996).

Temperature, salinity and food availability can strongly influence the occurrence and distribution of the zooplankton (e.g. Webber and Roff 1995b, Christou 1996). In this study, the environmental parameters temperature and salinity showed a strong seasonal pattern, whichdid not differ greatly between the two years (see Fig. 10). In contrast, the total abundance as well as the time of maximal occurrence of most mesozooplankton taxa did vary between the two years (see Figs. 13, 14). However, most copepod genera with peak abundances during thermal stratification of the water column (*Calocalanus*, *Mecynocera*, *Acartia* and *Lucicutia*) were positively while *Ctenocalanus* and *Parvocalanus*, two taxa with peak occurrence during vertical mixing were negatively correlated to the annual temperature changes. A correlation between the chlorophyll *a* concentration and the abundance of the different mesozooplankton taxa could not be established. This result is not surprisingly, as many species found in this study do not feed exclusive on phytoplankton, but are known to feed on a great variety of both autotrophic and heterotrophic organisms (e.g. Kleppel 1993), and a correlation with particulate organic matter would instead mirror the available food much better. Although there was no significant correlation between the chlorophyll *a* concentration and the abundance of any copepod taxon, the chlorophyll *a* distribution in 2003 might explain the high densities of some taxa in summer 2003. In contrast to 2002, high chlorophyll *a* values were found in spring 2003 during vertical mixing, indicating a phytoplankton bloom. The heterotrophic protists respond to the changes in the autotrophic phytoplankton (Kimor and Golandsky-Baras 1981) and in consequence the copepods. Hence, the summer maximum might be a response to this bloom.

It also has to be kept in mind, that the seasonal cycle has been shown for most taxa in terms of genera. The irregular seasonal pattern obtained can perhaps partly be explained by the differences in the seasonal cycle of the species combined. Great differences in their seasonal pattern are also evident in e.g. the family Paracalanidae: the four genera (*Acrocalanus*, *Paracalanus*, *Parvocalanus*, *Calocalanus*) found in the northern Gulf of Aqaba showed considerably different annual cycles (Figs. 12, 13). Different seasonal cycles for the *Clausocalanus* species have been described in the Mediterranean by Mazzocchi and Ribera D'Alcala (1995) and Peralba and Mazzocchi (2004). Copepods outnumbered all other taxa throughout the sampling period. In most regions of the world's oceans they are dominating the mesozooplankton (e.g. Longhurst 1985). In the upper 100 m they contribute between 70 and 80% to the total mesozooplankton in e.g. the SE Arabian Sea (Madhupratap and Haridas 1990), the Gulf of Naples (Mazzocchi and Ribera d'Alcala 1995) and the Sargasso Sea (Deevey 1971). In the northern Gulf of Aqaba, copepods have been found to make up 79 - 95% (Al-Najjar 2000, Cornils et al. in press) Recent investigations of Paffenhöfer and Mazzocchi (2003) have shown that the abundance of epipelagic copepods is about 10-fold higher when a smaller mesh size is used (63 μm vs. 200 μm). Therefore, sampling with 200 μm mesh size results in catching mainly the later copepodite stages and the adults of the smaller species. Since the young copepodite stages (CI-CIII) of the small species have rarely been found throughout the sampling period. Hence, only CIV, CV and adults were further considered in this study.

Due to the relatively large mesh size of 200 μm, calanoids dominated the copepod community throughout the investigation period. Compared to other subtropical regions (e.g. Sargasso Sea: Deevey and Brooks 1977, Arabian Sea: Smith et al. 1998), the diversity of all copepods in the Gulf of Aqaba was low, hardly changing throughout the investigation period (Shannon index H' = 2.603 - 3.238). A probably reason for the low diversity in the Gulf is, that the immigration of plankton organisms is restricted by several parameters: (i) the shallow Straits of Tiran (250 m), (ii) high temperatures at greater depths (>20°C), and (iii) high salinities (>40). Thus, mainly epipelagic plankton species with a tolerance of high salinities are able to survive in this basin, which explains the reduction of the number of plankton species from the Indian Ocean to the northern Red Sea and the Gulf of Aqaba (Halim 1969). The mainly epipelagic species of the Gulf of Aqaba are throughout most of the year confined to the upper 100 m of the water column (Almeida Prado-Por 1983, 1990, Farstey et al. 2002). Hence, vertical sampling of the upper 100 m should be sufficient to get a representative insight of the planktonic community.

The calanoid copepods were predominated by small sized taxa (*Clausocalanus*, *Ctenocalanus*, *Paracalanus*, *Calocalanus*, *Mecynocera*, *Oithona* and oncaeids). These taxa have been described as abundant in many other subtropical regions, e.g. in the Caribbean (Deevey 1971, Webber and Roff 1995a) or in the Mediterranean (Christou 1998, Siokou-Frangou 1996). Among the small sized calanoid species, the clausocalanids were particularly dominant in the northern Gulf of Aqaba (*Clausocalanus* spp., *Ctenocalanus vanus*). The genus *Clausocalanus* has been described as one of the widespread taxon (Frost and Fleminger 1968), and are often predominant in subtropical regions, e.g. in the Sargasso Sea (Deevey 1971, Schulz 1986), in the Red Sea (Weikert, 1982), in the Caribbean (Webber and Roff 1995a), off the Brazilian shelf (Lopez et al. 1999) and in the Mediterranean (Mazzocchi and Ribera D'Alcala 1995, Peralba and Mazzocchi 2004). The contribution of *Clausocalanus* spp. of the total copepod community varies e.g. in the Carribean and the Mediterranean between 14 and 40% (Webber and Roff 1995a, Siokou-Frangou et al. 1997), whereas *Ctenocalanus vanus* has a lower relative abundance (<5%).

Small calanoid copepods have been thought to be mainly herbivorous, i.e. feeding preferentially on phytoplankton. Under this assumption, Almeida Prado-Por (1990) described the calanoid copepod community in the Gulf of Aqaba. However, this view has to be revised since it has been shown that microzooplankton plays an important role in the nutrition of copepods, especially in oligotrophic regions where the primary producers are dominated by ultraplankton (review by Kleppel 1993). The diet of many calanoids is diverse and reflects the natural protist community (e.g. Kleppel 1993). Therefore, it is presumed that the copepods are able to respond to the variation of the food environment (Poulet 1976, 1978).

Feeding experiments with dominant copepods of the Gulf of Aqaba, *Clausocalanus farrani*, *Clausocalanus furcatus*, *Ctenocalanus vanus*, *Mecynocera clausi* and *Acartia negligens* have also shown a broad pattern of nutrition (Cornils et al. in press, unpubl. Data), and coincide with results obtained for *Paracalanus* spp. (Paffenhöfer 1984), and *Oithona* spp. and *Parvocalanus crassirostris* (Calbet et al. 2000). *Paracalanus*, *Parvocalanus* and *Oithona* are also dominant members of the mesozooplankton in the Gulf of Aqaba and hence, it can be assumed that the majority of the copepods are well adapted to the low primary production situation, and are opportunistic feeders. Hence, their seasonal cycles are probably more related to their tolerance of abiotic factors such as temperature. Apart from the predominant copepods, other taxa contributed also considerably to the abundance, like appendicularians, chaetognaths and molluscs. The appendicularians, the second most abundant holoplankton group, occurred in comparable abundance as known from the Red Sea (Böttger-Schnack 1995) and earlier investigations in the northern Gulf of Aqaba (19 - 145 ind. m^{-3}; Fenaux 1979). In the later study, appendicularians occurred in maximal abundance in June and August (Fenaux 1979), which coincide only with the second year of our study. Chaetognaths ranked third in abundance in our study and the abundance found are comparable to those observed by Schmidt (1973), studying the mesozooplankton taxa in the northern Gulf of

Aqaba.

Meroplanktonic larvae occurred in relatively high numbers in the northern tip of the Gulf of Aqaba (e.g. Cornils et al. in press). During our investigation they contributed between 3 - 30% to the mesozooplankton community. The steep slopes of the Gulf of Aqaba result in a close proximity between offshore and coastal waters. The coastal regime is covered with coral reefs and a high diversity of benthic organisms (e.g. Loya 1972, Schuhmacher 1977). The coastal currents, semidiurnal tides and winds are capable of transposing a high amount of meroplankton to the offshore waters, and e.g. a strong correlation between the tidal currents and the distribution of meroplankton larvae could be observed by Belgrano and Dewarumez (1995).

Despite the enclosure of the Gulf of Aqaba due to the sill, endemic species have hardly been found in the pelagic waters of the Gulf of Aqaba so far (Almeida Prado-Por 1983, 1990, Böttger-Schnack 1988, 2001). Most species are either circumglobal or common in the Indian Ocean. This might be an indication for the constant inflow of surface water from the Red Sea which contributes new individuals to the copepod community. For future research, genetic investigations might give an insight into the populations of species of the Gulf of Aqaba compared to the same species in other seas.

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Tables and Figures

Table 10: Relative composition (%) of the mesozooplankton taxa.

	Taxa	Mean	Minimum	Maximum
Cnidaria	Medusae	0.18	0.01	1.32
	Siphonophora	0.11	0.00	1.81
Rotatoria	Rotatoria	<0.10	0.00	0.18
Plathelminthes	Plathelminthes	<0.10	0.00	0.05
Nemathelminthes	Pilidium Larvae	<0.10	0.00	0.48
Mollusca	Pteropoda/Gastropoda Larvae	4.86	1.18	25.33
	Bivalvia Larvae	3.09	0.07	14.24
	Cephalopoda juv.	<0.10	0.00	0.01
Polychaeta	Polychaeta Larvae	0.20	0.00	6.71
	Polychaeta Adults	<0.10	0.00	0.30
Crustacea	Cladocera (*Evadne tergestina*)	0.16	0.00	3.24
	Copepoda	78.76	58.19	92.39
	Ostracoda	0.17	0.00	2.93
	Euphausiacea	0.19	0.00	2.25
	Decapoda Larvae	<0.10	0.00	3.90
	Cirripedia Nauplii	<0.10	0.00	0.28
	Mysiidacea	0.05	0.00	1.53
	Isopoda	<0.10	0.00	0.11
	Amphipoda	<0.10	0.00	0.43
	Cumacea	<0.10	0.00	0.04
Chaetognatha	Chaetognatha	2.41	1.14	5.45
Tunicata	Appendicularia	2.50	0.03	16.47
	Salpa	0.19	0.00	3.09
Echinodermata	Juveniles	<0.10	0.00	0.59
	Larvae	0.23	0.00	8.54
Hemicordata	Actinotrocha Larvae	<0.10	0.00	0.19
	Bryozoa Larvae	<0.10	0.00	0.12
Chordata	*Branchiostoma* sp.	<0.10	0.00	0.03
	Fish Larvae	<0.10	0.00	1.49
	Fish Eggs	<0.10	0.00	0.83

Table 11: Relative abundance (%) of copepod taxa during the investigation period (taxonomy after Boltovskoy, 1999).

Order	Familiy	Taxa	Mean	Minimum	Maximum
Calanoida			**61.71**	**41.85**	**83.23**
	Calanidae	*Mesocalanus tenuicornis* (F)	<0.10	0.00	0.31
		Nannocalanus minor (F)	0.10	0.00	1.11
		Undinula vulgaris (F)	0.12	0.00	1.71
		Calanidae (CI - CV, M)	0.50	0.08	4.35
	Paracalanidae	*Acrocalanus* spp.	0.45	0.00	2.93
		Calocalanus spp.	12.83	3.64	38.71
		Paracalanus spp.	12.89	0.71	37.07
		Parvocalanus crassirostris	0.81	0.00	12.40
	Mecynoceridae	*Mecynocera clausi*	3.94	0.00	33.89
	Eucalanidae	*Rhincalanus nasutus*	<0.10	0.00	0.28
	Clausocalanidae	*Clausocalanus* spp. (CIV, CV, F, M)	23.72	6.61	52.14
		Ctenocalanus vanus (CIV, CV, F, M)	10.41	0.79	46.00
		Clausocalanidae (CI - CIII)	1.28	0.00	19.12
	Euchaetidae	*Euchaeta* spp.	0.13	0.00	1.58
	Scolecitrichidae	Scolecitrichidae	0.14	0.00	1.62
	Augaptilidae	*Haloptilus* sp.	<0.10	0.00	0.10
	Lucicutiidae	*Lucicutia* spp.	0.25	0.00	3.46
	Metridinidae	*Pleuromamma indica*	0.11	0.00	2.37
	Centropagidae	*Centropages* spp.	0.28	0.00	2.62
	Temoridae	*Temoropia mayumbiensis*	0.14	0.00	1.26
	Candaciidae	*Candacia* spp.	0.27	0.00	2.10
	Pontellidae	*Calanopia* spp.	<0.10	0.00	0.63
		Pontellina plumata	<0.10	0.00	0.10
		Pontella spp.	<0.10	0.00	0.29
	Acartiidae	*Acartia negligens*	5.14	0.65	24.73
Cyclopoida	**Oithonidae**	***Oithona* spp.**	**22.66**	**8.38**	**46.38**
Poecilostomatoida			**12.20**	**5.62**	**26.91**
	Oncaeidae		4.58	0.69	15.57
	Corycaeidae		5.60	0.53	18.14
	Sapphirinidae		<0.10	0.00	0.42
Harpacticoida			**<0.10**	**0.00**	**0.36**

F: female, M: male, CI-CV: copepodite stages

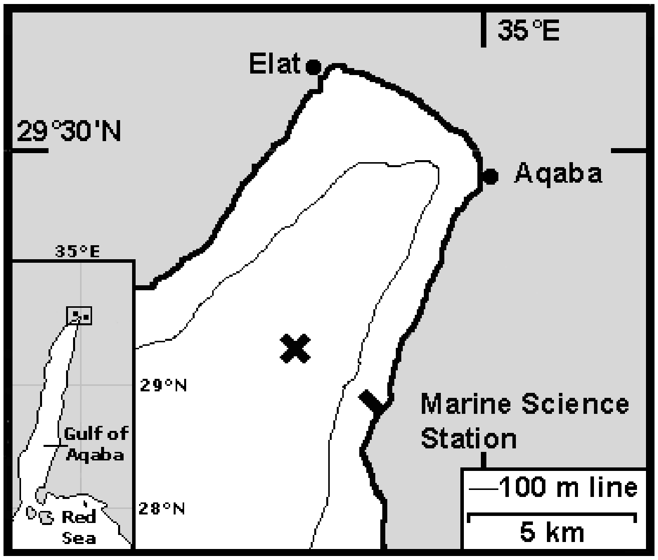

Figure 9: The Gulf of Aqaba with a detailed map of the sampling position (x).

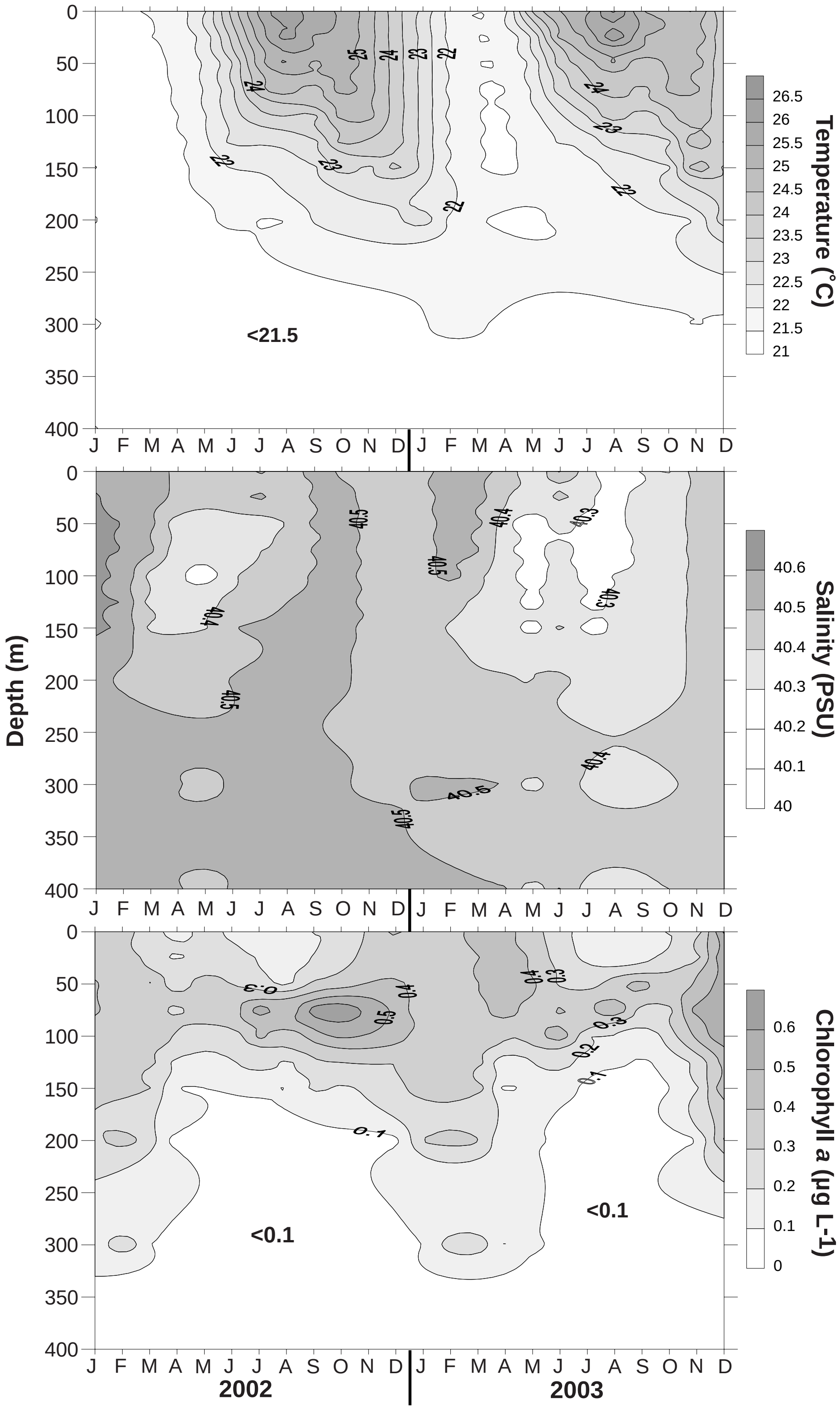

Figure 10: Temperature, salinity and chlorophyll *a* distribution at the sampling position in the Gulf of Aqaba during the years 2002 and 2003.

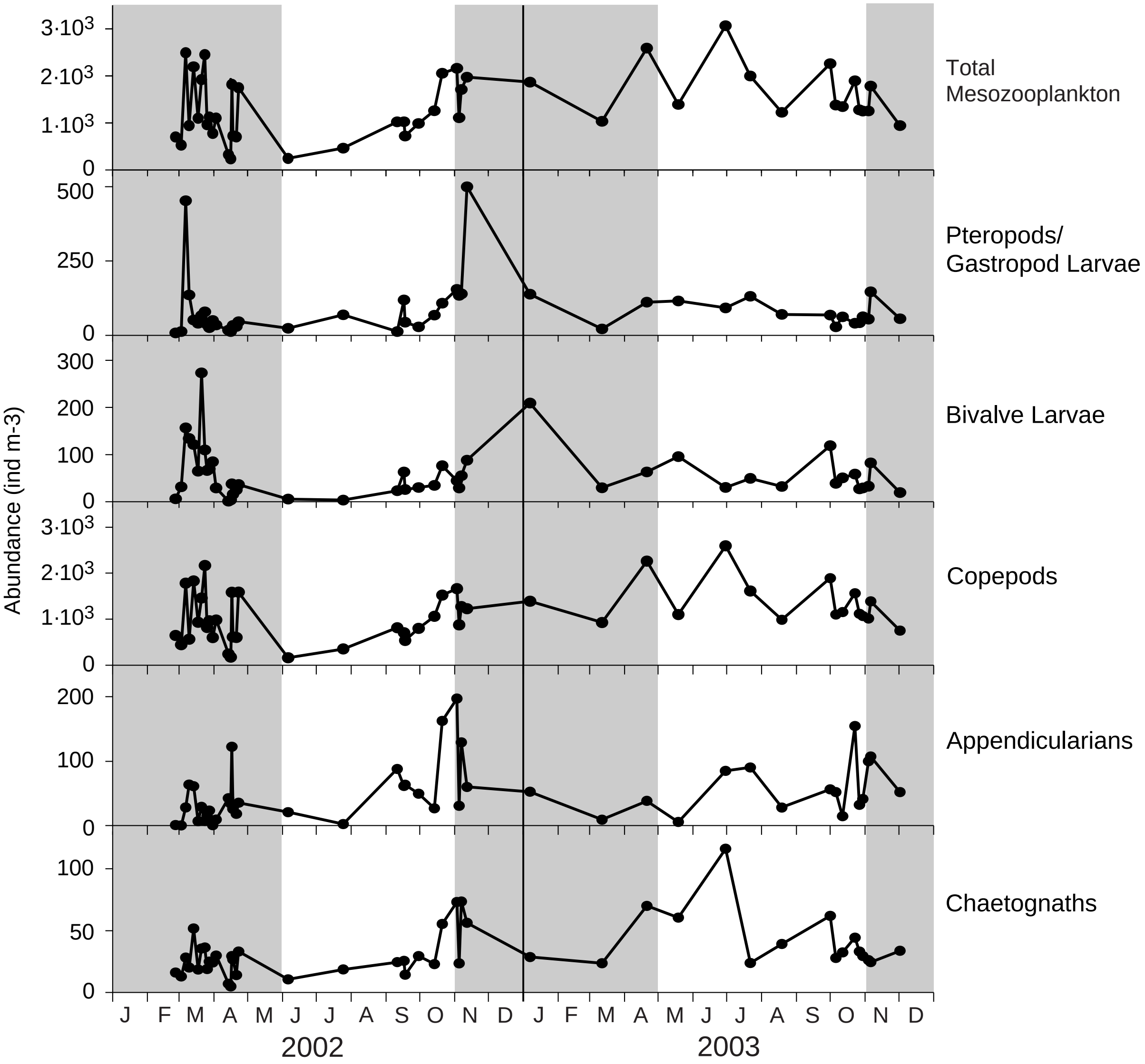

Figure 11: Seasonal abundance of the total mesozooplankton and selected groups of the holo- and meroplankton (grey areas: periods of vertical mixing).

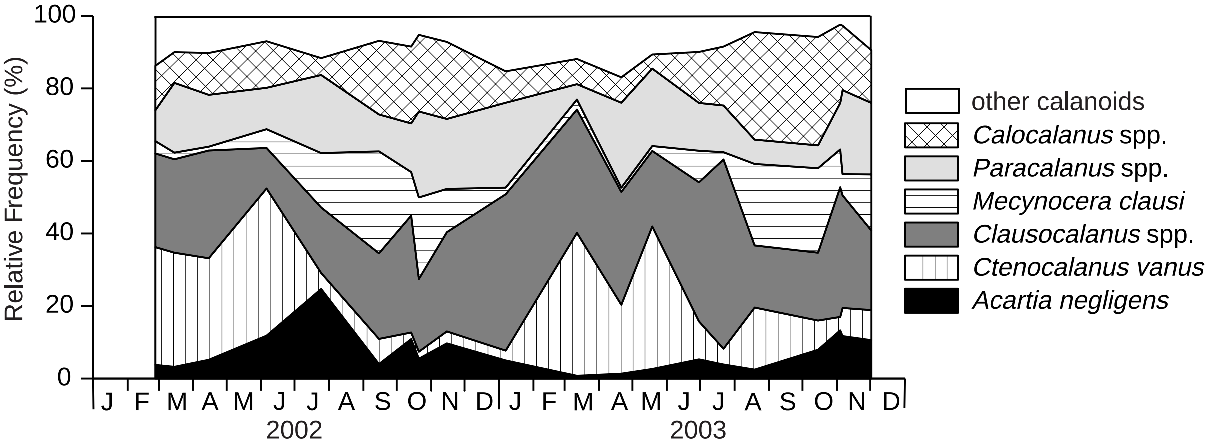

Figure 12: The relative abundance (%) of the calanoid copepods, displaying the major taxa.

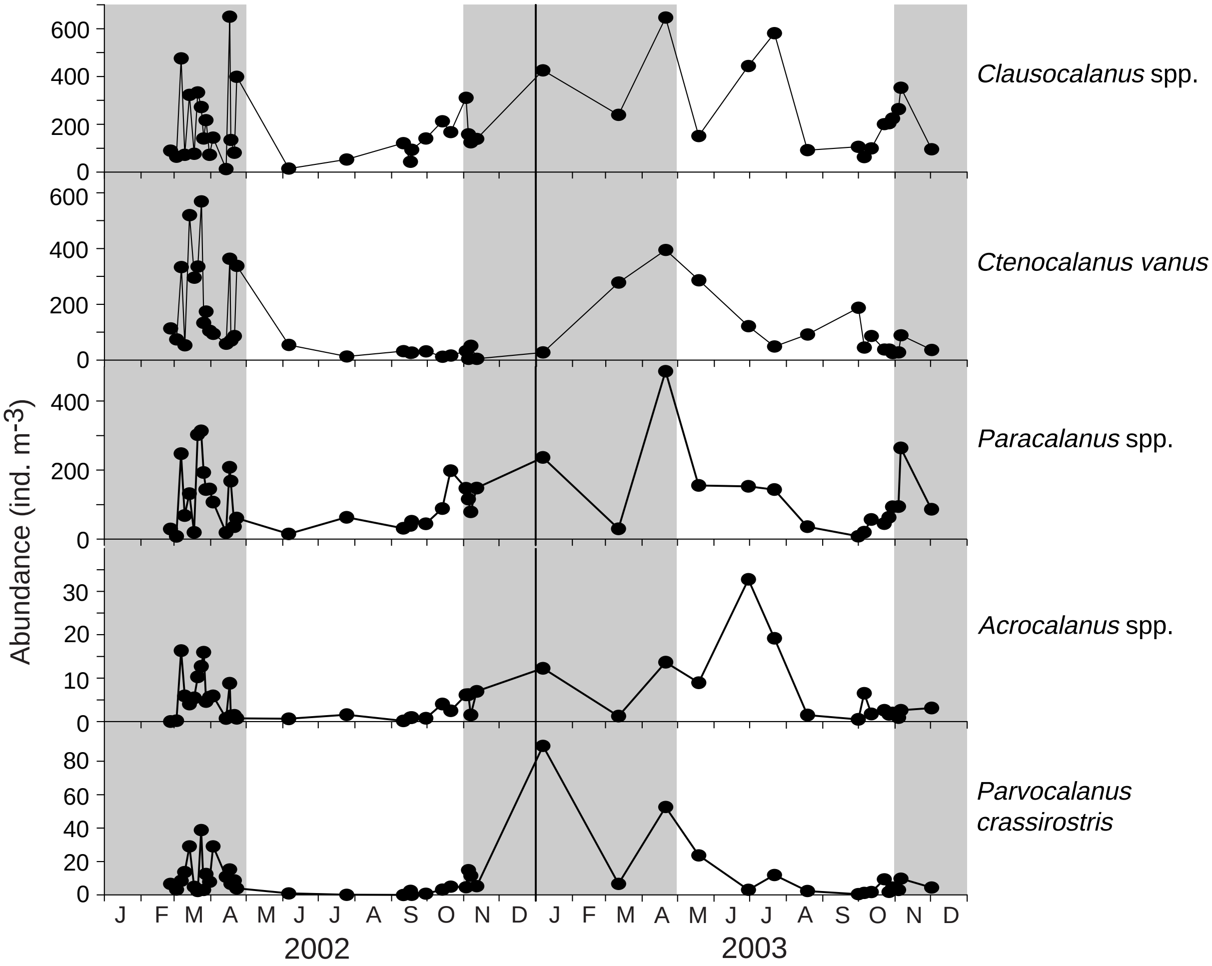

Figure 13: The seasonal cycle of calanoid taxa with higher density in spring and winter (grey areas: periods of vertical mixing).

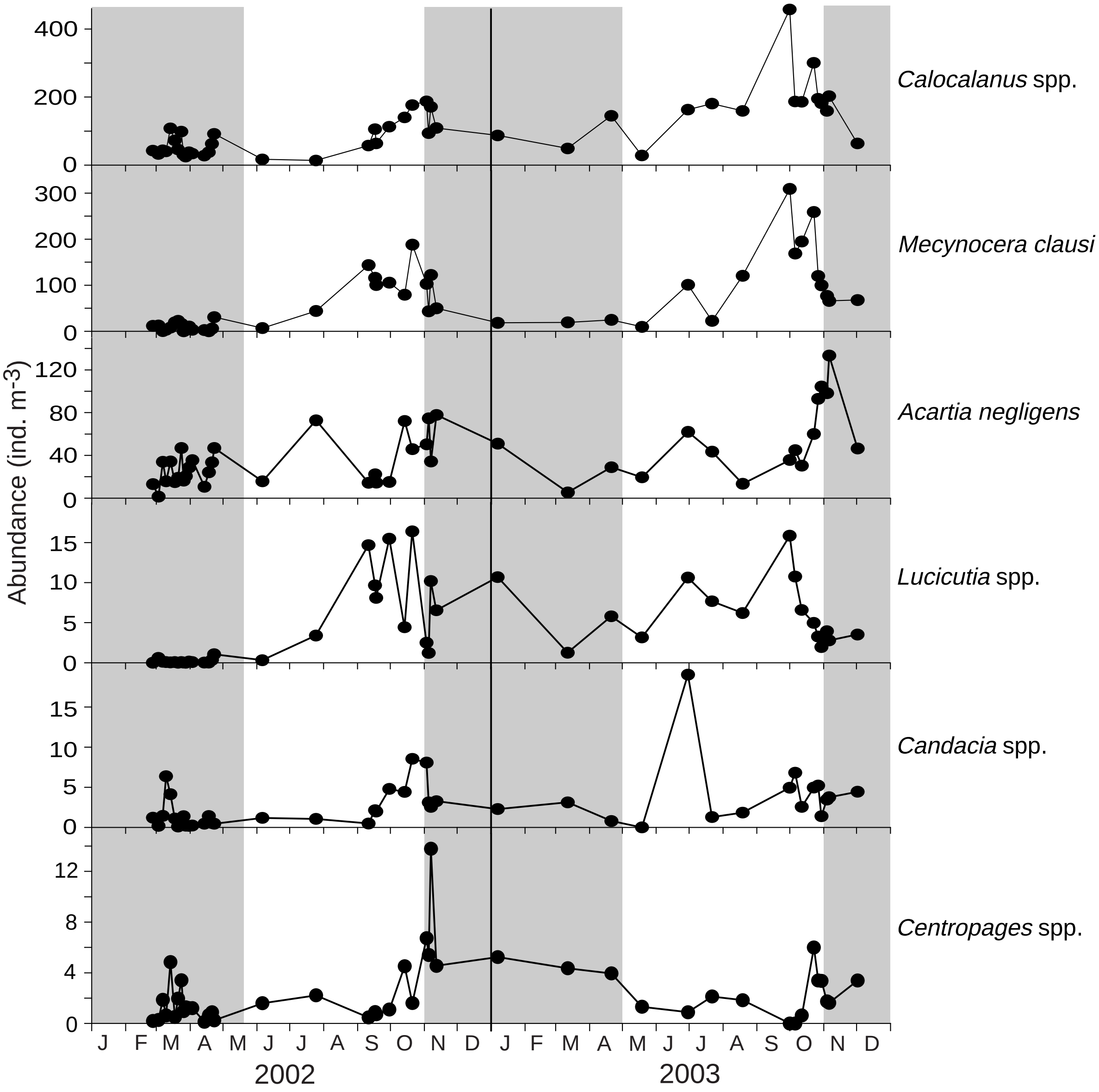

Figure 14: The seasonal cycle of calanoid taxa with higher density during autumn (grey areas: periods of vertical mixing).

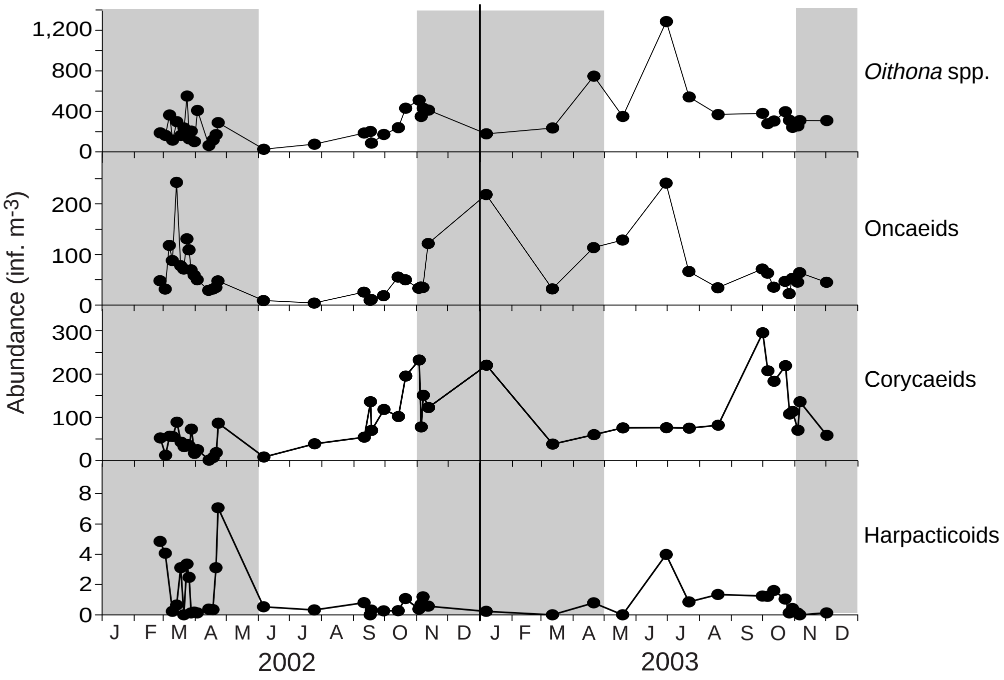

Figure 15: The seasonal abundance of cyclopoid copepods (grey areas: periods of vertical mixing).

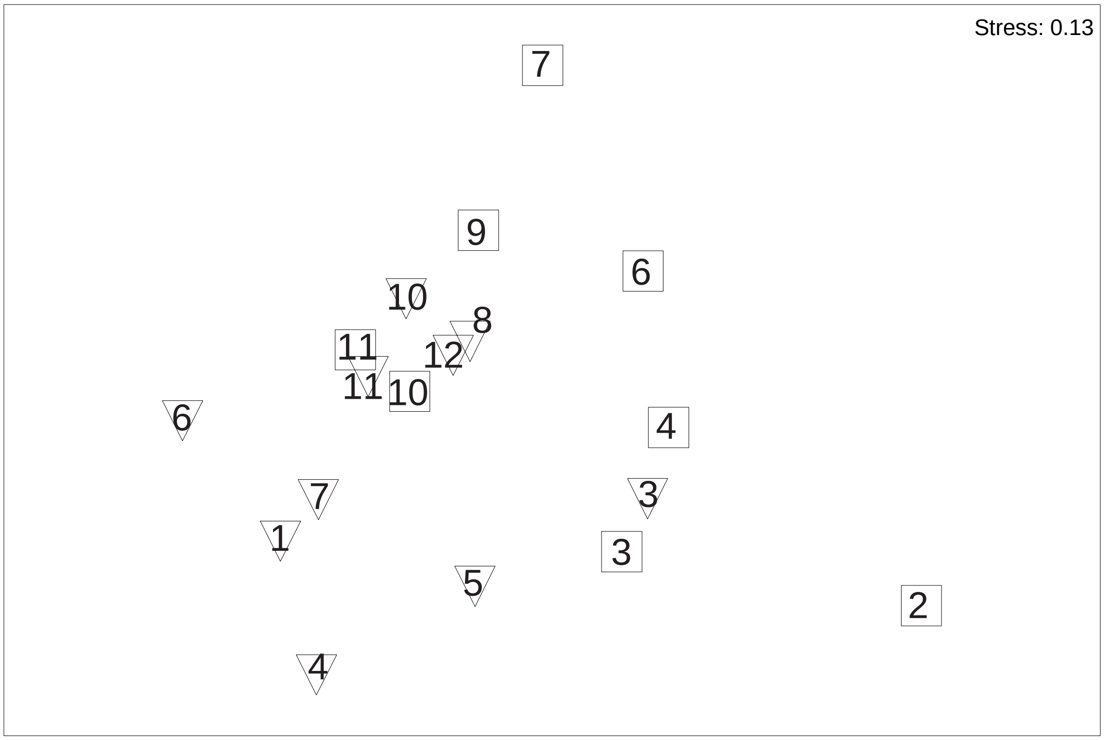

Figure 16: MDS Plot of the similarity between the sampling months for the copepod community (squares: samples 2002; triangles: samples 2003; the numbers 1-12 represent the sampling months).

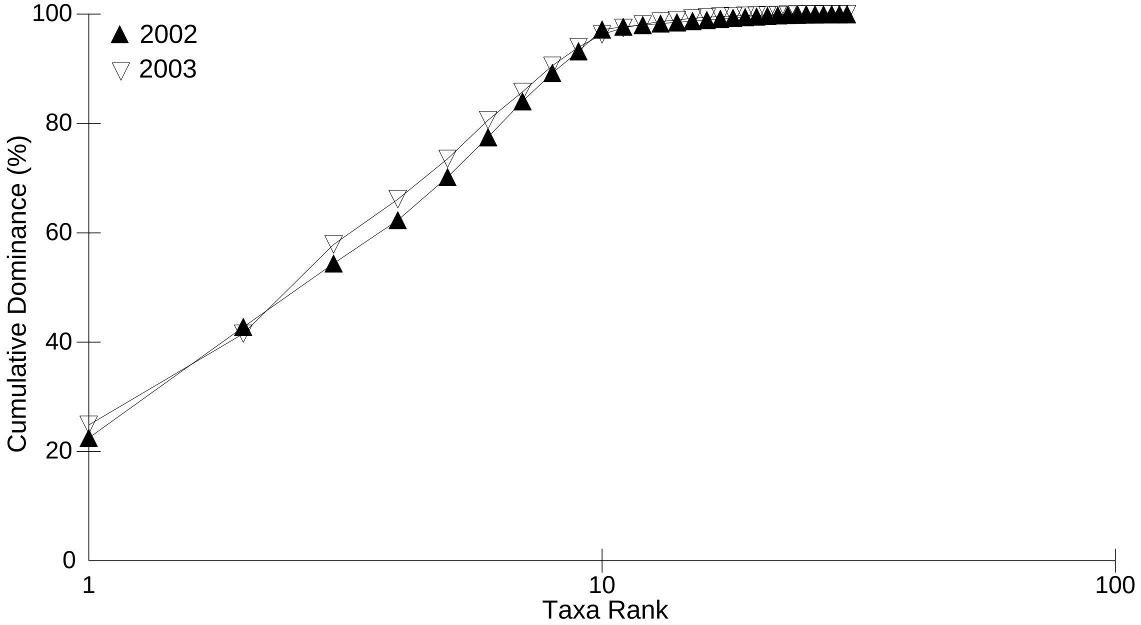

Figure 17: Dominance plot of the copepod taxa.

6.2 Publication II

submitted to: Marine Biology

FEEDING OF CLAUSOCALANIDS (CALANOIDA, COPEPODA) ON NATURAL OCCURRING PARTICLES IN THE NORTHERN GULF OF AQABA (RED SEA)

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Abstract

A total of 12 feeding experiments were conducted in the northern Gulf of Aqaba during spring (March/April) and autumn (September/October) 2002 at the Marine Science Station (MSS) in Aqaba. Females of three species of clausocalanids were selected: *Clausocalanus farrani*, *Clausocalanus furcatus* and *Ctenocalanus vanus*. Natural occurring particle (NOP) larger than 5 μm were investigated as food source. The ambient chlorophyll a concentration at sampling depth (70 m) ranged between 0.15 - 1.00 μg chl a L^{-1} and NOP concentrations ranged between 1.78 - 14.0 x 10^3 cells L^{-1} during the sampling periods. The division of particles into five size classes (5 - 10 μm, 10 - 20 μm, 20 - 50 μm, 50 - 100 μm and >100 μm) revealed that most of the particles were found in the size classes below 50 μm (81 - 98%), while most of the natural occurring carbon (NOC) was concentrated in the size classes larger than 20 μm (70 - 95%). Ingestion rates were food density dependent rather than size dependent ranging for chlorophyll a between 0.3 and 84.2 ng chl a ind.$^{-1}$ d^{-1}, for NOP between 0.02 and 1.65 x 10^3 cells ind.$^{-1}$ d^{-1}, for NOC between 0.01 and 0.41 μg C ind.$^{-1}$ d^{-1} and for the body carbon (BC) uptake between 0.4 and 51.8% BC d^{-1}. The share of the size classes to the total ingestion resembled in most cases the size class composition of the natural particle community.

Keywords:*Clausocalanus farrani*, *Clausocalanus furcatus*, *Ctenocalanus vanus*, grazing, natural occurring particles, Gulf of Aqaba

Introduction

In subtropical and tropical pelagic environments small calanoid copepods often form a dominant zooplankton group (e.g. Hopcroft et al. 1998). For example, the genus *Clausocalanus* of the family Clausocalanidae is one of the most dominant and widespread taxa within the small-sized calanoids (Frost and Fleminger 1968). They are found in high numbers, for example in the Caribbean (Webber and Roff 1995), the Sargasso Sea (Schulz 1986), the Mediterranean (Mazzocchi et al. 1997) and the Gulf of Aqaba (Almeida Prado-Por 1983,1985). Despite its wide distribution, the ecology of the clausocalanids has received little attention in comparison to its neritic and temperate counterpart Pseudocalanus (e.g. Poulet 1973, 1974, 1976; Ohman 1990; Dagg et al. 1998). Historically, small calanoid copepods were considered herbivorous which had to be revised after increasing evidence of omnivory was found (for review see Kleppel 1993). Protozoans, especially ciliates, are known to be an important food source to small calanoids (Kleppel et al. 1988; Stoecker and Mc Dowell Capuzzo 1990; Gifford 1991; Calbet and Landry 1999; Levinsen et al. 2000; Broglio et al. 2004). The importance of microzooplankton as a food source is extremely important in subtropical and tropical oligotrophic oceanic waters where most of the primary production is provided by pico-sized phytoplankton (<2 μm) (e.g. Campbell and Vaulot 1993, Lindell and Post 1995). This group is generally unavailable as a direct food source for mesozooplankton because of its small size. Nonetheless, the picoplankton is indirectly used by copepods via additional steps (protozoans) in the food chain. Feeding experiments with natural occurring particles (NOP) are more difficult to interpret compared to experiments using cultured phyto-or microzooplankton due to the diversity of particles, but certainly give a more realistic reflection on in situ copepod feeding. Feeding experiments of *Pseudocalanus minutus* with naturally occurring particulate matter have indicated that copepods seem to be rather unselective and opportunistic in what they ingest (e.g. Poulet 1973, 1974, 1976; Dagg and Grill 1980; Huntley 1981; Turner 1991). Also, it has been noted that the feeding behaviour alters with the seasonal changes in particle concentration (Poulet 1978, Dagg and Grill 1980, Kleppel et al. 1988). Hence, the copepods have to be able to adapt rapidly to changing natural particle composition.

The Gulf of Aqaba is an unique environment characterised by stronger seasonal fluctuation than other subtropical seas (Reiss and Hottinger 1984). Deep vertical mixing (down to 600 m) and repletion of nutrients in winter (December - March) is followed by summer stratification and depletion of nutrients in the euphotic zone. The changes in the mixing and stratification trigger a seasonal succession of the phytoplankton and microzooplankton community (Kimor and Golandsky 1977). During winter, diatoms and dinoflagellates are abundant due to the increased nutrient levels, but the main primary producers during summer and autumn are ultraplankton (<8 μm) which consists of *Prochlorococcus*, *Synechococcus* and small eucaryotic algae (Lindell and Post 1995, Sommer 2000). The calanoid copepod community of the Gulf of Aqaba is dominated by small-sized epipelagic species (Almeida Prado-Por 1990) whereby the clausocalanids play a significant role. The Gulf of Aqaba is inhabited by the following clausocalanid species: *Ctenocalanus vanus*, *Clausocalanus farrani* and *Clausocalanus furcatus* (Almeida Prado-Por 1990) and *Clausocalanus minor* (personal observation). Only few investigations have included data of feeding rates for *Clausocalanus* spp. and *Ctenocalanus vanus* (e.g. Kleppel et al. 1988, Peterson et al. 1989, Broglio et al. 2004). The most detailed studies were conducted on *Clausocalanus furcatus* (Mazzocchi and Paffenhöfer 1998, 1999). No feeding data are available for *Clausocalanus farrani* so far.

Feeding studies are often conducted under laboratory conditions with high quality foods where the concentration of food particles can be increased to a saturated feeding level. This is not applicable to the natural pelagic system where the food source comprises many different types and sizes of particles. Therefore we chose incubation experiments to determine ingestion rates of copepods with natural particle concentrations and composition. This study presents the first results on the feeding ecology of females of *Clausocalanus farrani*, *Clausocalanus furcatus* and *Ctenocalanus vanus* on naturally occurring particles (NOP) in the Gulf of Aqaba during spring and autumn in 2002. It will be considered to what extent particle size selectivity, composition or concentration influence the feeding patterns of the selected species.

Methods

A total of 12 experiments were conducted in the northern Gulf of Aqaba from February 26 to April 16 and September 11 to October 21, 2002. Naturally occurring particles, further referred to as NOP, were used as a food source to obtain information on the natural feeding preferences of the dominant calanoid copepod species *Clausocalanus farrani*, *Clausocalanus farrani* and *Ctenocalanus vanus*. Incubation experiments were conducted and ingestion rates were calculated based on the method of Frost (1972) within the facilities of the Marine Science Station (MSS) in Aqaba, Jordan.

Sampling

The sampling for the experiments took place in the northern Gulf of Aqaba off the MSS at E34°57.872, N29°27.868 during daytime (Fig. 19; Table 12). Water samples were collected with 10 L Niskin water samplers at 70 m depth, which was within the chlorophyll *a* maximum layer (Cornils et al., unpublished data). A CTD was run every time to determine the ambient water temperature (0 - 100 m). The copepods were obtained with a 200 μm mesh Nansen net equipped with a flow meter towed vertically from 100 m depth to the surface. The clausocalanid copepods are situated in the upper 100 m throughout most of the year (A. Cornils and V. Farstey, unpublished data). Two net hauls were taken for each experiment. The first haul was preserved in 4% buffered formalin for quantitative analysis. The content of the second was carefully poured into a large bucket and transferred to the laboratory for experimental studies.

Experiments

Females of *Clausocalanus farrani*, *Clausocalanus furcatus* and *Ctenocalanus vanus* were separated from the net sample, transferred into 250 ml beakers of screened seawater (200 μm sieve to remove larger zooplankton) and kept there for 1 - 2 hours to acclimatisation. Only free swimming specimens with intact antennae were selected for the experiments. For each species three experimental bottles and three control bottles (no copepod specimens) were prepared. 2.7 L Nalgene bottles, previously rinsed with 10% HCl, were filled with the 200 μm screened sea water samples. Nutrients (NO_3, PO_4, SiO_3) and vitamins were added to prevent limitation of phytoplankton growth. 20 - 25 pre-adjusted copepod specimens were placed in each experimental bottle, and all bottles were incubated for 8 to 24 hours. Incubation took place either on a plankton wheel in dim light at day and dark at night-time (March/April) or, due to higher air temperatures in the laboratory, in a shaded watertank with a flow through system (September/October). Bottles of the latter experiments were turned every few hours in order to prevent settlement. The temperature during the experiments was maintained within 2°C of ambient conditions (March/April 21 - 22°C and September/October 24 - 25.5°C).

Particle concentration was determined at the start and the end of the experiments. Triplicates of 2 L subsamples for chlorophyll *a* measurements were filtered onto Whatman GF/F filter paper and frozen. Subsamples of 500 ml were fixed with Lugol's iodine solution for NOP counts. Copepods were removed after the experiment, screened for mortality and transferred to pre-weighed tin caps for CN-measurements.

Analysis

The GF/F filters for chlorophyll *a* analysis were transferred to 10 ml of 90% acetone, homogenised and extracted for 24 h. Chlorophyll *a* measurements were done with a spectrofluorometer (SFM 25 BIO-TEK KONTRON Instruments). The volume of the subsamples for NOP counts was reduced by sedimentation to 100 ml and transferred to an 100 ml Utermöhl sedimentation chamber (Utermöhl 1958). After 24 hours of particle settlement the sedimentation cylinder was removed and $\frac{1}{2}$ of the Utermöhl chamber was counted for all naturally occurring particles at a magnification of 400x; using an inverted microscope (Zeiss Axiovert 35). The number of NOP was then calculated for 1 Liter. Determination of taxa was done according to Massuti and Margalef (1950), Brandt and Apstein (1964), Drebes (1974), Pankow (1990) and Tomas (1993, 1995). Individual cells were identified and later grouped in five size classes: 5 - 10 μm, 10 - 20 μm, 20 - 50 μ, 50 - 100 μm and >100 μm (Table 13) according to Poulet (1978), Cowles (1979) and Uye and Kasahara (1983). The classification of size classes was made under the assumption that copepods in oligotrophic regions are non-selective feeders (Poulet 1974, 1976). First results of feeding experiments in the Gulf of Aqaba with small copepods (4.36 ±1.02 μg C ind^{-1}) showed higher clearance rates for particles larger than 10 μm (Sommer et al. 2002). Particles smaller than 5 μm were therefore neglected since they could not be counted quantitatively with inverted light microscopy and have been claimed to be inefficiently fed on by copepods. Boyd (1976) stated that Clausocalanus arcuicornis retains only 50% of particles smaller than 8 μm, but virtually all particles above 20 μm. Carbon content (μg L^{-1}) estimates were made according to Smetacek (1975) referring to similar genuses of the same size. The derived natural occurring carbon (NOC) will only approximate the real carbon content, because the conversion factors for carbon were taken from another ecosystem.

For each experiment, the growth rate, the grazing coefficient, the mean cell concentration, the filtration rate and the ingestion rate were calculated according to the equations of Frost (1972). Selectivity was investigated according to Chesson (1983). The carbon content (body carbon) of the incubated copepod specimens was measured with a CHN-Analyser (EuroEA3000). The tin caps with the copepods were dried for 24 h, weighed and then combusted in the CHN-Analyser. The results were used to calculate the percentage of body carbon uptake per day.

Results

Ambient conditions

In spring 2002, the chlorophyll *a* concentration at the sampling depth of approximately 70 m varied between 0.26 and 1.00 μg L^{-1} and no clear trend was obvious, whereas in autumn 2002 it decreased from 0.42 to 0.15 μg L^{-1} within the study period (Table 12). The NOP concentration was highest during March (07.03. - 26.03.) and on April 16th, varying between 2.92 - 14.0 x 10^3 cells L^{-1}, while in autumn NOP concentrations ranged between 1.78 - 6.56 x 10^3 cells L^{-1} with highest values recorded on September 30th. The estimated natural occurring carbon (NOC) concentration varied in spring 2002 between 0.86 and 2.47 μg C L^{-1}, and in autumn 2002 between 1.28 - 1.67 μg C L–1 (Table 12).

Particles smaller than 50 μm were most abundant (0.3 - 5.7 x 10^3 cells L^{-1}) and comprised 80.7 to 97.5% of the total abundance of particles (Fig. 20, 21). Particles greater than 50 μm occurred only in small concentrations between 0.1 - 1.6 x 10^3 cells L^{-1}. The largest particles (>100 μm) were rarely found in the samples (on average 1.8%, Fig. 20). Therefore, these particles were not included in the calculation of ingestion. With regard to the NOC concentrations, the size classes 20 - 50 μm and 50 - 100 μm contributed the most (70 - 95% or 0.07 - 1.66 μg C L^{-1}) to the natural particle biomass larger than 5 μm (Fig. 20).

The size classes smaller than 20 μm consisted mainly of dinoflagellates and other "flagellates" (>75% by numbers, Fig. 21) with limited contributions of coccolithophorids, silicoflagellates and diatoms, while the size classes larger than 20 μm were composed mostly of ciliates and diatoms with small amounts of dinoflagellates, silicoflagellates and "other particles". The last section comprised copepod eggs, funghi, and unknown particles (Table 13). Comparing the two sampling seasons, spring and autumn 2002, it becomes clear that the importance of dinoflagellates and ciliates in the NOP composition increased, while that of small flagellates and diatoms decreased (Fig. 22).

Ingestion Rates

The ingestion rates varied considerably in spring and autumn 2002 with generally higher medians for chlorophyll *a* ingestion in spring (Table 14). The NOP ingestion rates varied between 0.02 - 1.65 x 10^3 cells ind.$^{-1}$ day^{-1} during the spring experiments. Only the NOP ingestion rates of *Clausocalanus farrani* showed a higher median in spring, 0.54 x 10^3 ind.$^{-1}$ day^{-1} compared to 0.23 x 10^3 ind.$^{-1}$ day^{-1} in autumn. For *Clausocalanus farrani* no positive ingestion rates were found for the NOC in autumn. For *C. furcatus* and *Ctenocalanus vanus* differences between spring and autumn were not significant (ANOVA posthoc test). Overall, *Clausocalanus furcatus* showed lower ingestion rates than both other species.

Table 14 indicated that ingestion rates for chlorophyll *a* and, partly for NOP, were higher during spring. However, figure 23 displays that the ingestion rates of spring experiments had comparable ingestion rates to experiments conducted in autumn at a similar mean food concentration. Therefore, changes in composition did not influence the total ingestion rates significantly (ANOVA posthoc-test). Figure 23 also shows that the low ingestion rates of *Clausocalanus furcatus* are similar to those of *C. farrani* and *Ctenocalanus vanus* at the same mean food concentration of chlorophyll *a*, NOP and NOC. The ingestion rates of *Clausocalanus farrani* and *Ctenocalanus vanus* rose with increasing mean food concentrations. Experiments with *Clausocalanus furcatus* were only conducted at a similar mean food concentration. However, the correlations between the food concentration and the ingestion rates were not significant (linear regression; Fig. 23).

The contribution of each size class to the total ingestion was calculated to reveal changes in the composition of the total ingestion. Generally, the composition of total ingestion resembled the composition of the natural occurring particles (Fig. 21) and of natural carbon. Nevertheless, some experiments showed a different composition of ingestion than the natural environment (February 26, March 3 and 31, April 16 and October 21). The composition of the NOP ingestion in terms of size classes showed that the three smaller size classes (<50 μm) made up more than 74% of the total ingestion for all three species, although the fluctuation within the size classes was rather high. The NOP ingestion of the smallest size class (5 - 10 μm) varied between 0 and 70% and the ingestion of the next larger size class (10 - 20 μm) ranged between 0 and 65%. For the size class 20 - 50 μm, the ingestion fluctuated between 0 and 85% and for the largest size class (50 - 100 μm) the ingestion varied between 0 and 25%. As mentioned above, the size classes between 5 - 20 μm were composed mostly of small "flagellates" and dinoflagellates, whereas the size class between 30 - 50 μm consisted mainly of diatoms and ciliates. However, preferences of prey types could not be revealed. In the experiments of March 31st and April 16th, we found high ingestion rates in the size class 20 - 50 μm for *Ctenocalanus vanus* where the proportion of ciliates was less than 15%. There was no ingestion of small flagellates (5 - 10 μm). However, this pattern was not found for the *Clausocalanus* species.

For the size class composition of NOC ingestion, the picture was reversed. Only little of the natural carbon of the smallest size class (5 - 10 μm) contributed to the carbon uptake of the females (<15%) and even the size class 10 - 20 μm contributed only a small percentage to total C uptake (<30%, neglecting the experiment at September 30th). The highest amount of carbon uptake was by the size classes 20 - 50 μm and 50 - 100 μm (>65%). These size classes were represented mainly by ciliates and diatoms. However, the uptake is not significantly related to either group. Both the composition of NOP and NOC revealed, that the females of *Ctenocalanus vanus*, *Clausocalanus farrani* and *Clausocalanus furcatus* fed on the abundant food particles in the water column without preferences; selectivity indices, calculated according to Chesson (1983), revealed no preference of food type. Therefore, it can be assumed that the diet of the selected females is diverse and predominantly reliant on food abundance rather than food type.

Statistical tests (ANOVA posthoc test) between the long (24h) and the short (8-12h) experiments showed no significant differences. A comparison between the experiments incubated on the plankton wheel and in the water tank revealed no significant differences (ANOVA posthoc test). Therefore, it can be assumed that these difference had no influence on the ingestion rates.

Discussion

The ingestion rates displayed in this study represent one of the few results of incubation experiments for the clausocalanids (Table 18). Only females have been selected, since the males of the clausocalanids have reduced mouthparts (Frost and Fleminger 1968; Heron and Bowman 1971) and are therefore unlikely to feed. Clausocalanids are epipelagic copepods and thus mainly found in epipelagic waters (e.g. Almeida Prado-Por 1990, Hure and Scotto di Carlo 1970), where the primary producers and consequently most of the heterotrophic protists are located (Kimor and Golandsky 1978).

Comparisons with the few data available on feeding rates for either *Clausocalanus* spp. or *Ctenocalanus* spp. revealed that the ingestion rates of the present study correspond well with the results of experiments with natural occurring particles as well as with algal monocultures (Table 18). Results of feeding experiments are available mainly for *Clausocalanus furcatus*, which had during our study a body carbon uptake of less than 4.5%. Low ratios for this species have been found also by Mazzocchi and Paffenhöfer (1998) under laboratory conditions with dinoflagellates as food source (Table 18). However, these ratios increased with rising cell concentrations. Mazzocchi and Paffenhöfer (1999) reported that low ratios were found despite their observations of high swimming activity. They suggested that continuous movement might be energetically better than 'stop-and-go' movement. Broglio et al. (2004) found ratios for *Clausocalanus* spp. between 10 - 40% body carbon in the NW Mediterranean, which is in the range of Clausocalanus farrani for this study (Table 14). Under natural conditions, the daily ratio can vary over a wide range, which has also been shown for other small calanoid species (e.g. *Centropages typicus*, 4 - 70%; Dagg and Grill 1980).

Ctenocalanus vanus, *Clausocalanus farrani* and *Clausocalanus furcatus* belong to the most dominant calanoid copepod species in the northern Gulf of Aqaba (Almeida Prado-Por 1990, Cornils et al. in press). During both spring and autumn 2002 the uptake of body carbon was less than 40%. The investigated females showed no significant differences in the feeding pattern of ingestion between spring and autumn 2002 which might be due to the fact that the size class composition hardly changed. The total ingestion rates for chlorophyll *a*, NOP, NOC and %BC were rather connected with the mean food concentrations. However, this pattern was not significant. The mean cell concentrations were too low to show a clear increase in ingestion. The impact of size classes on the ingestion rates of NOP and NOC revealed that the females fed mainly on small sized food items between 5 - 20 μm in terms of abundance while the main carbon uptake was found in the size classes larger than 20 μm. The small size classes were dominated by dinoflagellates and other "flagellates" while the larger size classes were dominated by diatoms and ciliates.

Gut content analysis of *Clausocalanus* spp. in the subtropical Atlantic at the Great Meteor Seamount revealed that the guts were filled with mainly unidentifiable particles, and histological pictures showed a good nutritional condition which is also an indication for good adaptation of clausocalanids to low phytoplankton biomasses (Fischer 2004). Feeding here takes place probably predominantly on naked cells which includes small dinoflagellates, other flagellates and ciliates as has been revealed in our study. Kleppel et al. (1988) investigated the carotenoids gut pigments of *Clausocalanus* spp. and found mainly carotenoids of heterotrophic particles followed by carotenoids of dinoflagellates. Al-Najjar (2000) found mainly the pigment peridinin as a marker for dinoflagellates in the guts of small-sized calanoid copepods in the northern Gulf of Aqaba.

Poulet (1974) assumed from his results that some copepods are able to adapt fast to changes in the structure of food sources. This enables the copepods to switch between size classes. This pattern may also be important also for the clausocalanids. They live in an oligotrophic environment where the primary producers in the food web are dominated by not directly available ultraplankton (Lindell and Post 1995) and where medium-sized phytoplankton is scarce (Sommer 2000). Therefore, the microzooplankton plays an important role as link between the small primary producers and the mesozooplankton (Gifford 1991, Calbet and

Landry 1999). In addition, clausocalanids have short life spans with 4 - 5 generations each year (Gaudy 1972, Shmeleva and Kovalev 1974). Selective feeding would inhibit the development of a continuous population, but the clausocalanids are one of the most successful calanoid group in the subtropical and tropical regions (Frost and Fleminger 1968). Therefore, non-selectivity and omnivory are a good strategy in subtropical waters with low food concentrations. Non-selectivity under conditions of low food concentration has been reported by other authors (e.g. Poulet 1976, 1978, Cowles 1979, Huntley 1981) as well as omnivory (Paffenhöfer and Knowles 1980). Poulet (1976) claimed that the copepod *Pseudocalanus minutus* was feeding on the dominant food type at high food concentrations, whereas they feed on a broader size range at low food concentrations. The low food concentrations in our study indicate a diverse food spectrum (Fig. 21). Omnivory has been shown in several publications with positive selection for microzooplankton, for example ciliates (Kleppel et al. 1998, Batten et al. 2001, Halvorsen et al. 2001, Broglio et al. 2004). Positive selection of ciliates could not be revealed during our investigation. Probably, non-living particles also play an important role as food source in regions with low living particle concentrations. The carbon-chlorophyll ratio in faecal pellets of *Clausocalanus arcuicornis* from Onagawa Bay (Japan) suggested that non-phytoplankton particles, presumably detritus, constitute a dominant fraction of particulate materials in their diet (Ayukai 1990). However, this pattern has not been investigated in this study.

The incubation of the experiments took place under different conditions and might therefore be susceptible to errors. One possible source of error was the duration of the experiments, which varied between 8 and 24 hours. Gut content analysis of clausocalanids revealed a diel variation of feeding with high values at midnight and dawn (Mayzaud et al. 1984; Kleppel et al. 1988; Landry et al. 1994; Atkinson et al. 1996; Halvorsen et al. 2001, Fischer 2004). In oligotrophic pelagic systems the microzooplankton plays an important role inside the food web (Gifford 1991). Recent investigations of microzooplankton grazing in the Gulf of Aqaba showed that microzooplankton grazing rates were high, but declined with algal size (Sommer et al. 2002). They showed that the grazing rates of microzooplankton were about two orders of magnitudes higher than those of the mesozooplankton and therefore the impact on the investigated community especially for the ingestion of the smaller size classes should not be neglected in further investigations. Nejstgaard et al. (2001a, b) offered a calculative solution for the problem of microzooplankton feeding in incubation experiments for mesozooplankton. Therefore, feeding of microzooplankton should also be expected in the experimental controls which implies that the feeding rates of the selected copepod species might be underestimated due to the microzooplankton grazing in the control, especially for the smallest size class. The ciliates contributed on average 8% (range: 1 to 28%) of the total NOP concentrations. Therefore, they could have had a considerable impact on the ingestion rates in the 5 - 10 μm size class. During the incubation experiments on March 31st and April 16th we found low proportions of ciliates coinciding with the lack of ingestion of small flagellates. This might indicate the missing impact of microzooplankton. However, this pattern was only detectable for *Ctenocalanus vanus*.

In conclusion, clausocalanids seem to be omnivorous, non-selective feeders on the abundant particles, which fits the oligotrophic conditions of the Gulf of Aqaba with its dominance of ultraplankton. The overall results of this study suggest that the clausocalanids are highly adapted to subtropical, oligotrophic regions.

Acknowledgements

We thank the director of the Marine Science Station (MSS) in Aqaba, Dr. M. Badran, and the staff for their kind welcome and their help in sampling and analysis, especially Ehab Eid, Maysara Emor, Khaled Al-Tarabeen, Hassan Abu-Taleb and the late Said H. Sirhan. Further we thank Eva-Maria Zetsche and Christian Undeutsch for their help in conducting the feeding experiments.

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Tables and Figures

Table 12: List of sampling dates for the feeding experiments and the natural chlorophyll *a* concentration, natural occurring particle and carbon concentration at the sampling depth (~70 m).

Date	Sampling	Experiments			Natural Concentrations		
		start	duration	species	chl *a*	particles	carbon
	time	time	h		μg L^{-1}	10^3 cells L^{-1}	μg C L^{-1}
26.02.	13:45	17:30	8	*C. vanus*; *C. farrani*	0.46	2.92	0.99
03.03.	15:00	18:30	12	*C. vanus*; *C. farrani*	0.28	3.29	2.08
07.03.	14:45	19:00	12	*C. vanus*; *C. farrani*	1.00	7.93	2.47
10.03.	14:57	18:45	12	*C. farrani*	0.53	5.97	1.48
21.03.	14:33	18:00	12	*C. vanus*	0.71	7.56	2.41
26.03.	13:45	17:30	20	*C. furcatus*	0.26	9.39	1.98
31.03.	10:22	13:00	24	*C. vanus*; *C. farrani*; *C. furcatus*	0.31	4.43	0.86
16.04.	09:00	12:00	24	*C. vanus*	0.72	14.0	2.24
11.09.	09:20	13:00	8	*C. vanus*	0.42	1.78	1.42
18.09.	11:00	15:00	8	*C. furcatus*	0.38	4.55	1.28
30.09.	09:47	13:30	8	*C. vanus*; *C. farrani*; *C. furcatus*	0.30	6.56	1.54
21.10.	11:09	14:00	8	*C. farrani*	0.15	2.33	1.67

Table 13: Occurrence of taxonomical groups in the five selected size classes; x: no further taxonomic determination; quotation marks a type of taxonomic group.

Taxa		Size class (μm)				
		5 - 10	10 - 20	20 - 50	50 - 100	>100
”Flagellates”		x	x			
Silicoflagellates			*Distephanus* sp.	*Dictyocha* sp.		
Coccolithophorids		x				
Dinoflagellates		x	x	x	*Oxytoxum* sp.	
					Dinophysis spp.	
					Ceratium spp.	
						Ceratium spp.
Diatoms	pennate		x	x	x	
					Nitzschia spp.	
					Thalassionema sp.	
	centric		x	x	x	x
		Bacteriastrum sp.	*Chaetoceros* spp.	*Chaetoceros* spp.	*Chaetoceros* spp.	
			Thalassiosira sp.	*Thalassiosira* sp.		
				”*Coscinodiscus*”	”*Coscinodiscus*”	”*Coscinodiscus*”
					”*Rhizosolenia*”	”*Rhizosolenia*”
					Leptocylindrus spp.	
					Eucampia sp.	
Ciliates				Strombidiae	Strombidiae	
					Holotricha	
					Tintinnidae	Tintinnidae
					Proplectella sp.	*Salpingella* sp.
						Dadayiella sp.
Foraminifera						x
Radiolaria						x
others				copepod eggs		copepod nauplii
				funghi; spores		copepodites
				unidentified		

Table 14: Total ingestion rates chlorophyll *a* (chl *a*), natural occurring particles (NOP), natural occurring carbon (NOC) and percentage of body carbon (%BC) in females of *Clausocalanus farrani*, *Clausocalanus furcatus* and *Ctenocalanus vanus*. in brackets: number of experiments/number of replicates.

Species	Season	Ingestion			
		chl *a* ng chl *a* ind.$^{-1}$ d^{-1}	NOP 10^3 cells ind.$^{-1}$ d^{-1}	NOC μg C ind.$^{-1}$ d^{-1}	% BC % BC d^{-1}
Ctenocalanus vanus	Spring (6/18)	5.3 - 84.2	0.15 - 1.65	0.01 - 1.21	0.5 - 38.8
	Median	15.1	0.29	0.23	7.3
	Autumn (2/6)	1.9 - 11.3	0.04 - 0.50	0.35	11.4
	Median	3.0	0.25	0.35	11.4
Clausocalanus farrani	Spring (5/15)	0.3 - 61.7	0.06 - 1.47	0.01 - 1.90	0.4 - 51.8
	Median	12.9	0.54	0.41	13.0
	Autumn (2/6)	2.4 - 6.7	0.23	——	——
	Median	5.2	0.23	——	——
Clausocalanus furcatus	Spring (2/6)	0.5 - 9.2	0.08 - 0.40	0.01 - 0.10	0.4 - 2.3
	Median	6.1	0.18	0.04	1.7
	Autumn (2/6)	1.0 - 9.8	0.02 - 0.20	0.10	4.5
	Median	3.7	0.15	0.10	4.5

Table 18: Feeding data of clausocalanids derived from incubation experiments.

Species	Incubation Experiments			Food type	Region	Reference
	Ingestion rate	Clearance rate	% BC			
C. furcatus (females)	0.15 µg C ind^{-1} h^{-1}	1.98 ml ind^{-1} h^{-1}		dinoflagellates	SE Georgia	Mazzocchi and Paffenhöfer (1999)
C. furcatus (females)		2.06 ml ind^{-1} h^{-1}		NOP	Gulf of Naples	Mazzocchi and Paffenhöfer (1999)
C. furcatus (females)	2.3 cells ind^{-1} h^{-1} 7.3 cells ind^{-1} h^{-1} 208.5 cells ind^{-1} h^{-1}	1.21 ml ind^{-1} h^{-1} 1.96 ml ind^{-1} h^{-1} 0.40 ml ind^{-1} h^{-1}	10.3 – 33.6 %	*Gymnodinium nelsoni* (2 cells ml^{-1}) *Gymnodinium nelsoni* (4 cells ml^{-1}) *Rhodomonas* sp.(208.5 cells ml^{-1})	SE Georgia	Mazzocchi and Paffenhöfer (1998)
C. furcatus (females)			3.8 – 11.7% 1.5 – 2.1%	*Prorocentrum triestium*, *Scripsiella* sp. (0.3 mm L-1)	Gulf of Naples	Mazzocchi and Paffenhöfer (1998)
Clausocalanus spp.	61/180 ng C ind^{-1} d^{-1} 16/205 ng C ind^{-1} d^{-1}	37 ml ind^{-1} d^{-1} 6 ml ind^{-1} d^{-1}	5/37%	Ciliates Phyto >5µm NOP	NW Mediterranean	Broglio et al. 2004
Clausocalanus spp.	<10 pg C ind^{-1} h^{-1}	1.49 – 2.08 ml ind^{-1} d^{-1} 1.5 – 3.1 ml ind^{-1} d^{-1}		Ciliates Dinoflagellates NOP Heterotrophic Nanoflagellates	NW Spain	Batten et al. (2001)
Ctenocalanus vanus	7.8 ng Chl *a* taxa^{-1} d^{-1} 7.1 ng Chl *a* taxa^{-1} d^{-1}	0.5 ml L^{-1} d^{-1} 1.9 ml L^{-1} d^{-1}		17.2 µg Chl *a* L^{-1} 3.8 µg Chl *a* L^{-1} NOP	Benguela upwelling	Peterson et al. 1989
Small calanoids		2 ml ind^{-1} d^{-1} 9 ml ind^{-1} d^{-1} 22 ml ind^{-1} d^{-1} 16.5 ml ind^{-1} d^{-1}		*Chlorella* sp. Pennate diatoms *Thalassiosira* sp. *Nitzschia* sp.	Gulf of Aqaba	Sommer et al. 2002

Figure 18:

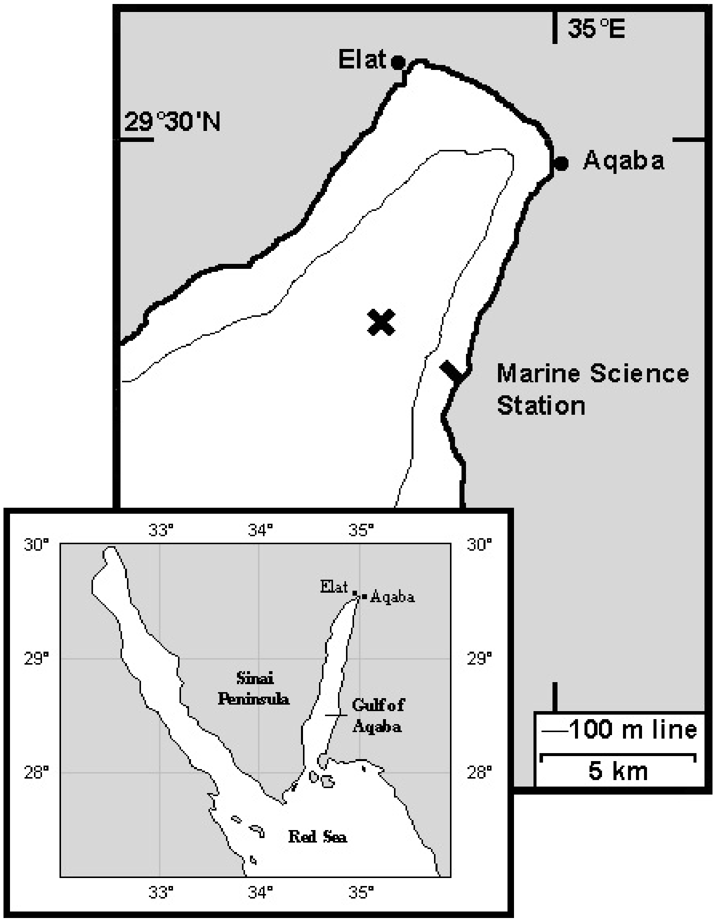

Figure 19: Map of sampling position (x) in the northern Gulf of Aqaba; overview of the northern Red Sea (scale 1:5,000,000)

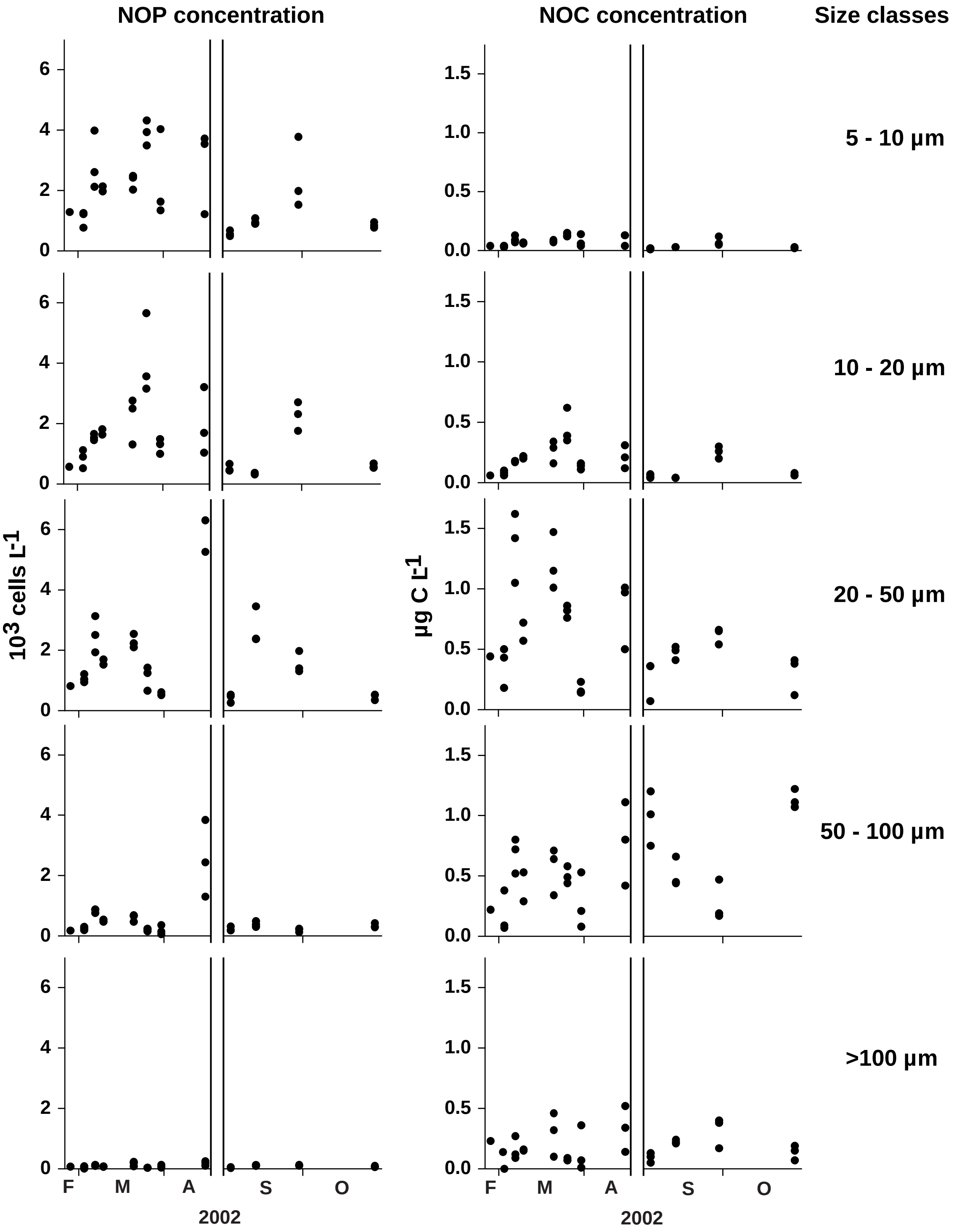

Figure 20: Natural concentrations of (a) naturally occurring particles (NOP) concentration and (b) estimated natural occurring carbon (NOC) at sampling depth (70 m), displayed in size classes.

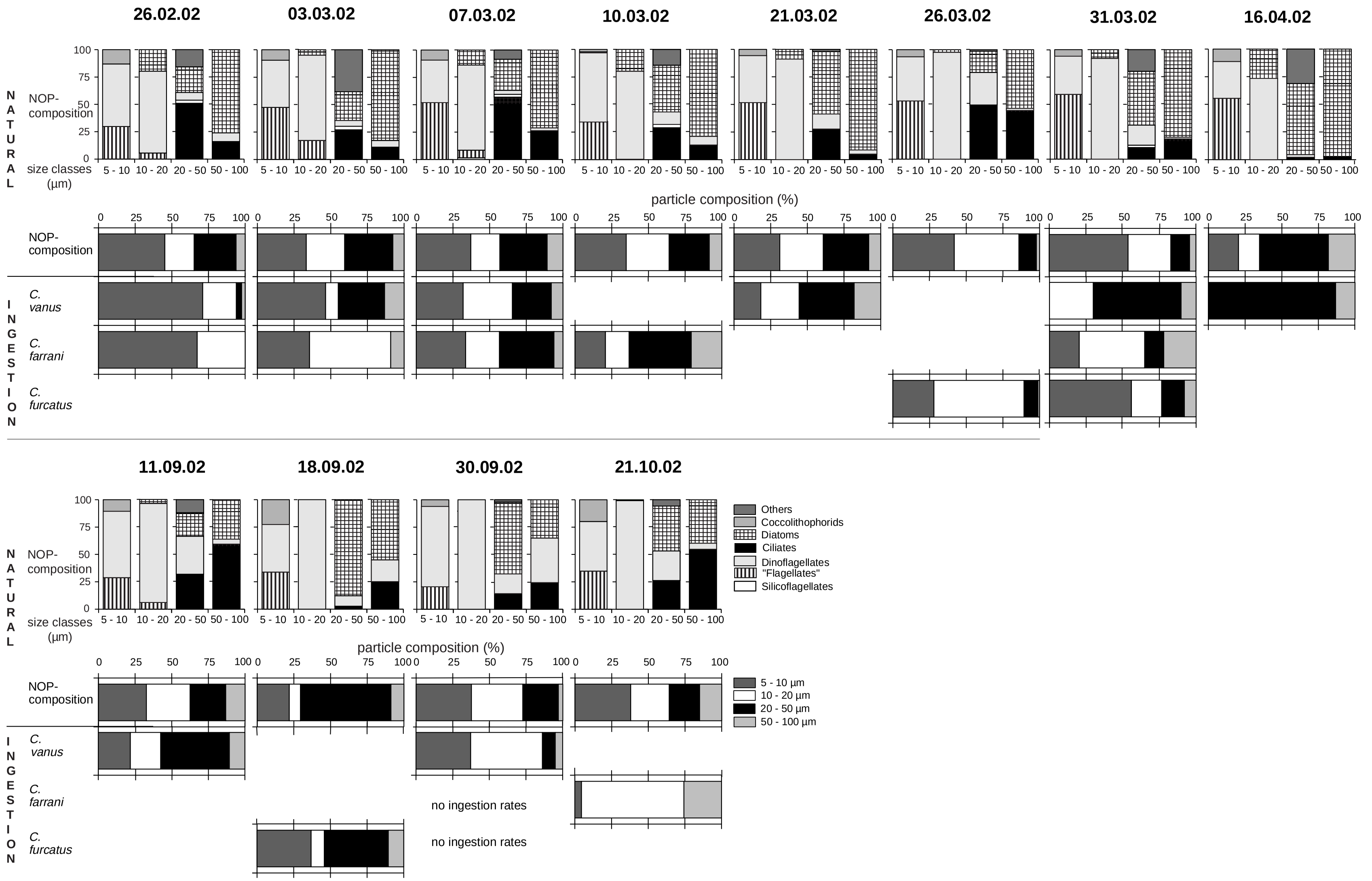

Figure 21: Naturally occurring particles (NOP). The natural composition of taxonomic groups, the natural composition of the size classes and their composition of the ingestion by the three selected species.

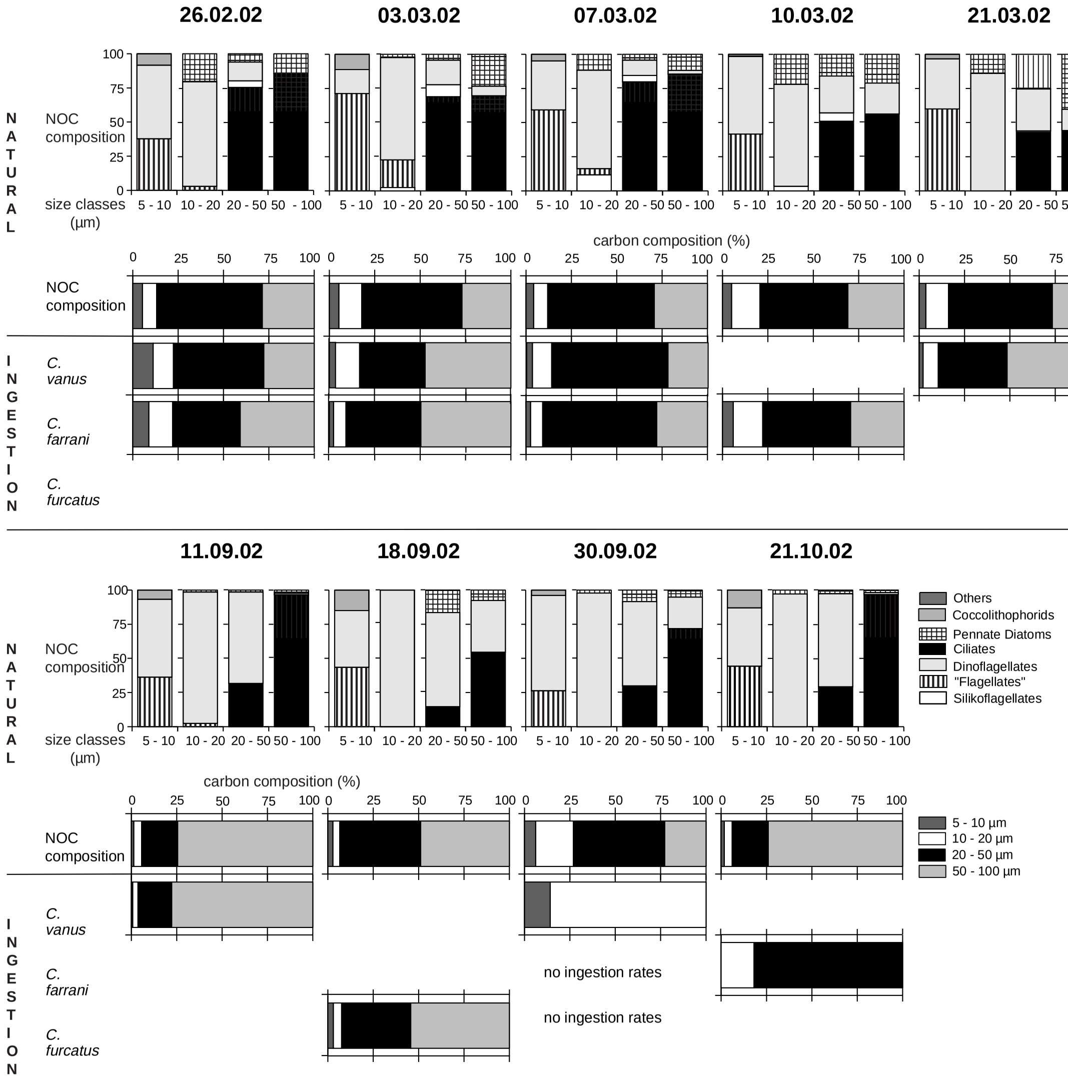

Figure 22: Carbon of the natural occurring particles (NOC). The natural composition of taxonomic groups, the natural composition of the size classes and their composition of the ingestion by the three selected species.

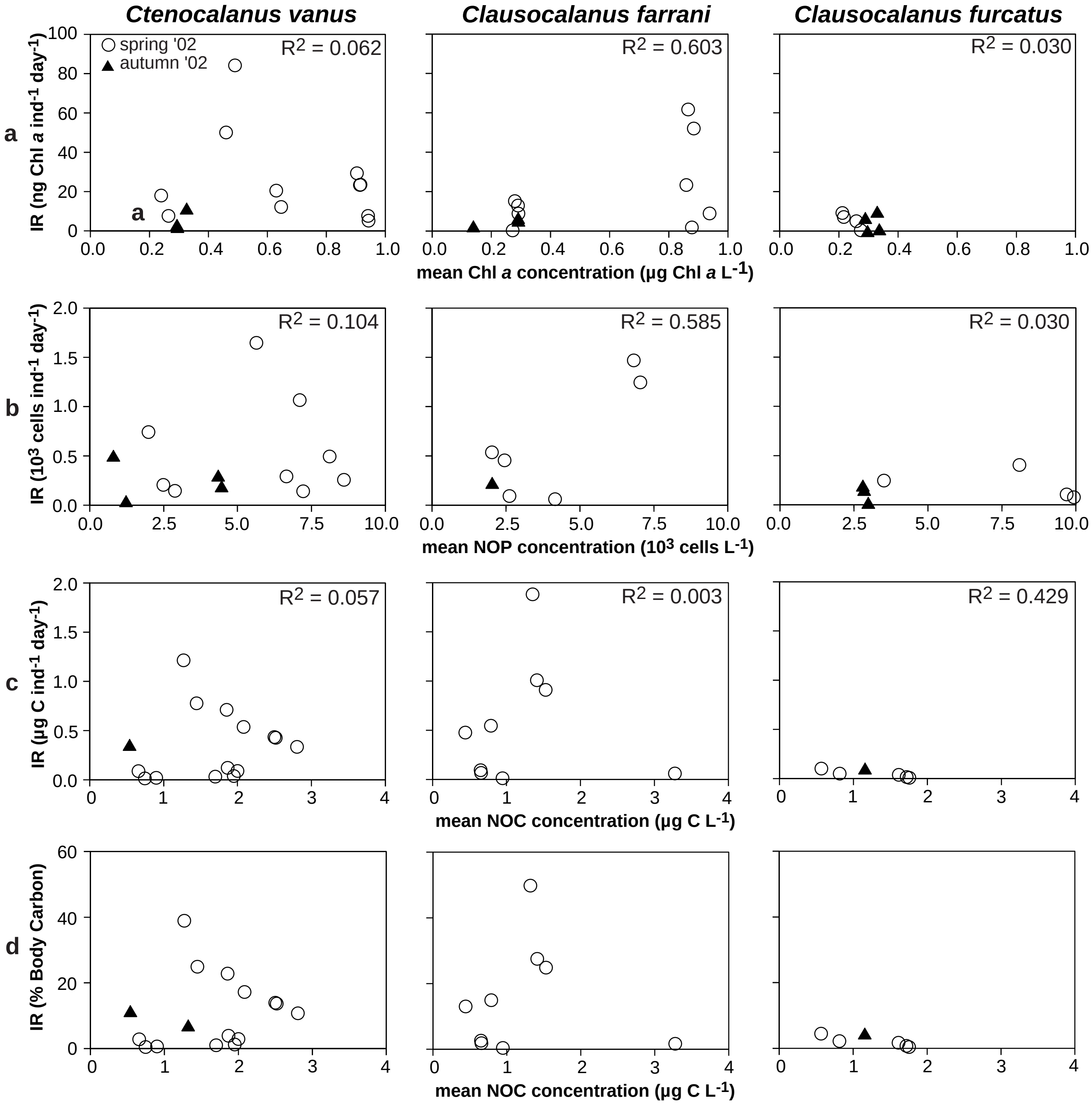

Figure 23: Ingestion rates of the females of *C. farrani*, *C. furcatus* and *C. vanus* in dependence of average cell concentration for (a) chlorophyll *a*, (b) NOP, (c) NOC and (d) % body carbon. Numbers display linear regression between cell concentrations and ingestion rates (95% confidence level); IR: Ingestion rates.

6.3 Publication III

Manuscript

SEASONALITY OF THE ABUNDANCE AND REPRODUCTION OF THE CLAUSOCALANID COPEPODS OF THE NORTHERN GULF OF AQABA (RED SEA)

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Abstract

Clausocalanids dominate subtropical mesozooplankton communities. Their life cycles, however, are widely unknown. Here, we follow the seasonal population development and reproductive biology of Red Sea clausocalanids in the northern Gulf of Aqaba, between February 2002 and December 2003. Monthly vertical hauls taken with a Nansen net (200 μm mesh size) between 100 m and the surface revealed four species, including a new record (*Clausocalanus minor*) for the area. Overall, *Ctenocalanus vanus* dominated during the first, and *Clausocalanus furcatus* during the second half of the year, whereas the frequency of *C. farrani* remained fairly stable throughout both years. *Ctenocalanus vanus* abundances peaked during winter and spring, followed by *Clausocalanus farrani* peaking in spring and additionally, in June 2003. In 2002, the abundance of *C. furcatus* showed no distinct seasonal cycle of abundance, whereas in 2003, it reached high densities in January, July and November. The proportion of mature gonads, determined from preserved females, was not significantly related to changes in temperature or food in any of the four species. Incubation experiments showed that egg production rates varied between 0-3.3 and 1.8-9.2 eggs female^{-1} d^{-1} in *C. farrani* and *C. furcatus*, respectively. Endoparasitism by dinoflagellates was found in all three species, *C. farrani* being the most infested.

Keywords: *Ctenocalanus vanus*, *Clausocalanus farrani*, *Clausocalanus furcatus*, Gulf of Aqaba, reproduction, seasonality

Introduction

Clausocalanids are common in many parts of the world's oceans. These comparably small copepods are often dominant components of the mesozooplankton and are thus believed to be an important link within the pelagic food web (e.g. *Pseudocalanus*: Corkett and McLaren 1978, *Clausocalanus*: Frost and Fleminger 1968). While species from temperate regions, such as *Pseudocalanus* spp., have been intensely studied (e.g. Corkett and McLaren 1978, Jonasdottir 1989, Bucklin et al. 1998), our knowledge on the dominant subtropical and tropical oceanic genera *Clausocalanus* and *Ctenocalanus* is still very limited. The few investigations available to date focus on the regional and vertical distribution (e.g. North Atlantic: Williams and Wallace 1975, off Brazil: Björnberg 1980, Gulf of Aqaba: Almeida Prado-Por 1983, 1990, Mediterranean Sea: Fragopoulu et al. 2001, Antarctic: Schnack-Schiel and Mizdalski 1994) and seasonal variability (e.g. Mediterranean Sea: Mazzocchi and Ribera D'Alcala 1995, Peralba and Mazzocchi 2004). Species of the genus *Clausocalanus* are found to coexist in the same water mass throughout the year (Mazzocchi and Ribera D'Alcala 1995). In the subtropical Gulf of Aqaba, the abundant clausocalanids are represented by *Ctenocalanus vanus* Giesbrecht 1888, *Clausocalanus farrani* Sewell 1929, *Clausocalanus furcatus* Brady 1883, and *Clausocalanus arcuicornis* Dana 1849 (Halim 1969, Almeida Prado-Por 1983, 1990, Abd El-Rahman 1999). These species were probably recruited from the Indian Ocean through the Red Sea (Halim 1969) and are hence of tropical origin.

Recent studies on the feeding patterns of clausocalanids in the Gulf of Aqaba have shown that these species are unselective particle feeders (Cornils et al. submitted), which is concurrent with results from other regions and genera of the family (e.g. Poulet 1973, Peterson et al. 1989, Mazzocchi and Paffenhöfer 1999, Broglio et al. 2004). The reproductive biology was studied in *Clausocalanus furcatus* (Webber and Roff 1995b, Mazzocchi and Paffenhöfer 1998, Hopcroft and Roff 1998) and *Clausocalanus lividus* (Saiz and Calbet 1999, Calbet et al. 2002). Mazzocchi and Paffenhöfer (1998) found an inverse relationship between egg production and food concentration in *C. furcatus*, and conclude that this species is adapted to oligotrophic environments.

In contrast to the adjacent Red Sea proper and other subtropical oligotrophic systems, the Gulf of Aqaba provides a unique environment for the clausocalanids as it is characterized by seasonal phytoplankton succession driven by thermal winter convection (Genin et al. 1995 Levanon-Spanier et al. 1979, Lindell and Post 1995, Al-Najjar 2000). The Gulf of Aqaba is the deep (max. depth 1800 m) and narrow (5 - 26 km) northeastern extension of the Red Sea, a semi-enclosed basin separated from the Red Sea by a shallow sill at the Straits of Tiran (250 m), which allows only superficial exchange of nutrient-depleted surface waters. In late fall, sea surface cooling creates a deep vertical mixed layer of more than 250 m depth (Klinker et al. 1976, Paldor and Anati 1979). The convective mixing is probably the most important source of nutrient transport into the euphotic zone (Klinker et al. 1978, Badran 2001). In late spring, the warming of the air and sea surface creates a thermal stratification, setting the stage for a phytoplankton bloom (diatoms). The intensity of the bloom is strongly correlated with the mixing depth of the previous winter (Kimor and Golandsky 1977, Genin et al. 1995). During the summer stratification, the surface layer becomes nutrient depleted (Reiss and Hottinger 1984, Badran 2001), ultraplankton (<8 μm) dominates the phytoplankton (Prochlorophytes, eucaryotic flagellates). The influences of the seasonal development of hydrography and phytoplankton on the abundance of the offshore mesozooplankton of the Gulf of Aqaba have been described by Almeida Prado-Por (1983), Farstey et al. (2002) and Cornils et al. (submitted).

In 2002 and 2003 the seasonal cycle of hydrography and plankton was studied in the northern Gulf of Aqaba. The present study focuses on the response of the population dynamics and reproduction activity of the clausocalanid copepods to the seasonal changes in water temperature and phytoplankton development. We studied the occurrence, vertical distribution, population structure, maturity stage, and reproductive activity of the dominant clausocalanids.

Methods

Sampling

The material was collected in the northern Gulf of Aqaba from February 2002 to December 2003 at an offshore station (E 34°57,872; N 29°27,868) with a depth of 300 m. Vertical hauls were conducted from 100 m depth to the surface with a Nansen net (0.4 m^2 aperture, 200 μm mesh size), equipped with a flowmeter, at a towing speed of 1 m s^{-1}. Sampling was performed between 9 a.m. and 15 p.m. on a monthly basis with additional samplings in spring 2002 (March/April), autumn 2002 (September - November) and autumn 2003 (October/November). The samples were preserved in borax-buffered 4% formaldehyde seawater solution. For further processing the samples were divided with a Folsom-Splitter. The clausocalanid specimens were sorted either from one quarter of the sample, or, if occurring in numbers <40, from the total sample. The copepodite stages I, II and III of the clausocalanids are not considered in this study as they are likely to be under-represented in the samples due to the large mesh size. The *Clausocalanus* females were determined to species level after Frost and Fleminger (1968). The CIV and CV stages, and the males of *Clausocalanus*, however, were not distinguished due to ambiguities in the morphological characters. The specimens of *Ctenocalanus vanus* were divided into CVI and CV stages, males and females.

Gonad morphology

Gonad maturity was established from 40 - 50 preserved females of each species using a stereo microscope (Leica M16). As the female gonads of both *Ctenocalanus* and *Clausocalanus* are similar to those of *Pseudocalanus*, the gonad development stage (GS) was subdivided according to the classification of Niehoff (2003). GS1 characterises females with empty diverticula. GS2 describes the females carrying small opaque oocytes in the diverticula. In GS3, the oocytes in the diverticula are large and their nuclei are clearly visible.

Similar to *Pseudocalanus* (Niehoff 2003), the oocytes in the GS3 of *Ctenocalanus vanus* were brownish in colour, whereas the oocytes of *Clausocalanus* spp. remained opaque throughout the development. Prior to spawning, the nucleus is not visible anymore, and the mature oocytes form a single ventral band in the diverticula (GS4). Females in GS3 and GS4 are considered as mature, i.e. ready to spawn, as here final oocyte development processes take place (Niehoff 2003). In addition to the determination of gonad maturity stages, developing oocytes in the diverticula of *Ctenocalanus vanus* were counted. Due to the lacking pigmentation, single oocytes in the diverticula of *Clausocalanus* spp. were impossible to identify correctly and hence, the oocytes were not counted. In all females, prosoma length was measured.

The gonad maturation stages and egg production rates of *Clausocalanus minor* were not determined as less than 20 specimens per samples were found.

Egg production

Egg production experiments were carried out during periods of high frequent sampling (March/April, October/November 2002, and October/November 2003) with *Clausocalanus farrani*, *C. furcatus* and *Ctenocalanus vanus*. For the experimental studies, separate samples were taken with the Nansen net (200 μm mesh size) and transported to the laboratory immediately after capture. Of each species, 30 - 90 actively swimming, healthy looking females were sorted using a stereo microsope (Nikon) and individually placed in multi-wells (5 ml) filled with 150 μm pre-screened sea water. After an incubation period of 24 hrs at ambient water temperatures (23 - 27°C), the multi-wells were checked for the number of eggs released, nauplii and mortality of the females (Table 15). The mortality rate was quite high during the experiments. However, during periods of high egg production, 90% of the dead females spawned before death. The reproductive activity was expressed as percentages of spawning females and as eggs female^{-1} d^{-1}.

Except for *Clausocalanus lividus* and *C. mastigophorus*, all *Clausocalanus* species are considered to carry egg sacks (Saiz and Calbet 1999, Peralba and Mazzocchi 2004). The egg sacks of *C. furcatus* are supposed to be fragile, and the eggs are easily released from it at disturbance (Mazzocchi and Paffenhöfer 1998). In our experiments, the eggs of *C. furcatus* were released from the sacks quickly after spawning, while in *C. farrani* more than 50% of the egg sacks remained attached to the females within the observation period. In 10% of these females the eggs could not be separated and counted. In contrast to the *Clausocalanus* species, *Ctenocalanus vanus* is a free spawning species.

Endoparasites

At close stereo microscopical observation, endoparasites were found in the clausocalanid females. Two types of dinoflagellate parasites were detected following the descriptions of Ianora et al. (1990): 1. A parasite infesting the gut of female specimens was identified as *Blastodinium* sp. 2. Abnormalities in the P5 of the females were ascribed to infestation by *Syndinium* sp..

Statistics

Linear regression was used to identify possible relationships between the environmental (sea surface temperature, depth-integrated chlorophyll *a*) and the biological parameters (clausocalanid abundance, gonad maturity, female prosoma length, oocyte number). A time lag of one month between the biological and the environmental data was chosen to account for the generation time of the clausocalanids.

Results

Environmental parameters

The environmental conditions during the study period have been described in detail by Cornils et al. (submitted a), and are therefore only briefly summarized. The sea surface temperature varied between 21.3°C in February and 26.7°C in August (Fig. 24). Deep vertical mixing (>300 m) occurred in winter (January -April). Due to sea surface warming in late spring the water column became stratified with the shallowest mixed surface layer in July (<50 m). The chlorophyll *a* concentration fluctuated between 20.8 and 58 mg m^{-2} (depth-integrated, 0-100m, Fig. 24). During the deep vertical mixing in winter, the chlorophyll *a* concentration was homogeneously distributed down to 150 m depth. At the onset of thermal stratification in spring 2003 (March/April) a bloom developed within the upper 75 m persisting until May. In summer (July/August) a deep chlorophyll *a* maximum was found between 50 - 100 m persisting until November/December in both years, but more pronounced in 2002.

Clausocalanid occurrence

In the northern Gulf of Aqaba, the clausocalanid species contributed on average 27% (range 10 - 64%) to the total copepod community (Cornils et al. submitted). Four species of clausocalanids were distinguished in females: *Ctenocalanus vanus*, *Clausocalanus farrani*, *C. furcatus* and *Clausocalanus minor*. The proportion of each species changed seasonally: *Ctenocalanus vanus* was dominant between March and June in both years with a percentage of 40 - 80% of all clausocalanid females (Fig. 25) while *Clausocalanus furcatus* was predominant between July 2002 - January 2003 (50 - 60%) and July and November 2003

(60/65%). The percentage of *Clausocalanus farrani* remained fairly stable throughout both years (30 - 50%). *Clausocalanus minor* was reported for the first time in the Gulf of Aqaba and contributed only little to the *Clausocalanus* population (between 0 and 3.9% throughout the year).

In *Clausocalanus* spp. the annual cycles differed between the two years. In 2002, the highest abundance of both CIV and CV was found in spring (March/April) and in autumn (October). In 2003, the abundance of CIV reached high densities in April and July (Fig. 26), while the abundance of CV peaked in January, April, July and November. The densities of *Clausocalanus* spp. males were low throughout the investigation period, contributing between 0 and 10.3% to all *Clausocalanus* specimens, with highest densities in April and July 2003.

The females of *C. farrani* were more abundant during the first half of both years (Fig. 26). The highest densities occurred in March/April 2002 (66 ind. m^{-3}) and in June 2003 (144 ind m^{-3}). In 2002, no major peaks of abundance occurred for the females of *C. furcatus*, the density ranged between 1.7 and 49.5 ind. m^{-3}. In 2003, the abundance peaked in January, July and November with 140, 126 and 97 ind. m^{-3}, respectively (Fig. 26). Although in neither of the two species, the abundance was significantly correlated with the sea surface temperature or the depth-integrated chlorophyll *a* (Table 16), there was a tendency towards a positive and negative relationship in *C. furcatus* and *C. farrani*, respectively. *Clausocalanus minor* females occurred only in low numbers (0.8 ±1.9 ind. m^{-3}, max. 8.6 ind. m^{-3} in Jan. 2003) without a seasonal trend (Fig. 26).

Overall, the abundance of all developmental stages studied of *Ctenocalanus vanus* significantly changed between seasons with highest numbers in spring (Fig. 27, Table 16). The males had the lowest abundance throughout the study period (<7 ind. m^{-3}). During the frequent sampling in March and April 2002, the abundance of the clausocalanids showed a high variability in all development stages.

Gonad development

The determination of gonad maturation stages of *Clausocalanus farrani* revealed that mature (GS3-GS4) and immature (GS1-GS2) females were present in roughly equal proportions during most of the investigation period (Fig. 28). High percentages of immature gonads (>80%) were only found in March, April and July 2002, and in January and July 2003. When egg production experiments were conducted in March, and autumn (October/November) 2002 and 2003, the percentage of spawning females was highly variable, fluctuating between 0 and 39% (Fig. 29). In spring and autumn 2002, the egg production rate of *Clausocalanus farrani* varied between 0.0 and 3.3 eggs $female^{-1}$, whereas in 2003 the egg production rate was lower at 0.0 to 1.1 eggs $female^{-1}$ (Table 15).

The proportion of mature gonads (GS3 and GS4) in *Clausocalanus furcatus* ranged between

60 and 100%, except for March and April 2002, when more than 80% of the gonads were immature (Fig. 28). Most of the mature females were in GS3 (>53%, average 94%), the percentage of females in GS4 was usually less than 12%, except for April 2003 (47%). Consistent with the high percentages of mature gonads, the proportion of spawning females of *C. furcatus* varied between 20 and 60% during autumn of both 2002 and 2003 (Fig. 29). Due to the low abundances in spring 2002, only one experiment was conducted which revealed that 25% of the females were spawning. In autumn 2002, the egg production rate of *C. furcatus* varied between 1.8 and 9.2 eggs female^{-1}, whereas in autumn 2003 the egg production rate was lower with 1.2 to 5.6 eggs female^{-1} (Table 15).

The determination of the gonad maturation stages of *Ctenocalanus vanus* revealed a high percentage of mature gonads (GS3 and GS4) during winter and spring (March - June 2002, January - April, December 2003), reaching densities between 40 and 95% (Fig. 28). In autumn and summer, the percentage of mature gonads was lower than 40%. Females in GS4 occurred only in low numbers (0 - 3.8%). In winter and spring when most females were mature, the highest numbers of mature oocytes were found in the diverticula of the gonads, varying between 8 - 15 oocytes per female (Fig. 30). In summer and autumn, (July - November), the number of mature oocytes was below 4 oocytes per female. The number of oocytes is significantly related to the sea surface temperature as well as the prosoma length (Table 16).

The egg production experiments in spring 2002 showed only one spawning event in early March with 83% spawning females (Fig. 29) coinciding with a high percentage of mature females (83%). In autumn, egg production was low (0 - 19% in 2003) or nil (2002), in agreement with the low percentage of mature gonads during this period.

The proportion of mature gonads of the clausocalanid females was not significantly correlated to the sea surface temperature or the chlorophyll *a* concentration (Table 16).

Prosoma length

The females of *Clausocalanus minor* were the largest with 0.838 mm (±0.025) followed by *Ctenocalanus vanus* (0.808 ±0.050 mm) and *Clausocalanus farrani* (0.792 ±0.035 mm). The smallest species was *C. furcatus* with 0.741 mm (±0.037) prosoma length. The seasonal cycle of prosoma length could only be established for the three abundant species, showing a distinct seasonality which was reversed to the annual cycle of temperature (Fig. 31). The largest individuals occurred during the cold seasons with sea surface temperatures between 19 and 22°C and smallest specimens were found during the warm months, when the sea surface temperature had increased to 27°C. The correlation between the sea surface temperature and the prosoma length was significantly negative for all three species (linear regression; Table 16). The positive relationship between the chlorophyll *a* concentration and the prosoma length was only significant for *Ctenocalanus vanus* ($p = 0.04$, $r = 0.4986$).

Parasitism

A considerable incidence of endoparasitism was found in the preserved females of *Clausocalanus farrani* (7.8%), *Clausocalanus furcatus* (4.8%) and *Ctenocalanus vanus* (3.1%) (Fig. 32, Table 17). Endoparasites were also seen in *Clausocalanus minor*, but not counted quantitatively.

In *Clausocalanus farrani* and *C. furcatus* the impact of **Syndinium** sp. prevailed (Table 17), while the parasitized females of *Ctenocalanus vanus* were all infested by *Blastodinium* sp., except for three females during spring 2003 (12.03.) which showed abnormalities at the P5, indicating an infestation with *Syndinium* sp. However, these three females were found to have mature gonads (GS3). Endoparasitism of *Clausocalanus farrani* was highest during June/July 2002, December/January 2002/2003 and November 2003 (Fig. 32). Highest percentage of parasitized female *C. furcatus* was observed in summer and autumn (August - October). The percentage of parasitized female *Ctenocalanus vanus* showed no seasonal variation. In general, higher numbers of infestations were found in 2003.

During the egg production experiments, some of the putatively *Syndinium*-infested females of *Clausocalanus farrani* and *C. furcatus* (but not *Ctenocalanus vanus*) were found to eject tiny (10 - 15 μm diameter) spheres through the anus, suggesting expulsion of the free-living stage of the parasite. Spawning was never observed in these females. The highest proportion of females in the incubations with this phenomenon was found for *Clausocalanus farrani* (0 - 54%; average 8.8%), while the percentage of infested females of C. furcatus was considerably lower (0 - 13%; average 2.4%; Table 15).

Discussion

Our study confirms the importance of clausocalanid copepods in the northern Gulf of Aqaba pelagic system. We found *Ctenocalanus vanus*, *Clausocalanus farrani*, *Clausocalanus furcatus* and *Clausocalanus minor*, whereas *Clausocalanus arcuicornis* previously reported from this region (Halim 1969, Almeida Prado-Por 1983, 1985, Abd El-Rahman 1999, Al-Najjar 2000) was lacking in our samples. During investigations on the vertical distribution of mesozooplankton in the Gulf of Aqaba and the northern Red Sea in 1999 (S. Schiel and W. Hagen, unpublished data) and during 1991/1992 in the northern Gulf of Aqaba (A. Cornils and V. Farstey, unpublished data) also *C. minor* was found instead of *Clausocalanus arcuicornis*. Females of *C. minor* and *Clausocalanus arcuicornis* are of similar size and distinguishable only by the differences of the morphology of the genital segment (Frost and Fleminger 1968), and hence taxonomical difficulties might have led to inconsistent species determination.

The three *Clausocalanus* species found in the Gulf of Aqaba, though widely distributed, are restricted to subtropical and tropical regions of the oceans. *Clausocalanus furcatus* occurs circum-globally in the epipelagial (Frost and Fleminger 1968) and may dominate zooplankton communities in oligotrophic environments (Schulz 1986, Webber and Roff 1995a, Siokou-Frangou et al. 1997). *Clausocalanus farrani* and *C. minor* are confined to the Indian and Pacific oceans (Frost and Fleminger 1968, Haq et al. 1973, Madhupratap and Haridas 1986). In contrast, *Ctenocalanus vanus* is also common in temperate and subantarctic waters (e.g. Heron and Bowman 1971). Copepods in temperate waters are subjected to distinct seasonal changes, *C. vanus* is, hence, more likely to respond to the seasonal changes in temperatures, resulting in a significant relationship between the abundance and the sea surface temperature (Table 16). The observed differences in the seasonal occurrence of *Clausocalanus* species and *Ctenocalanus vanus* might result from their different latitudinal distribution.

In the Gulf of Aqaba as well as in other regions, *Ctenocalanus vanus* reaches highest densities during the cold months (winter, spring) and lowest densities in summer (e.g. Sargasso Sea: Deevey 1971, Eastern Mediterranean: Siokou-Frangou 1996, Christou 1998). The seasonal cycle of abundance for *Clausocalanus farrani*, *C. furcatus* and *C. minor* females differed not only between 2002 and 2003, but also between the three species. In the Mediterranean, *C. furcatus* reached its highest densities during the period of highest insolation in summer and autumn comparable to our results, whereas the co-occurring *Clausocalanus* species had their abundance maximum in spring or winter (Peralba and Mazzocchi 2004). Differences in the seasonal cycles between the *Clausocalanus* species have also been reported by Williams and Wallace 1975 or Mazzocchi and Ribera D'Alcala (1995).

In agreement with previous studies (e.g. Kouwenberg 1993, Schnack-Schiel and Mizdalski 1994) the proportion of *Clausocalanus* and *Ctenocalanus* males was rather low. Kouwenbwerg (1993) concluded that the pronounced female dominance in potentially herbivorous species, such as *Clausocalanus* spp., may be a survival strategy, relating to swarming behaviour and a limited food supply. Another possible reason for the absence of males in our samples is that they might inhabit layers below 100 m in the water column. However, investigations of the vertical distribution of clausocalanids in the Gulf of Aqaba showed that the few *Clausocalanus* males were mostly distributed within the upper 100 and hardly detected below 200 m (S. Schiel, unpublished data). This did not apply to the males of *Ctenocalanus vanus* which occurred predominantly below 100 m. Therefore, these males might indeed be underrepresented in our study. Similar to the Mediterranean (Fragopoulu et al. 2001, Peralba and Mazzocchi 2004) the Gulf of Aqaba copepodids and females of *Clausocalanus* and *Ctenocalanus* are mainly present in the upper 100 m of the water column (S. Schiel, unpublished data).

The structure of the female gonads of *Ctenocalanus vanus* and *Clausocalanus* spp. was similar to those of *Pseudocalanus* (Niehoff 2003) and *Ctenocalanus citer* (Niehoff et al. 2002) indicating that the morphology of gonads does not vary much within the Clausocalanidae.

A major difference between the oocytes of *Clausocalanus* and *Ctenocalanus* was their colouring. The oocytes of *Ctenocalanus vanus* darkened with progressing development as shown previously for *Pseudocalanus* (McLaren and Corkett 1978, Niehoff 2003) and many other calanoid copepod taxa (e.g. Calanus, Sømme1934, Runge 1985, 1987). In contrast, *Clausocalanus farrani* and *C. furcatus* did not show any changes in colour during maturation, which made it difficult to distinguish between GS3 and GS4 and to count the oocytes.

The relationship between the environmental parameters and the proportion of mature gonads was not significant for either *Clausocalanus furcatus*, *Clausocalanus farrani* or *Ctenocalanus vanus*. A tendency, however, could be seen for an inverse relationship between the temperature and proportion of mature gonads of *Ctenocalanus vanus*(Fig. 28). Breeding in *Clausocalanus farrani* and *C. furcatus* seemed to be independent to the seasonal temperature and chlorophyll *a* concentration changes.

In *Pseudocalanus*, laboratory studies have shown that gonad maturation and egg production is closely related to food supply (Corkett and McLaren 1984, Jonasdottir (1989), Niehoff 2003). In field studies, however, the reproductive activity of clausocalanoid species (*Pseudocalanus* in the North Sea, Halsband and Hirche 2001, *Ctenocalanus citer* in the Bellingshausen Sea, Niehoff et al. 2002) did not show any correlation to chlorophyll *a* concentration, a widely-used proxy for food availability. The same was true for our study. This indicates that reproduction was not food limited in the Gulf of Aqaba and supports previous reports, that clausocalanoids are able to reproduce at low food concentrations (e.g. Mazzocchi and Paffenhöfer 1998, 1999). In fact, Mazzocchi and Paffenhöfer (1998) showed that under laboratory conditions *Clausocalanus furcatus* egg production was higher when food (dinoflagellates, diatoms) concentrations were low, than when provided high food concentrations, suggesting a strong adaptation of this species to oligotrophic conditions. Chlorophyll *a*, however, shows only the autotrophic part of the full food spectrum, and recent studies have shown that protozoans are a significant part of the diet of many copepods, including clausocalanids (e.g. Kleppel 1993, Broglio et al. 2004). To what extent protists may have contributed to the reproductive activity of clausocalanids was beyond the scope of this study.

Halsband and Hirche (2001) have shown that egg production of *Pseudocalanus* was correlated to prosome length which in turn was a function of temperature. The same seems to be true for *Ctenocalanus vanus* in our study in which gonad maturation and hence temperature were significantly correlated ($r=0.7$, $p<0.001$). It is interesting, that though the prosome length of the *Clausocalanus* spp. changed with temperature as did the length of *Ctenocalanus vanus*, the reproductive activity, however, did not. Webber and Roff (1995a) did not find marked changes in the prosome length, concurrent with the lack of seasonal changes in temperature. During the 24 hrs of observation only one spawning event occurred in *Clausocalanus farrani*, *C. furcatus* and *Ctenocalanus vanus*. The spawning interval of *Clausocalanus furcatus* is approx. one to two days (Mazzocchi and Paffenhöfer 1998), becoming longer at the end of the reproduction period, if we assume a life span of less than 23 days (egg production stopped in general 5 - 10 days before death). The egg development time at more than 25°C fluctuates between 8 - 31 hrs (Bjoernberg 1972). *Clausocalanus furcatus* and *C. farrani* nauplii of stage one were found within the 24 hrs incubations for egg production confirming the findings of Bjoernberg (1972). In contrast to the findings of Mazzocchi and Paffenhöfer (1998) hatching occurred not only within the egg sack, but also on isolated eggs.

The egg production rates of *Clausocalanus furcatus* obtained in the Gulf of Aqaba (1.8 - 9.2 eggs females^{-1} d^{-1}) and *Clausocalanus farrani* (0 - 3.3 eggs female^{-1} d^{-1}) were similar to those observed in the Caribbean (4.5 eggs female^{-1} d^{-1}, Webber and Roff 1995b), but considerably lower than the egg production of a free spawning representative of *Clausocalanus*, *C. lividus* (2.2 - 35 eggs female^{-1} d^{-1}, Calbet et al. 2002). The egg production of clausocalanids, especially in those producing egg sacks, seems to be low compared to other calanoids (review in Mauchline 1998).

The effect of endoparasitism on the reproductive biology of marine copepods and its potential role in regulating the seasonal fluctuations in copepod reproduction and densities has been poorly studied. Clausocalanid copepods are known to be infested by two types of dinoflagellates: *Blastodinium* and *Syndinium*. Ianora et al. (1990) postulated an infestation of endoparasites in 13% of *Paracalanus parvus* females in the Mediterranean. Clausocalanids were found to host less endoparasites than paracalanids. During our investigation the infestation of the clausocalanids varied between 0 and 32%. The percentage of parasitized females was higher in *Clausocalanus farrani* than in *Clausocalanus furcatus* and *Ctenocalanus vanus*.

In conclusion, the results of this investigation show that there were differences in the seasonal occurrence of the species. The relative frequency of the females showed that the dominance changed between *Ctenocalanus vanus* and *Clausocalanus furcatus*, whereas the proportion of *Clausocalanus farrani* was rather stable. Differences were also visible in the reproductive activity. In *Ctenocalanus vanus* indications for the correlation between the seasonal changes in hydrography were found, whereas the reproductive activity of the *Clausocalanus* species seemed to be independent of season. In all clausocalanid species, a considerable proportion of endoparasitic dinoflagellates were found.

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Tables and Figures

Table 15: Egg production experiments.

Species	Parameter	Season		
		Spring 2002	Autumn 2002	Autumn 2003
Clausocalanus farrani	No. of Exp.	5	6	8
	Mortality (%)	20	13.4	12.7
	Egg sacks (%)	86	50	80
	Eggs female^{-1} d^{-1}	0 - 3.3	0 - 3.16	0 - 1.1
	Parasitism (%)	0	17.1	5.9
	Clutch size	0 - 8.7	0 - 9.8	0 - 6.2
Clausocalanus furcatus	No. of Exp.	1	6	8
	Mortality (%)	3.3	26.5	24.5
	Egg sacks (%)	26.7	1.7	11.2
	Eggs female^{-1} d^{-1}	no data	1.8 - 9.2	1.2 - 5.6
	Parasitism (%)	no data	3.9	1.6
	Clutch size	no data	5.8 - 13.4	1.5 - 13.6
Ctenocalanus vanus	No. of Exp.	4	3	7
	Mortality (%)	19.1	16.2	26.5
	Eggs female^{-1} d^{-1}	0/20.8	0	0 - 2.3
	Parasitism (%)	0	0	0
	Clutch size	0/25.7	0	0 - 22.0

Table 16: Linear regression of sea surface temperature and biological data of the clausocalanids; n: number of samples, p: significance level, r: correlation coefficient.

Parameter	Species	n	p	r	significance	p	r	
Abundance	*C. farrani*	18	11.92%	-0.3776		65.90%	0.113	
	C. furcatus	18	12.96%	0.3682		80.03%	0.0625	
	C. vanus	18	0.07%	-0.7382	++	38.57	0.2192	
Frequency of mature gonads	*C. farrani*	17	73.80%	0.0872		57.73%	0.1478	
	C. furcatus	17	29.31%	0.2709		54.97%	0.1585	
	C. vanus	17	37.64%	-0.2305		27.14%	0.2825	
No. of oocytes female^{-1}	*C. vanus*	17	1.37%	-0.5821	+	14.38%	0.3675	
Prosoma length	*C. farrani*	17	0.014%	-0.8246	++	13.16%	0.3780	
	C. furcatus	17	0.003%	-0.8799	++	48.00%	0.1864	
	C. vanus	17	0.024%	-0.8012	++	3.96%	0.4986	+

+ significant, ++ highly significant

Table 17: Percentage of endoparasitic dinoflagellates (%) in preserved clausocalanid females.

Species	*Blastodinium*		*Syndinium*		Total	
	Average	Min. - Max.	Average	Min. - Max.	Average	Min. - Max.
C. farrani	1.82	0 - 14.1	5.64	0 - 27.5	7.8	0 - 39.4
C. furcatus	1.66	0 - 9.8	3.09	0 - 20.0	4.8	0 - 24.6
C. vanus	2.95	0 - 12.8	0.14	0 - 4.9	3.1	0 - 12.8

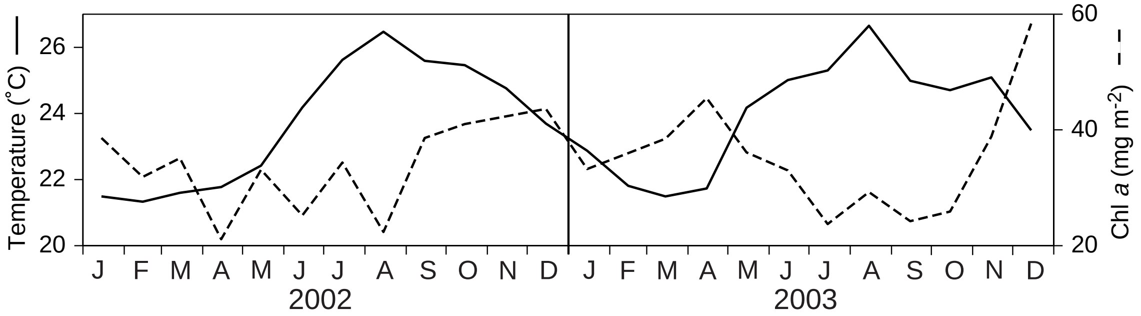

Figure 24: Annual cycle of sea surface temperature and depth-integrated chlorophyll *a* (mg m^{-2}).

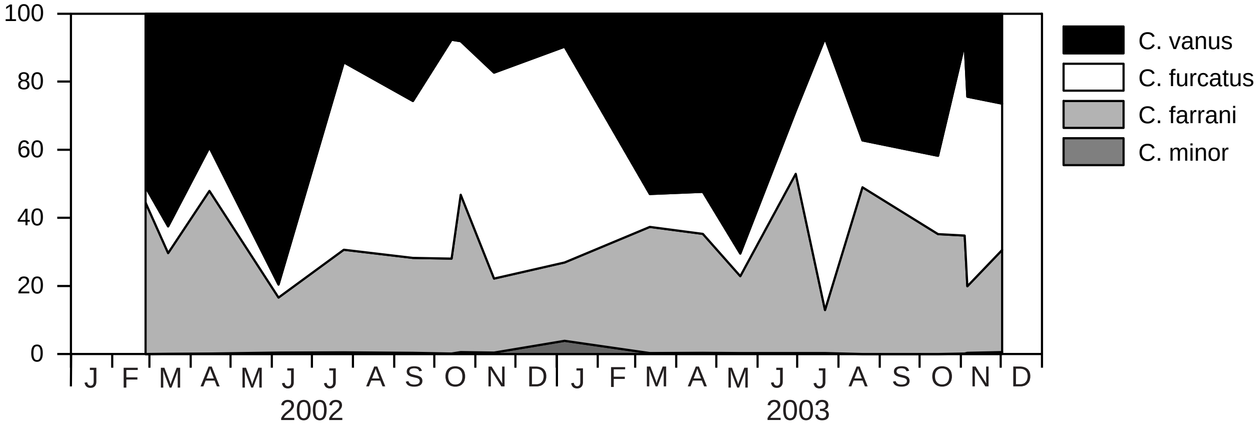

Figure 25: Relative frequency of the clausocalanid females over the investigation period.

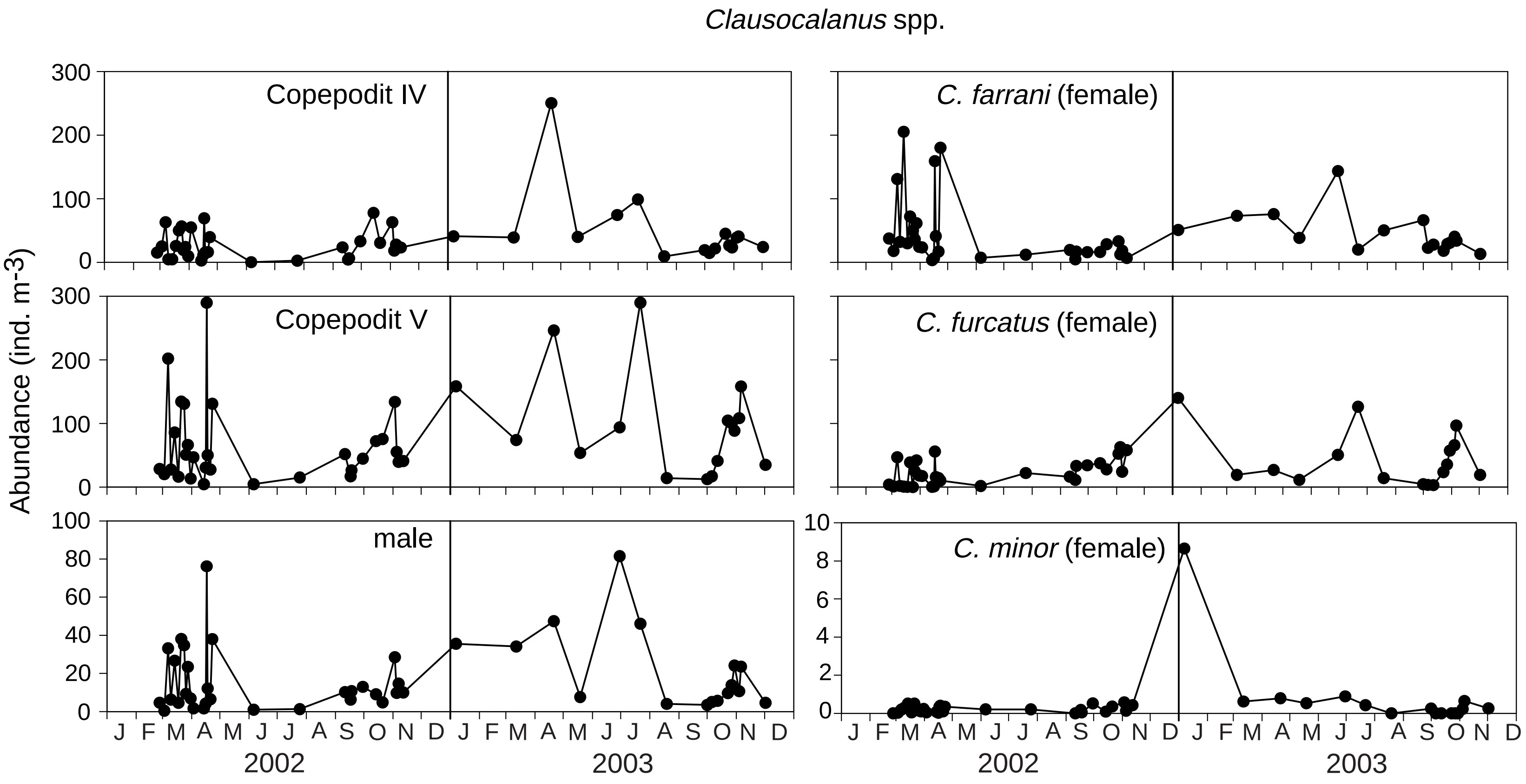

Figure 26: Seasonal abundance of *Clausocalanus* spp..

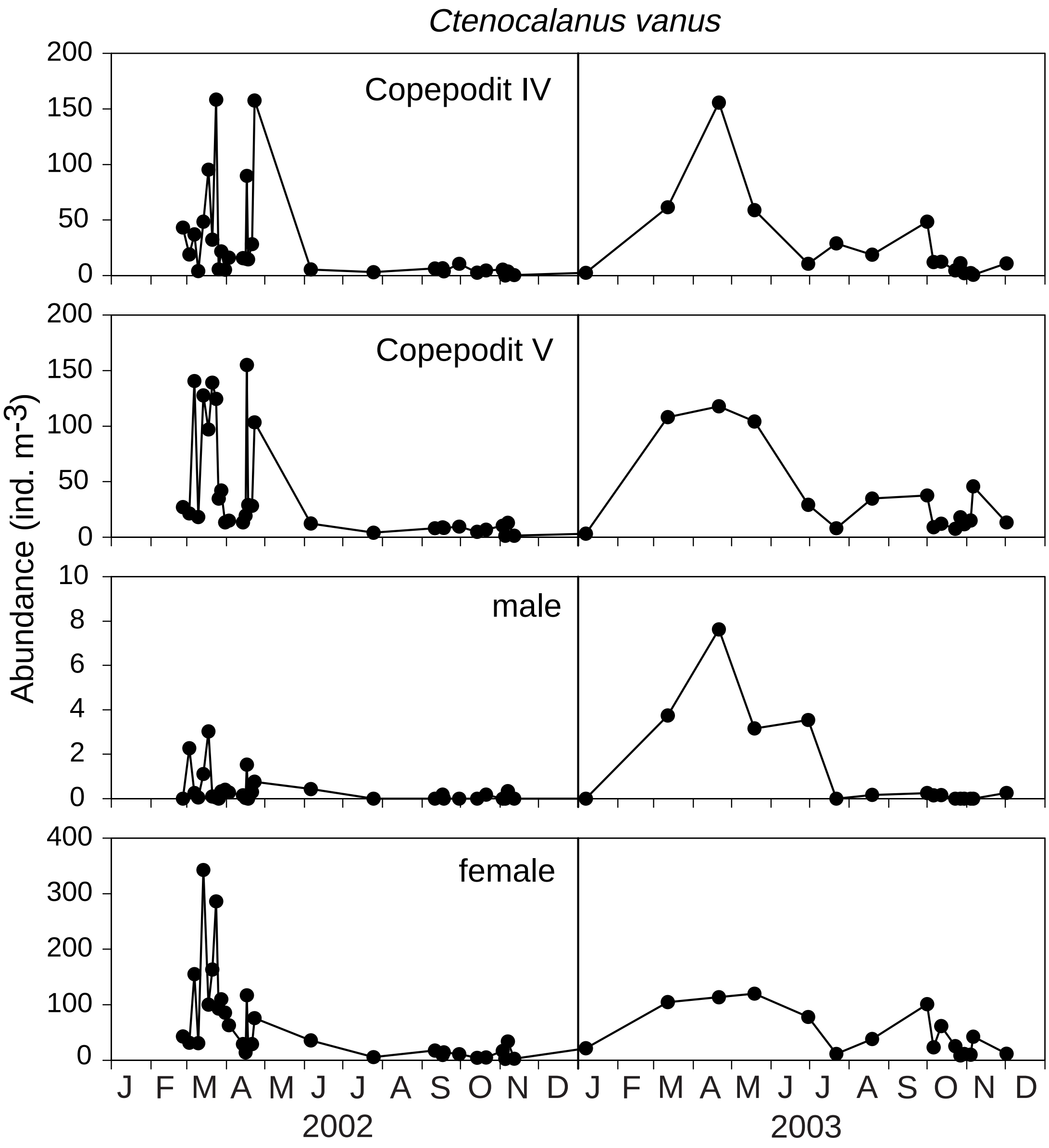

Figure 27: Seasonal abundance of *Ctenocalanus vanus*.

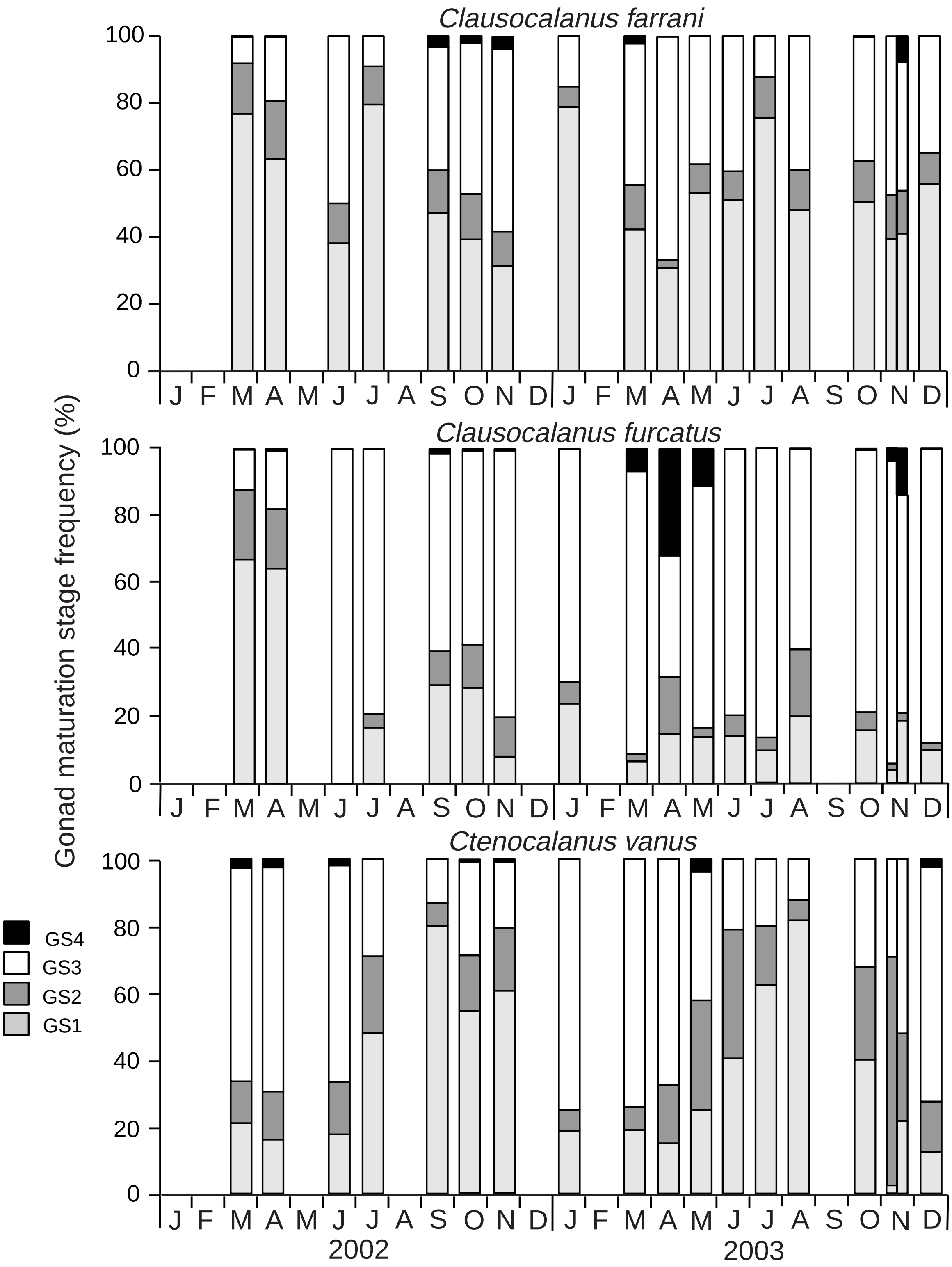

Figure 28: Annual gonad development of the clausocalanids (GS: Gonad maturation stage).

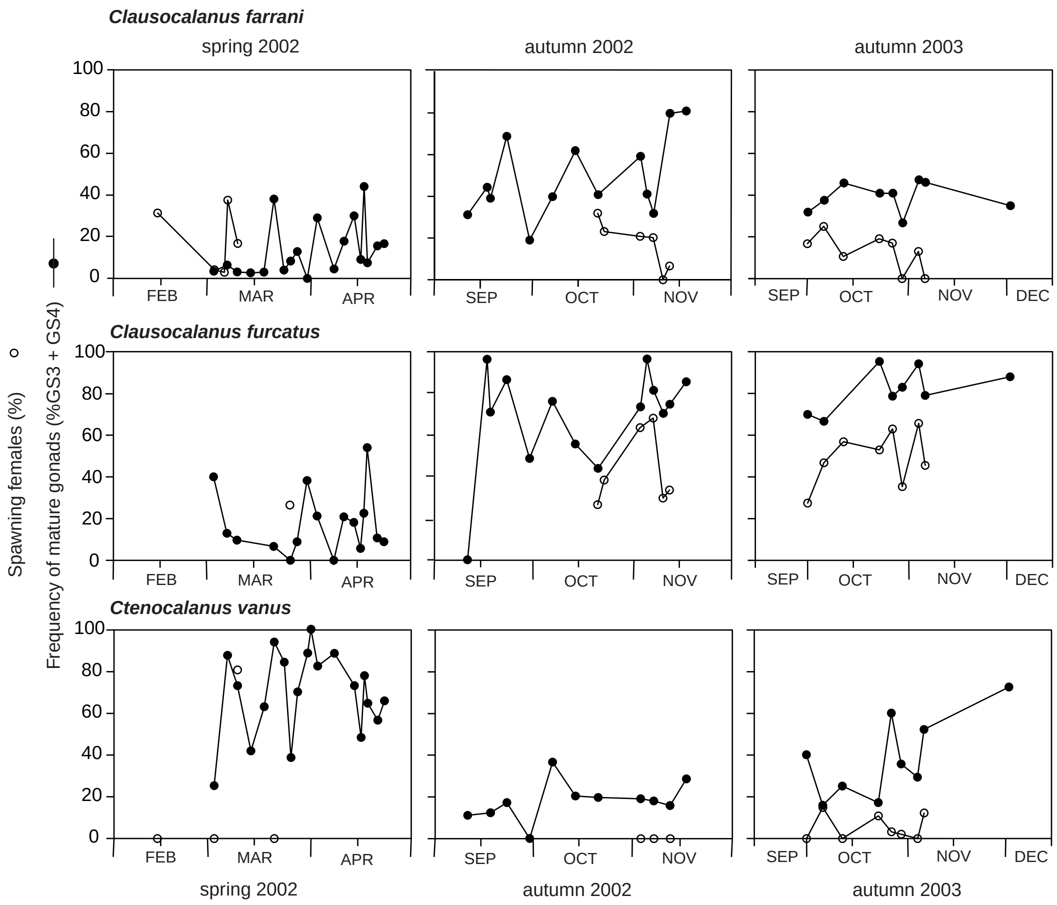

Figure 29: Percentage of spawning females (O) and the proportion of mature gonads (●) in the clausocalanids.

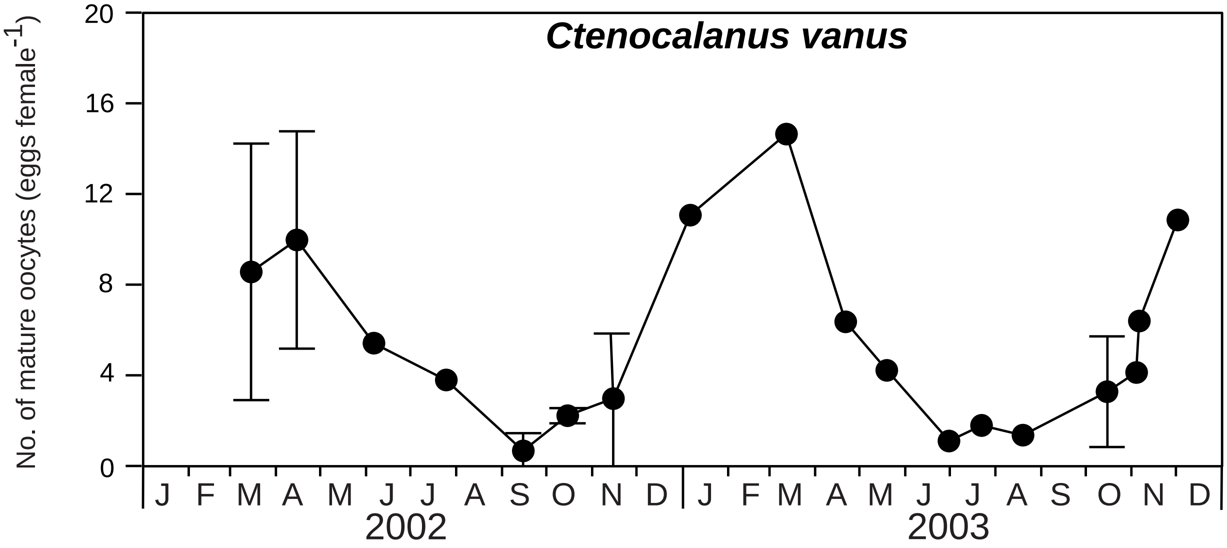

Figure 30: Number of oocytes (eggs female^{-1}) in the gonad diverticula of *Ctenocalanus vanus*.

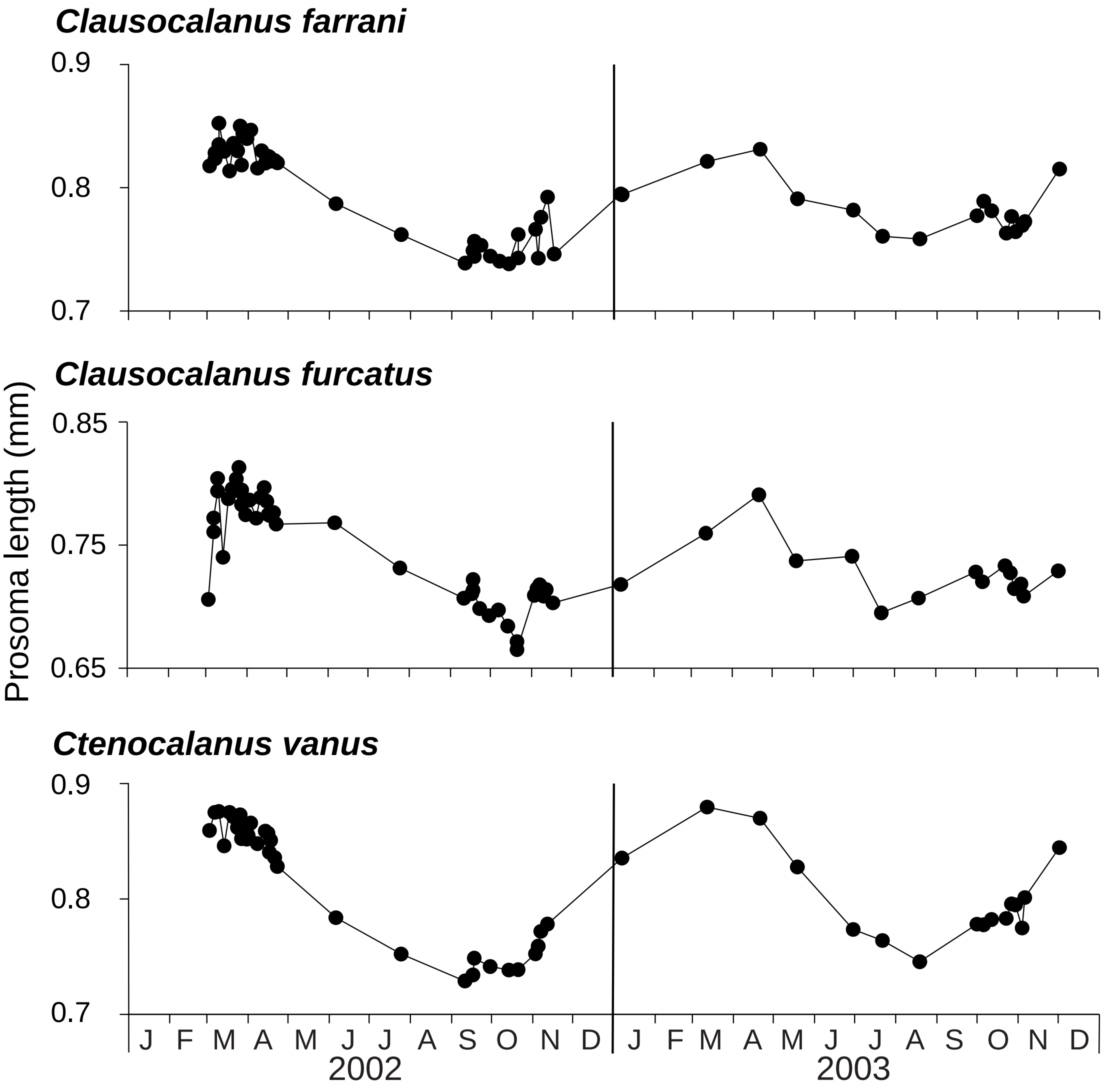

Figure 31: Prosoma length of clausocalanid females.

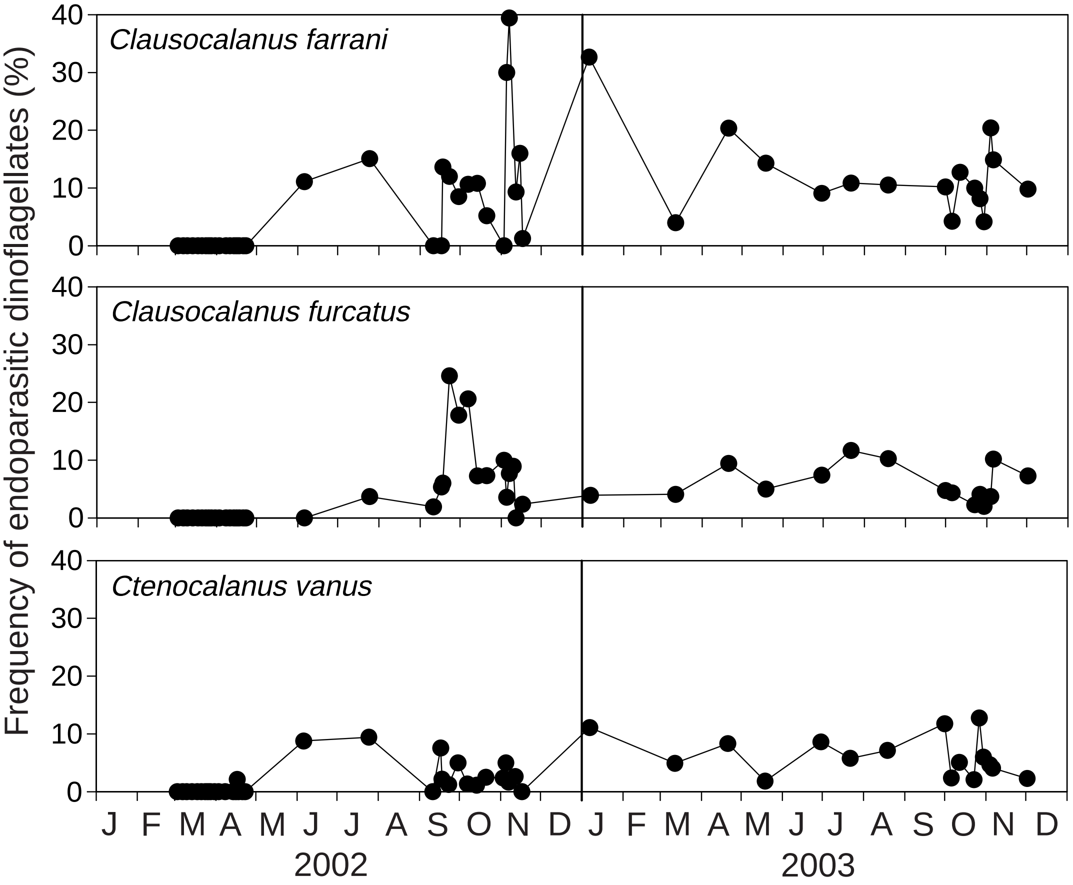

Figure 32: Frequency of dinoflagellate endoparasitism in preserved clausocalanid females.

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