

**A comparison of phytoplankton and ciliate feeding
by marine calanoid copepods**

Dissertation

zur Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Christian-Albrechts-Universität

zu Kiel

vorgelegt von

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Kiel

2006

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Tag der mündlichen Prüfung: 01. Februar 2007

Zum Druck genehmigt: 01. Februar 2007

gez. J. Grotemeyer, Dekan

**Everything is drifting,
The whole ocean moves ceaselessly...
Just as shifting and transitory as human theories.**

- Fridtjof Nansen -

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Summary

The feeding behaviour of the marine calanoid copepods *Calanus finmarchicus* and *Centropages hamatus* was studied in several laboratory experiments, and the trophic position of *C. finmarchicus* in the Trondheim Fjord in 2004 was determined through stable isotope analyses.

Calanus finmarchicus showed a feeding threshold on algal prey (dinoflagellates) at a concentration of $\sim 60 \mu\text{g C l}^{-1}$ (stage CV), whereas ciliates (oligotrichs) were ingested irrespective of ciliate concentration (adult females). The ingestion rate as a function of ciliate concentration could be described by a Holling type III functional response with beginning saturation at $\sim 150 \mu\text{g C l}^{-1}$. At prey concentrations $>120 \mu\text{g C l}^{-1}$ ingestion of algae was higher than that of ciliates, but did not follow typical saturation kinetics. Due to missing data no maximum ingestion could be identified, and at high concentrations ingestion of algal prey declined, probably due to aggregation of cells. Furthermore, *C. finmarchicus* (adult females) seemed to prefer larger cells out of a mixture, regardless of species specific or total concentration, and to avoid cells $<9 \mu\text{m}$ when larger cells were available. The trophic position of *C. finmarchicus* in the Trondheim Fjord in 2004 was trophic level 2.2, thus indicating a moderate degree of omnivory under natural conditions.

Centropages hamatus (adult males and females) started feeding on algal (flagellates, diatoms) and ciliate prey (oligotrichs) at concentrations of $\sim 5 \mu\text{g C l}^{-1}$, and the ingestion rate as a function of prey concentration could be described by a Holling type III functional response. In general, ingestion of ciliates was higher than ingestion of algae, and adult males showed lower feeding rates than adult females at prey concentrations $>50 \mu\text{g C l}^{-1}$. When diatoms and ciliates were offered together *C. hamatus* (both sexes) fed exclusively on ciliates as soon as those contributed with more than 5% to the mixture. This indicates the capability of active prey selection and switching.

Zusammenfassung

Das Fraßverhalten der marinen calanoiden Copepoden *Calanus finmarchicus* und *Centropages hamatus* wurde in mehreren Laborexperimenten untersucht, und die trophische Position von *C. finmarchicus* im Trondheimfjord im Jahr 2004 wurde durch Analysen stabiler Isotope bestimmt.

Calanus finmarchicus im Copepoditstadium CV zeigte eine Fraßschwelle für Algen (Dinoflagellaten) bei einer Konzentration von $\sim 60 \mu\text{g C l}^{-1}$, wohingegen Ciliaten (Oligotricha) von adulten Weibchen unabhängig von der Konzentration ingestiert wurden. Die Ingestionsrate als eine Funktion der Ciliatenkonzentration konnte durch eine Holling Typ III Funktionelle Reaktion mit beginnender Sättigung bei $\sim 150 \mu\text{g C l}^{-1}$ beschrieben werden. Bei Beutekonzentrationen $> 120 \mu\text{g C l}^{-1}$ war die Ingestion von Algen höher als von Ciliaten, folgte aber nicht der typischen Sättigungskinetik. Aufgrund fehlender Daten konnte keine Maximalingestion identifiziert werden, und bei hohen Konzentrationen sank die Ingestion der Algen, wahrscheinlich aufgrund von Zellaggregationen. Desweiteren scheint *C. finmarchicus* (adulte Weibchen) größere Zellen aus einer Mischung unabhängig von der artspezifischen oder der Gesamtkonzentration zu bevorzugen, und Zellen $< 9 \mu\text{m}$ zu meiden, wenn größere Zellen vorhanden sind. Die trophische Position von *C. finmarchicus* im Trondheimfjord im Jahr 2004 war trophische Ebene 2,2, was unter natürlichen Bedingungen auf ein gewisses Maß an Omnivorie hindeutet.

Centropages hamatus (adulte Männchen und Weibchen) begann Algen (Flagellaten, Diatomeen) und Ciliaten (Oligotricha) bei Konzentrationen von $\sim 5 \mu\text{g C l}^{-1}$ zu ingestieren, und die Ingestionsrate als eine Funktion der Beutekonzentration konnte für alle Beutearten durch eine Holling Typ III Funktionelle Reaktion beschrieben werden. Im allgemeinen war die Ingestion von Ciliaten höher als die Ingestion von Algen, und adulte Männchen zeigten niedrigere Raten als adulte Weibchen bei Beutekonzentrationen $> 50 \mu\text{g C l}^{-1}$. Wenn Diatomeen und Ciliaten zusammen angeboten wurden, fraß *C. hamatus* (beide Geschlechter) ausschließlich Ciliaten, sobald diese mehr als 5% der Mischung ausmachten. Dies läßt die Fähigkeit zur aktiven Beuteselektion und ein „Switching“-Verhalten erkennen.

Sammendrag

Beiteadferden til de marine calanoide kopepodene *Calanus finmarchicus* og *Centropages hamatus* ble undersøkt i flere labforsøk, og den trofiske posisjonen til *C. finmarchicus* i Trondheimsfjorden i 2004 ble bestemt ved analyser av stabile isotoper.

Calanus finmarchicus i kopepoditstadium CV viste en beiteterskel på alger (dinoflagellater) ved en konsentrasjon på $\sim 60 \mu\text{g C l}^{-1}$, mens voksne hunner spiste ciliater (oligotrichia) med en hastighet som var uavhengig av konsentrasjonen. Spiseraten som funksjon av ciliatkonsentrasjon kunne beskrives ved en Holling type III funksjonell respons med begynnende metning ved $\sim 150 \mu\text{g C l}^{-1}$. Ved byttekonsentrasjoner $>120 \mu\text{g C l}^{-1}$ var spisehastigheten av alger høyere enn av ciliater, men fulgte ikke den typiske metningskinetikk. På grunn av manglende data kunne det ikke ble bestemt en maksimal spisehastighet, og ved høye konsentrasjoner sank spisehastigheten av alger, noe som sannsynligvis skyldes cellaggregering. *C. finmarchicus* (voksne hunner) ser ut til å foretrekke større celler når de blir gitt en blanding uavhengig av om artene er gitt i likt antall eller lik biomasse, og de spiser ikke celler $<9 \mu\text{m}$ hvis større celler er til stedet. Den trofiske posisjonen av *C. finmarchicus* i Trondheimsfjorden i 2004 var trofisk nivå 2,2, som antyder en viss grad av omnivori under naturlige betingelser.

Centropages hamatus (voksne hanner og hunner) begynte å spise alger (flagellater, diatomeer) og ciliater (oligotricha) ved konsentrasjoner av $\sim 5 \mu\text{g C l}^{-1}$, og spiseraten som funksjon av byttekonsentrasjon kunne beskrives ved en Holling type III funksjonell respons for alle arter av bytter. Generelt var spisehastigheten av ciliater høyere enn for alger, og voksne hanner viste lavere beiterater enn voksne hunner ved byttekonsentrasjoner $>50 \mu\text{g C l}^{-1}$. Når diatomeer og ciliater ble tilbudt i blanding, spiste *C. hamatus* (begge kjønn) utelukkende ciliater så snart de utgjorde mer enn 5% av blandingen. Dette tyder på evne til aktiv bytteseleksjon og switching.

1 Introduction

Copepods are small creatures in huge oceans. The word 'copepod' consists of two parts with Greek origin: 'kope' means 'oar' and 'podos' means 'foot'. Hence a copepod is oar-footed, which refers to the pairs of swimming legs on the same somite, which are moved together, as would be the oars of a sculling shell. [<http://www.nmnh.si.edu/iz/copepod/>]

Maybe Norwegian fishermen were among the first to discover their importance, at least the importance of one species, since the Norwegian language with 'røddate' ('red bait') has a common name for the marine calanoid copepod that feeds 'Norwegian' fish. This species, today known as *Calanus finmarchicus* (Giesbrecht 1892), was first described in 1767 by Johan Ernst Gunnerus (1718-1773), the archbishop of the city of Trondheim during the years 1758 to 1773, who also gave it its first scientific name *Monoculus finmarchicus* (Marshall and Orr 1955a). With time researchers looked closer into the water masses, which cover our planet, and discovered approximately 9,000 to 9,500 different marine copepod species worldwide. These are classified into nine orders of which the three most widely known are: Calanoida, Cyclopoida and Harpacticoida. The order Calanoida is divided into 22 families (Boxshall and Halsey 2004). Among these families are the Calanidae and the Centropagidae with their name-giving genera *Calanus* and *Centropages*, respectively. In my studies I concentrated on two species: *Calanus finmarchicus* (Calanidae) and *Centropages hamatus* (Centropagidae). (See table 1 for detailed taxonomic classification.)

The marine copepods *C. finmarchicus* and *C. hamatus* are pelagic species, but there are also benthic (both on the surface of and within the sediment) and epibiotic (parasites and commensals) forms. A few copepod families also colonized freshwater habitats such as lakes and other standing freshwater bodies. The dominant freshwater families are: Diaptomidae (500 species), Cyclopidae, Temoridae and Centropagidae (Boxshall and Halsey 2004). In brackish water masses, e.g. the Baltic Sea, marine species as well as freshwater species can be found depending on their salinity tolerance. It has been proposed that copepods might be the most abundant animals in the world, both in total numbers and in percentage of total animal biomass (Beck et al. 1991).

1.1 Copepod Anatomy

Species belonging to the phylum Arthropoda have a body which is segmented. In calanoid copepods the two main body parts are called prosome (cephalothorax, followed by usually five, sometimes four, free segments) and urosome with up to five segments, depending on the developmental stage. The segment numbers are the tool to determine the age of individuals because the size of copepods depends on temperature and food source (Tiselius 1989, Tiselius and Jonsson 1990, Murray and Marcus 2002). The free prosome

segments carry a pair of swimming legs each. The antennules at the cephalothorax are very prominent in calanoid copepods and exceed the whole body in length. They have a species dependent amount of setae and carry mechanoreceptors (Légier-Visser et al. 1986). The mouth parts (mandibles, maxillules, maxillas, maxillipeds) are used for feeding, but also for slow swimming, and have chemoreceptors (Friedman and Strickler 1975, Poulet and Marsot 1978). By moving the swimming legs calanoid copepods can carry out rapid jumps (Westheide and Rieger 1996). Copepods have a so-called nauplius eye. The internal anatomy of copepods includes the circulatory, nervous, muscular, digestive, excretory, and reproductive systems.

(Reference if not further mentioned: Schriever et al. 1986)

1.2 Copepod Life Cycle

Copepods have a complex life cycle from the egg to the adult form, which includes six naupliar and five copepodite stages. Depending on the species and / or the distribution area, copepods produce from less than one (if individual development takes longer than one year) and up to 4 generations per year (Yamaguchi et al. 2003). Some copepod species undergo a diapause to survive unfavourable conditions or produce resting eggs to synchronise the hatching of the nauplii. Resting eggs lie on the sediment or float in a certain depth and the nauplii hatch when the environmental conditions again support the development into adult copepods. For example the development of *Temora longicornis* follows this pattern with the production of resting eggs in spring-summer (Castellani and Lucas 2003). Some copepods, e.g. *Calanus finmarchicus*, descend to deeper waters (up to 2000m) in winter to diapause as stage V copepodite, moult into adults in the following year, and lay eggs so that the new generation hatches, often synchronised with the beginning of the algal spring bloom (Hopkins et al. 1984, Madsen et al. 2001).

1.3 Copepod Feeding

The perception of the trophic role of calanoid copepods has changed during the last decades. Traditionally they were viewed as pure herbivores that act as a link between primary production and planktivorous fish (Lowndes 1935, Marshall and Orr 1955a, Anraku and Omori 1963). Further research revealed the importance of the microbial loop, and showed that copepods are not herbivorous but mostly omnivorous, with microzooplankton being a component of their diet (Greene 1988, reviewed in Stoecker and Capuzzo 1990, Carlotti and Radach 1996, Kiørboe et al. 1996, Vincent and Hartmann 2001). To which extent the different prey groups (phytoplankton and microzooplankton) contribute to copepod diet is subject to much research and discussion.

In the 1990s the scientific community introduced the term “diatom-paradox” in the discussion about the role of diatoms as copepod food. Diatoms often form the majority of the phytoplankton in spring blooms, whereas post-bloom communities mainly are dominated by flagellates. The diatom-rich phytoplankton has been seen as the basis for copepod production in spring (Runge 1988, Turner 1984, Mann 1993). Diatoms as a group contain less lipids, carbohydrates and proteins per cell volume than dinoflagellates (Hitchcock 1982) and were questioned to be important and high quality food for copepods (Kleppel et al. 1991). Some species of diatoms were found to be inferior food for copepod egg production and / or hatching success, e.g. because of their lack of certain fatty acids (Støttrup and Jensen 1990, Kleppel 1993, Jónasdóttir and Kiørboe 1996, Turner et al. 2001). While some authors stated that diatoms are not only poor food, but toxic for developing embryos because of certain aldehydes and thus are “in fact inferior for copepod reproduction” (Ban et al. 1997), other authors commented that “neither field observations nor laboratory experiments have so far provided conclusive and ecologically meaningful tests of the hypothesis that diatoms in general are toxic to copepods and prevent their embryos from developing normally” (Jónasdóttir et al. 1998). Murray and Marcus (2002) showed for *Centropages hamatus* that simple unialgal or mixed diets are not the best food supply at all developmental stages, but that “an optimal diet fosters growth and survival at all stages and maximizes viable egg production, to ensure high recruitment to the next generation”.

Shifts in the relative extent of herbivory and carnivory have consequences for food chain length, the efficiency of energy transfer to higher trophic levels and the top-down control on phytoplankton (Williams et al. 1994, Sommer and Stibor 2002, Ward et al. 2005, Sommer and Sommer 2006). Omnivorous organisms can ingest their food in two different ways: unselectively proportional to the offer or via active selection of a preferred prey. In the first case a copepod would ingest 80% algal and 20% ciliate prey, if a mixture contains 80% algal and 20% ciliate prey. In the second case the copepod has the possibility either always to switch towards the most abundant prey or selectively towards rare prey items if a balanced diet is necessary, i.e. to gain special fatty acids (Murray and Marcus 2002).

The mechanistic basis for feeding differences lies in the morphology of feeding appendages (Petipa 1975, Schnack 1982) and determines together with the size of the copepods the size range of food particles that can be ingested. Copepods are thought to use different feeding modes depending on their species specific mouthparts and the movements that are possible with them (reviewed in Sanders and Wickham 1993, Greene 1988, Tiselius and Jonsson, 1990, Ohman and Runge 1994, Nejstgaard et al. 1997).

Feeding behaviour of copepods is linked to their swimming behaviour (Greene 1988). The nowadays most common way of categorization is to distinguish between: (1) slow-moving or stationary suspension feeding (*Temora longicornis*, *Pseudocalanus elongatus*, and *Paracalanus parvus*); (2) fast swimming interrupted by sinking periods (*Centropages typicus* and *C. hamatus*); (3) motionless sinking combined with short jumps (*Acartia clausi*) (Tiselius and Jonsson 1990). For *C. hamatus* Hwang and co-workers (Hwang et al. 1994) defined four possible behavioural modes: (1) slow-swim (movement of feeding appendages only); (2) break (no appendages moving); (3) fast-swim (posteriorly-directed movement of first antennae and pereopods); (4) groom (brushing of first antennae through feeding appendages).

The two mostly discussed feeding modes are suspension and ambush feeding.

Suspension feeding copepods move slowly and generate a feeding current by movements of their feeding appendages. Thus they drive a flow field along their mouthparts (Jonsson and Tiselius 1990) and hold back or reject the particles within, depending on size, shape and "taste". According to the general opinion, suspension feeding is most efficient on non-motile prey. In order to find enough food at low food concentrations, copepods have to increase the rate of the water processed. At maximal water through-put the ingestion rate has to correlate linearly to food concentration. Below a certain concentration limit they could end up with spending more energy on the production of the feeding current than will be gained from the food. Therefore, it seems adaptive that suspension feeding should stop below a threshold concentration. When low food concentration is considered in terms of biovolume this would apply to few larger prey items, or food particles that have a relatively high concentration in numbers but are very small. On the other hand also moving prey might be captured by suspension feeding when the escaping speed of the prey item is insufficient for avoiding the feeding current created by the copepod. In this case suspension feeding could be energetically more favourable than ambush feeding on motile but small prey when the concentration is high enough (Jonsson and Tiselius 1990).

Ambush feeding copepods hang motionless in the water column or sink slowly while waiting for prey signals. Moving prey items induce a deformation of the laminar flow around them and the copepod can detect these hydromechanical signals with sensory detectors located at the antennules (Barrientos Chacon 1980, Landry 1980, DeMott and Watson 1991, Svenson and Kiørboe 2000, Maar et al. 2006). Then the copepod jumps towards the source of the signal and captures the prey item if it is of suitable size and does not escape (Jonsson and Tiselius 1990, Bundy et al. 1998). Copepods do not react on chemical or visual signals when it comes to moving prey (DeMott and Watson 1991), but chemical signals (e.g. odour of amino acids) play an important role for copepods feeding on sinking detrital aggregates (Kiørboe and Thygesen 2001, Maar et al. 2006). Large non-motile prey could also cause

hydromechanical signals by streamline deformations around them in their paths and therefore can be detected by an ambush feeding copepod (Bundy et al. 1998). The calanoid freshwater copepod *Diaptomus sicilis* generates a feeding current in slow swimming bouts and phytoplankton cells (*Cyrtomonas reflexa*, ESD: 12µm) are entrained in flow toward the mouthparts. The capture of large inert particles (polystyrene beads, ESD: 50 µm) by the same copepod species on the other hand did not involve the feeding current. The stimulus in this case must be a hydromechanical signal (Haurey et al. 1980 in: Bundy et al. 1998). Therefore, swimming behaviour plays an integral role in prey detection (Bundy et al. 1998). But if the motile prey is relatively small and occurs in high concentrations ambush feeding could be less effective, speaking in amount of prey ingested per time, than suspension feeding. The threshold concentration for ambush feeding copepods should be lower than that for suspension feeding because the copepods react specifically on received signals and therefore do not “waste” any energy for searching or creating a feeding current.

Non-motile prey is usually algal prey (except for eggs at appropriate size) and copepods which can / do only capture non-motile prey therefore are strictly herbivorous. Motile prey consists of moving algae (e.g. flagellates) and microzooplankton, such as ciliates. But sometimes ciliates contain pigments because of endosymbionts. In this case the copepod that only feeds on the ciliates cannot be defined as carnivorous *per se*, but is rather omnivorous. Furthermore, algae and ciliates that are suitable copepod food often overlap in their size range (Hansen et al. 1994). This leads to the idea that most of the copepods that feed on the microfraction of plankton are omnivorous.

Koehl and Strickler (1981) used high-speed filming to reveal the movement of the feeding appendages in calanoid copepods during the feeding process (see Fig. 1 for configuration of copepod mouthparts). They found that the feeding appendages which are only fractions of a millimetre long move at rates of 20-80 Hz. The second maxillae periodically actively capture parcels of water containing algal cells, which are then pushed into the mouth by the endites of the first maxillae. Algal cells are usually redirected without actually being touched by the feeding appendages (Fig. 2).

The length of the functionally wide and smooth, rather than comblike, setae of the second maxillae and the spacing between them surely determine which physical types of particles that likely to bump into the second maxillae, and which algae are retained in the closing basket. Intersettle distance of maxillary setae, which is thought to be indicative of the minimum particle size that can be removed from the water, varies between 3.5 and ~6.0 µm (Yamaguchi et al. 2003).

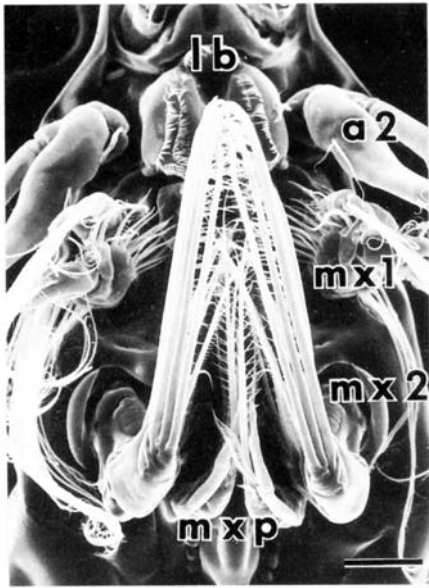


Figure 1 - Ventral view of the mouthparts of a female *Labidocera japonica* (Pontellidae). The species is omnivorous. SEM. The mouthparts shown are: lb-labrum; a2-second antenna; mx1-first maxilla; mx2-second maxilla; m xp-maxilliped. Scale bar is 0.1 mm. (After Ohtsuka and Onbé 1991)

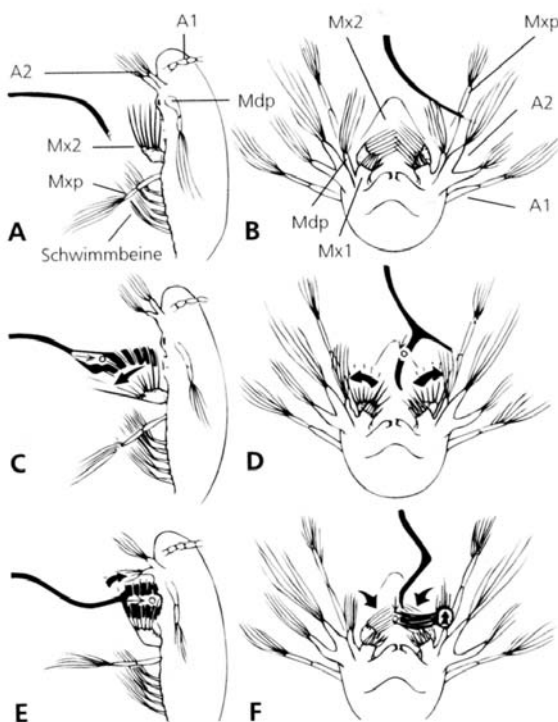


Figure 2 - Feeding mechanism of *Eucalanus pileatus*. Feeding appendages are: A2-second antenna; Mdp-mandibular palp; Mx1-first maxilla, Mx2-second maxilla; Mxp-maxilliped. Other structures labelled are: A1-first antenna and swimming legs. Black streaks are dye streams from a micropipette. Heavy arrows indicate movements of the second maxillae (and of the first maxilla in F). Circles represent the positions and fine arrows indicate the movement of algae observed during appendage motions. In the first column the copepod is viewed from its left side and the first maxilla has been left off for clarity. In the second column the copepod is viewed from its anterior end. Feeding currents bypass the second maxillae (A-B) until an alga nears them. The alga is captured by an outward fling (C-D) and an inward sweep (E-F) of the second maxillae. (After Koehl and Strickler 1981)

Koehl and Strickler (1981) examined the copepods *Eucalanus pileatus* and *Centropages typicus* and found that *E. pileatus* rejects captured material by pushing the second maxillae, and thus shoves the material away from the body and “detaches” it from the second maxillae by spreading the medial maxillary setae and expelling water between them as they rapidly move inward (Fig. 2). The authors concluded that variations of this basic pattern of scanning and capturing movements seem to be characteristic of different copepod species. Additionally, *E. pileatus* and *C. typicus* move their swimming legs slightly rearward

at the beginning of the scanning bout and then hold them stationary. *Calanus finmarchicus* keeps up a rapid vibration (about 600 per minute) of the mouthparts, with their setae spread out as a fan. The antennae, mandibular palps and first maxillae create a swirl on each side with the swimming *Calanus* in the centre, reaching to the first free thoracic segment (Marshall and Orr 1955a).

Feeding movements of an individual copepod seem to be modified under different food conditions, such as different sizes and concentrations of food particles (Koehl and Strickler 1981). If copepods are herbivorous or carnivorous, and whether they switch between different feeding modes has consequences for phyto- and microzooplankton communities as well as for food web interactions (Stibor et al. 2004). By feeding mainly on microphytoplankton they can suppress the primary production and even the phytoplankton standing stock (Li and Wang 2000, Halvorsen et al. 2001, King and LaCasella 2003). If copepods prefer microzooplankton, e.g. ciliates, as prey, they could trigger a cascading effect where the reduced grazing pressure by ciliates can result in an increase of nanophytoplankton (Vadstein et al. 2004, Sommer et al. 2005).

1.4 Functional Response Types

A functional response is the “change in the rate of exploitation of prey by an individual predator as a result of a change in prey density” (Ricklefs 2001). Functional responses of predators are determined by their behaviour. Therefore a variety of responses differing in form, rate of rise, and final level reached is possible. If ecologists nowadays speak of a ‘Holling functional response’ they refer to one of the three types defined by the Canadian researcher in the late 1950’s (Holling 1959) (Fig. 3):

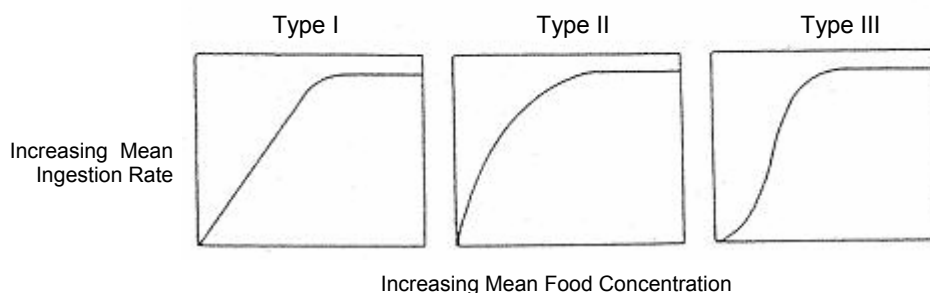


Figure 3 - Functional response types after Holling, 1959.

Type I – The searching pattern of the predator is random, and the rate of searching remains constant at all prey densities below the incipient limiting end. This means prey encounter is directly proportional to prey density, so that the rising phase is a straight line.

Type II – The number of prey attacked per predator increases very rapidly with initial

increase in prey density. Thereafter the increase becomes more slow approaching a certain fixed level. The searching rates become progressively less as prey density increases.

Type III – The final form of functional response is S-shaped. Rates of searching of the predator at first increase with increasing prey density, and then decrease.

The shape of the functional response types I and II has to do with whether the handling time (the time the copepod needs to process a food particle) is of significance or not.

1.5 Stable Isotopes

The data collected on copepod feeding behaviour help to determine the role of copepods in complex food webs. The knowledge about their trophic position is crucial for the development of models which calculate and predict food web interactions under changing environmental conditions (Gismervik and Andersen 1997, Neumann et al. 2003, Thingstad 2005). One tool to determine trophic positions is analysing the stable isotope ratio of some elements. In food web studies these elements usually are carbon ($^{12}\text{C}/^{13}\text{C}$ ratio) and nitrogen ($^{14}\text{N}/^{15}\text{N}$ ratio).

Carbon ($\delta^{13}\text{C}$) shows an average enrichment of only 1‰ per trophic level (DeNiro and Epstein 1976). Because the enrichment of carbon per trophic level is so small, it is rather used to identify the carbon source in a food web. Different carbon sources, e.g. benthic or pelagic, frequently have different $\delta^{13}\text{C}$ signals (e.g. Dunton and Schell 1987).

The enrichment in nitrogen ($\delta^{15}\text{N}$) of a consumer compared to its prey is approximately 3 to 4‰ (Minagawa and Wada 1984). The molecular bonds that contain the isotopically 'light' ^{14}N are preferentially broken during metabolic processes (Macko et al. 1986). Therefore excretion products are enriched in the 'lighter' ^{14}N isotope and the body tissue of the consumer becomes enriched in the 'heavier' ^{15}N isotope (DeNiro and Epstein 1976 and 1981).

A problem with the stable isotope ratios is that their fractionation obviously depends on the nutritional condition of the organisms, e.g. planktonic algae. Their stable isotope signal for nitrogen ($\delta^{15}\text{N}$) varies with their nitrogen source (NO_3^- , NH_4^+ , N_2). Several algae grown on different nitrogen sources showed a fractionation factor (ϵ) for nitrogen stable isotopes between -27.2‰ and 0‰. These fractionation differences caused variation in the $\delta^{15}\text{N}$ value of up to 50‰ (Pennock et al. 1996, Waser et al. 1998). Nitrogen limitation is another factor that influences the $\delta^{15}\text{N}$ signal of phytoplankton. If algal cells are limited by nitrogen, e.g. during a spring bloom, their fractionation factor will approach zero (Soyka 2006). Therefore the same algal species in laboratory cultures can have stable isotope ratios which markedly differ from each other, depending on their nitrogen supply (limiting or not).

Natural samples of the same species can also show variation within species depending on the nitrogen source they use (Montoya and McCarthy 1995). Furthermore, nitrogen isotope fractionation seems to be species dependent, ranging from $2.2 \pm 0.2\text{‰}$ to $6.2 \pm 0.4\text{‰}$ for several phytoplankton species grown under the same conditions (Needoba et al. 2003). This variation in algal fractionation of stable isotopes can cause difficulties in interpreting stable isotope signals of higher trophic levels, since algal stable isotope signals are necessary to get a baseline for trophic position one. Because of the high variability in algal $\delta^{15}\text{N}$ some researchers used filter feeding mollusc as a baseline for trophic position two when analysing food web relationships via stable isotopes (e.g. Post 2002). In animals the stable isotope values depends additionally to their food source also on the tissue of which the sample originates (DeNiro and Epstein 1981).

1.6 *Calanus finmarchicus* and *Centropages hamatus*

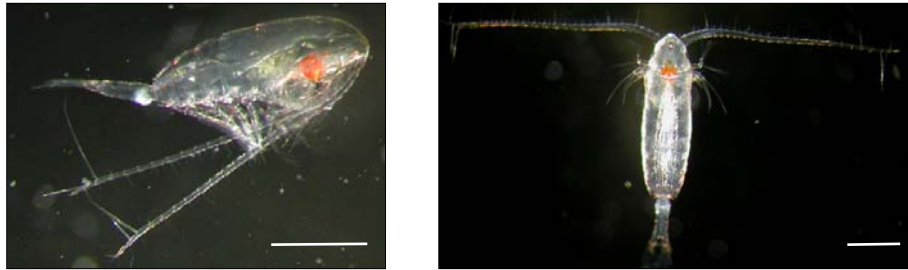


Figure 4 - *Calanus helgolandicus* (sibling species to *Calanus finmarchicus*). Photographs of living specimens found in the Kiel fjord, Germany in spring 2006. Scale bars are 1 mm. Photographies by A. Saage.

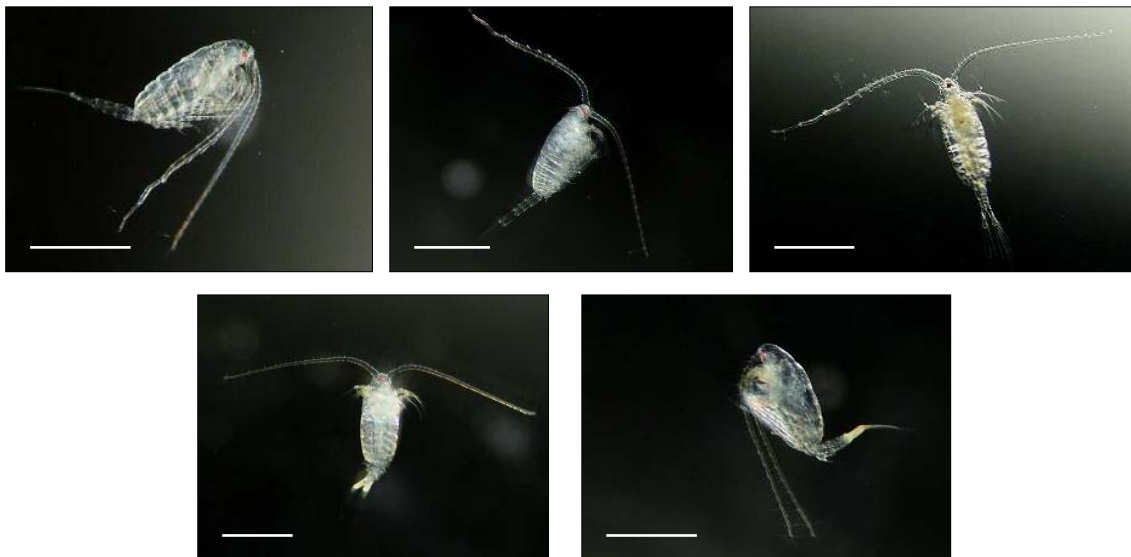


Figure 5 - *Centropages hamatus*. Photographs of living males (upper row) and females (lower row) found in the Kiel fjord, Germany in summer 2006. Scale bars are 1 mm. Photographies by A. Saage.

1.6.1 General Biology

Calanus finmarchicus is a cold water species with a distribution that covers the Northern Atlantic Ocean ranging from Greenland in the west to the island of Novaya Zemlya (Новая Земля) in the east, and from the Svalbard archipelago in the north to the Gulf of Maine in the south (30°N to 80°N, 80°W to 90°E) (Schriever et al. 1986, Speirs et al. 2006). It even has been reported in the icy Polar basin up to and beyond 85° of latitude, and as far east as the Bering Islands and the Ochotsk Sea (Sars 1903, Mori 1964). The distribution is limited by temperature and salinity ranges from -2 to 22°C and 29 to 35 ‰, respectively (Marshall and Orr 1955a). As many pelagic copepods *C. finmarchicus* has a pellucid body, sometimes more or less tinged or red (Sars 1903). Its total length is temperature dependent and varies between 2.7 to 5.4 mm for adult females, whereas adult males can reach 2.3 to 3.6 mm (Sars 1903, Marshall and Orr 1955a, Brodskii 1950). The weight can vary between 0.19 mg dry weight in the English Channel and 0.67 mg dry weight in the Barents Sea (Marshall and Orr 1955a). The life cycle of *C. finmarchicus* starts with an egg of an average size of 145-151 µm (Marshall and Orr 1955a, McLaren et al. 1988). Individual development time from hatching until adult form varies with temperature between 30 and 140 days (Uye 1988). Consequently the total life span covers a very wide range from approximately 70 to 80 days in the Gulf of Maine and the English Channel, where three generations per year are possible, to more than one year in the Norwegian Sea and further north (Marshall and Orr 1955a). If *C. finmarchicus* has only one generation per year, e.g. along the Norwegian coast, the diapause of CV copepodites starts in June, and they rely completely on the energy stored in the prominent oil sac during the winter months in deeper waters. In arctic regions lipids in the oil sac can account for 50 to 70% of the copepod dry weight and are mostly wax esters. In the following February / March CV stages moult into adult females and males and ascent to the surface. Spawning takes place in April and the new generation develops during the following months (Corner and O'Hara 1986). In Arctic regions with lower temperatures the cycle starts already in January / February with the ascent of adult *C. finmarchicus* to surface waters, and the new generation descends to the depth not before July / August (Marshall and Orr 1955a). In the Norwegian Sea *C. finmarchicus* is more abundant adjacent to shelf slopes than in oceanic areas. Its typical overwintering abundance (600-1200 m depth) is 30.000 – 38.000 individuals m⁻² (Edvardsen et al. 2006). Around Iceland an average annual biomass (upper 100m) of ~1500 mg C m⁻² and ~600 mg C m⁻² has been reported on the shelf and oceanic area, respectively. Maximum values of up to ~2200 mg C m⁻² were reached in early summer (Gislason 2005).

Calanus finmarchicus is of considerable economic importance as an important prey item for the juvenile stages of cod (*Gadus morhua*) and whiting (*Merlangius merlangus*)

(Fjøsne and Gjørseter 1996, Brander et al. 2001), as well as for planktivorous fish such as herring (*Clupea harengus*) and mackerel (*Scomber scombrus*), and whales, such as the sei-whale (*Balaenoptera borealis*), in the North Atlantic and adjacent seas (Sars 1903, Brodskii 1950, Melle et al. 1994).

The genus *Centropages* was established as early as 1848 by Krøyer and in 1853 the Swedish zoologist Wilhelm Lilljeborg (1816-1908) described the copepod *Ichthyophorba hamata* which today is known as *Centropages hamatus* (Sars 1903). It is an epipelagic planktonic species, found primarily in coastal waters (Boxshall and Halsey 2004). It is distributed in the Atlantic Ocean from 35° to 81° northern latitude, as well as in the North and Baltic Sea (Sars 1903, Klekowski and Weslawski 1991). A maximum field concentration of 722 individuals m⁻³ has been reported for the Westport River estuary, Massachusetts (Conley and Turner 1985). Both sexes are highly pellucid and nearly colourless as typical for planktonic copepods (Sars 1903). The average length of wild *C. hamatus* varies for adult females between 1.1 and 1.7 mm, for males between 1.3 and 1.5 mm (Sars 1903, Line 1980, Klekowski and Weslawski 1991, Hirche 2004). *C. hamatus* can be found the whole year round in the plankton of the Baltic Sea. Reproduction takes place in cycles and starts, in the Baltic Sea, in spring when the water temperature reaches 6°C (Line 1980). Adult females produce eggs with branched spines of a mean diameter not including the spines of 78.8 ± 1.3 µm. The spine length is 7.5 ± 2.5 µm (Castellani and Lucas 2003) and the carbon content is 37.4 ng (Kiørboe et al. 1985). Dependent on the temperature in the upper water layers *C. hamatus* can produce 3 to 4 generations per year. In the Baltic Sea the individual developmental time from hatching to the adult form is approximately 60 days in spring and 30 to 45 days in summer. At the end of October the individual development stops and the copepodites of stage III to IV descend to deeper water layers (Line 1980). Fryd and colleagues (Fryd et al. 1991) reported a developmental time of ~17 days from egg to adult for laboratory reared *C. hamatus* (25‰, 16.5 - 17.5°C).

C. hamatus, as *C. finmarchicus*, forms an essential part of the food of pelagic planktivorous fish, such as herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) (Sars 1903).

1.6.2 Feeding Behaviour

The description of the feeding behaviour of *Calanus finmarchicus* in the literature has changed with time. Marshall and Orr (1955a) cite Lowndes (1935) who described *Calanus* as a mainly selective feeder, but stated in the same publication that it is a filter feeder. Mullin (1963) observed that copepods of the genus *Calanus* generally removed large cells at higher rates when feeding on a phytoplankton mixture. Nevertheless, *Calanus* was still categorised

as an unselective herbivorous filter feeder by Anraku and Omori (1963), Petipa (1975) and Runge (1980). Schnack (1982) described the maxillae of the genus *Calanus* as passive, stationary organs which only serve as a filter. Huntley and colleagues (Huntley et al. 1983) found that the species *Calanus pacificus* can discriminate between the diatom *Thalassiosira weissflogii* and similar sized polystyrene beads. With further research the feeding behaviour of *Calanus* then was described as omnivore (Greene 1988, Stoecker and Capuzzo 1990, Carlotti and Radach 1996). Publications that confirm that the genus *Calanus* is capable of switching between different feeding modes are e.g. from Sanders and Wickham (1993), Ohman and Runge (1994) and Nejstgaard and colleagues (Nejstgaard et al. 1997). In 1998 Irigoien and coworkers (Irigoien et al. 1998) stated that it also ingests detritus. Since then further research has been carried out to determine feeding rates of *Calanus* on different prey items under different feeding conditions, e.g. Nejstgaard et al. (2001a), Calliari and Tiselius (2005), Poulsen and Kiørboe (2005).

Centropages hamatus is considered to be an omnivorous copepod (Anraku and Omori 1963, Conley and Turner 1985) which feeds on microzooplankton such as ciliates in addition to phytoplankton (Tiselius 1989). It spends feeding time either swimming or sinking. Greene (1988) observed switching between slow-swimming and fast-swimming modes. Tiselius and Jonsson (1990) described the feeding behaviour of *C. hamatus* as fast (ca 5 mm s⁻¹) cruising swimming interrupted by sinking periods, whereas Hwang and co-workers (Hwang et al. 1994) observed slowly upward swimming during suspension feeding, or sinking while on break.

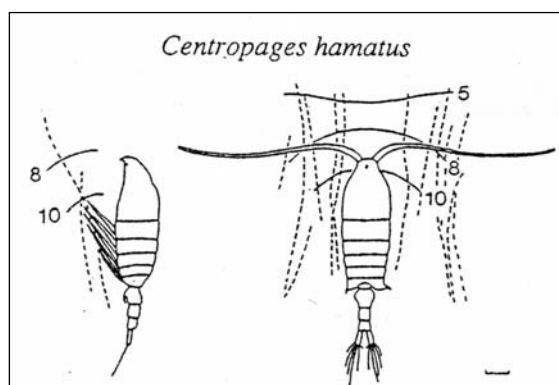


Figure 6 - Flow fields based on tracing of particles. Broken lines indicate trajectories of single particles and continuous isolines show flow velocity (mm s⁻¹) relative to the copepod. Scale bar = 0.2 mm. (After Tiselius and Jonsson 1990)

1.6.3 The Experiments

Does *Calanus finmarchicus* feed selectively and does it switch between feeding modes when prey items are changing in quality and quantity?

To answer this question I performed:

- a functional response experiment with an algal prey species (*Gymnodinium galatheanum*, equivalent spherical diameter (ESD): 12 μm).
- a functional response experiment with ciliate prey (*Strombidium* sp., ESD: 25 μm).
- two size selectivity experiments with a mixture of different sized algae (*Prymnesium patelliferum*, ESD: 6 μm , *Tetraselmis* sp., ESD: 9 μm , *Prorocentrum minimum*, ESD: 15 μm , *Scrippsiella trochoidea*, ESD: 20 μm , and *Gyrodinium aurelium*, ESD: 22 μm) in varying individual concentrations at limiting and saturating food concentrations.

(see table 1 for taxonomic details of the prey items)

To investigate the trophic position of *C. finmarchicus* in the Trondheim Fjord I took monthly samples of wild specimens and determined their $\delta^{15}\text{N}$ signals. A lab experiment was set up to determine isotopic fractionation of ^{15}N by various stages of the species which were fed a pure algal diet.

Does *Centropages hamatus* feed selectively and does it switch between feeding modes when prey items are changing in quality and quantity? Is there a difference in feeding behaviour between male and female specimens?

To answer these questions I performed:

- two functional response experiments with algal prey (*Rhodomonas* sp., equivalent spherical diameter (ESD): 11 μm ; *Thalassiosira weissflogii*, ESD: 14 μm).
- a functional response experiment with ciliate prey (*Rimostrombidium caudatum*, ESD: 45 μm).
- a switching experiment with an algae-ciliate-mixture as food source (*Thalassiosira weissflogii* and *Rimostrombidium caudatum*).

(see table 1 for taxonomic details of the prey items)

Feeding Behaviour Of Marine Calanoid Copepods

Table 1 - Taxonomic classification of the organisms used in the experiments.
(Sars 1903, Kahl 130-1935, Tomas (ed.) 1993, Tomas (ed.) 1996, Storch and Welsch 1999, Agatha 2004)

Kingdom	Metazoa
Phylum	Arthropoda
Subphylum	Crustacea
Class	Maxillopoda
Subclass	Copepoda
Order	Calanoida
Family	Calanidae
Genus	<i>Calanus</i>
Species	<i>Calanus finmarchicus</i>
	Family
	Centropagidae
	Genus
	<i>Centropages</i>
	Species
	<i>Centropages hamatus</i>
Kingdom	Protista
Phylum	Ciliophora
Class	Oligotrichea
Subclass	Oligotrichia
Order	Oligotrichida
Family	Strombidiidae
Genus	<i>Strombidium</i>
Species	<i>Strombidium sp.</i>
	Order
	Choreotrichida
	Family
	Strombidiidae
	Genus
	<i>Rimostrombidium</i>
	Species
	<i>Rimostrombidium caudatum</i>
Division (Phylum)	Chromophyta
Class	Cryptophyceae
Order	Cryptomonadales
Family	Cryptomonadaceae
Genus	<i>Rhodomonas</i>
Species	<i>Rhodomonas sp.</i>
	Class
	Dinophyceae [dinoflagellates]
	Order
	Prorocentrales
	Family
	Prorocentraceae
	Genus
	<i>Prorocentrum</i>
	Species
	<i>Prorocentrum minimum</i>
	Order
	Gymnodiniales
	Family
	Gymnodiniaceae
	Genus
	<i>Gymnodinium</i>
	Species
	<i>Gymnodinium galatheanum</i>
	Genus
	<i>Gyrodinium</i>
	Species
	<i>Gyrodinium sp.</i>
	Order
	Peridinales
	Family
	Calciodinellaceae
	Genus
	<i>Scrippsiella</i>
	Species
	<i>Scrippsiella trochoidea</i>
	Class
	Prymnesiophyceae
	Order
	Prymnesiales
	Family
	Prymnesiaceae
	Genus
	<i>Prymnesium</i>
	Species
	<i>Prymnesium patelliferum</i>
	Class
	Bacillariophyceae [diatoms]
	Order
	Biddulphiales [centric diatoms]
	Family
	Thalassiosiraceae
	Genus
	<i>Thalassiosira</i>
	Species
	<i>Thalassiosira weissflogii</i>
Division (Phylum)	Chlorophyta
Class	Prasinophyceae
Order	Chlorodendrales
Family	Chlorodendraceae
Genus	<i>Tetraselmis</i>
Species	<i>Tetraselmis sp.</i>

2 Material and Methods

2.1 Culture and Maintenance of Experimental Organisms

Calanus finmarchicus was caught in the Trondheim fjord (salinity 34‰) with a 100 µm-plankton-net (Nansen Closing Net, Hydro-Bios Kiel, Germany) with an opening diameter of 70 cm and a length of 300 cm. The net had a closed collecting cylinder (diameter 9.5 cm, length 22 cm) at the bottom end to avoid the copepods from being damaged. The catching depth varied between 150 and 300 metres depending on the sampling sites. Until I used the copepods in experiments they were kept in three litre jars with filtered, pasteurized seawater (salinity 34‰) at 15°C in darkness, and fed with the dinoflagellate *Gymnodinium galatheanum*.

The algal species used in the experiments were *Gymnodinium galatheanum*, *Tetraselmis* sp., *Prymnesium patelliferum*, *Prorocentrum minimum*, *Gyrodinium aurelium* and *Scrippsiella trochoidea*. They were grown in F/2-medium (Guillard 1983) at 15°C. *G. galatheanum*, *Tetraselmis* sp., *P. patelliferum*, *P. minimum* and *G. aurelium* originated from stock cultures at Trondheim Biological Station, Norway. *S. trochoidea* was obtained from the University in Oslo, Norway.

The ciliate *Strombidium* sp. was cultivated in tissue culture flasks in F/2-medium without macronutrients (only vitamins and microminerals were added to the filtered, pasteurized seawater with a salinity of 34‰) and fed the flagellate *Nephroselmis pyriformes*. The ciliate and its food alga *N. pyriformes* were also obtained from the University in Oslo, Norway.

Centropages hamatus was caught in the Kiel fjord (salinity 15-18‰) with a 200 µm-plankton-net (WP2 Closing Net, Hydro-Bios, Kiel). The net had a closed collecting cylinder (diameter 16 cm, length 30 cm) at the bottom end to avoid the copepods from being damaged. The maximum catching depth was 18 metres. Until I used the copepods in the experiments adult males and females were kept separately in three litre jars with filtered, pasteurized seawater (same salinity as in the fjord) at 10 to 15°C, and regularly fed the flagellate *Rhodomonas* sp. and the diatom *Thalassiosira weissflogii*.

Rhodomonas sp. and *T. weissflogii* were grown at 15°C in Drebes-medium (von Stoch and Drebes 1964), but the nutrient concentrations were increased to values typical of F/2-medium (Guillard 1983). The algae species originated from stock cultures at the Leibniz Institute for Marine Sciences, Kiel.

In March 2006 I isolated *Rimostrombidium caudatum*, an oligotrich ciliate, from the Kiel fjord. I used it as a prey item in the experiments with the copepod *C. hamatus*. The ciliate culture was kept in cell tissue flasks filled with 0.2 µm filtered, pasteurized sea water in a climate chamber at a temperature of 10° C at a light intensity between 100 and 150 µE m⁻² s⁻¹. In regular intervals the ciliates were fed the marine flagellate *Rhodomonas* sp. grown on the same medium as mentioned above.

I took photographs of fixed samples to identify the ciliate species used as prey. Samples fixed with Lugol's iodine (1% final solution) were photographed with the digital camera Nikon Coolpix 5000 through an inverted microscope (Zeiss Axiovert 200). Some of the Lugol-fixed samples were coloured with DAPI and photographs were taken, with the same digital camera mentioned above, under UV-light conditions using the microscope Leica Leitz DM RB. Some other samples were fixed with formalin (1% final solution) and prepared to be processed by a scanning electron microscope (SEM) (Zeiss DSM 940). These studies identified the ciliate as the species *Rimostrombidium caudatum* (Kahl, 1932) (Agatha and Riedel-Lorjé 1998, Agatha personal communication). In some culture flask *R. caudatum* was forming resting stages because of unknown reasons. These cysts are documented here by photographs, and samples have been sent to Dr. S. Agatha and Prof. W. Foissner, University Salzburg, Austria for further analyses. Unfortunately, no results have been available before this study was printed.

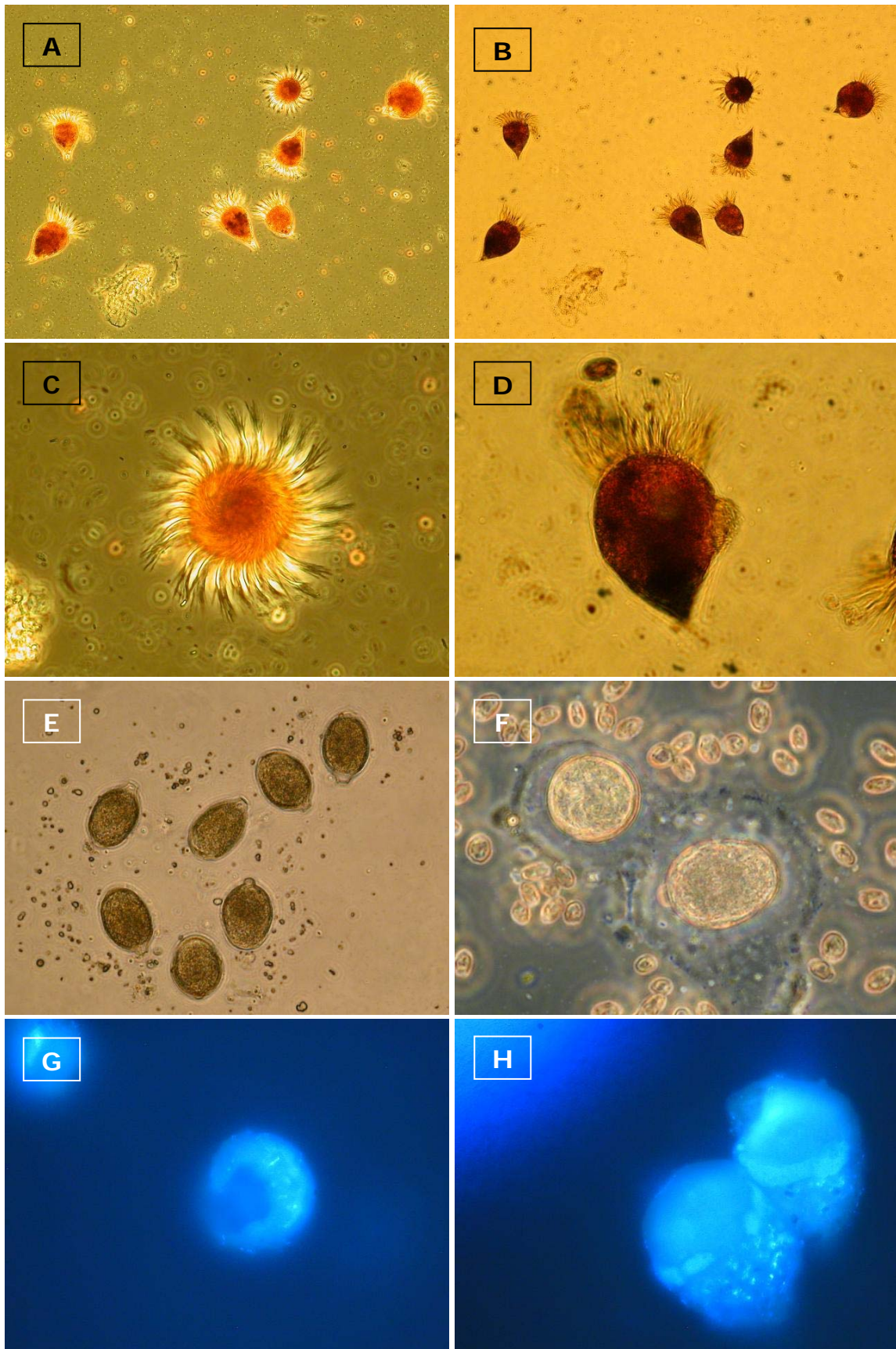


Figure 6 - *Rimostrombidium caudatum*. Cell size of the living ciliate is 35 - ~50 μm . Lugol-fixed sample of the ciliate in phase contrast (A, C) and in light field (B, D). The observed cyst (see text for further details) alive in light field (E) and phase contrast (F). DAPI coloured ciliate samples under UV-light which show the horse-shoe shaped macronucleus (G, H). Photographies by A. Saage.

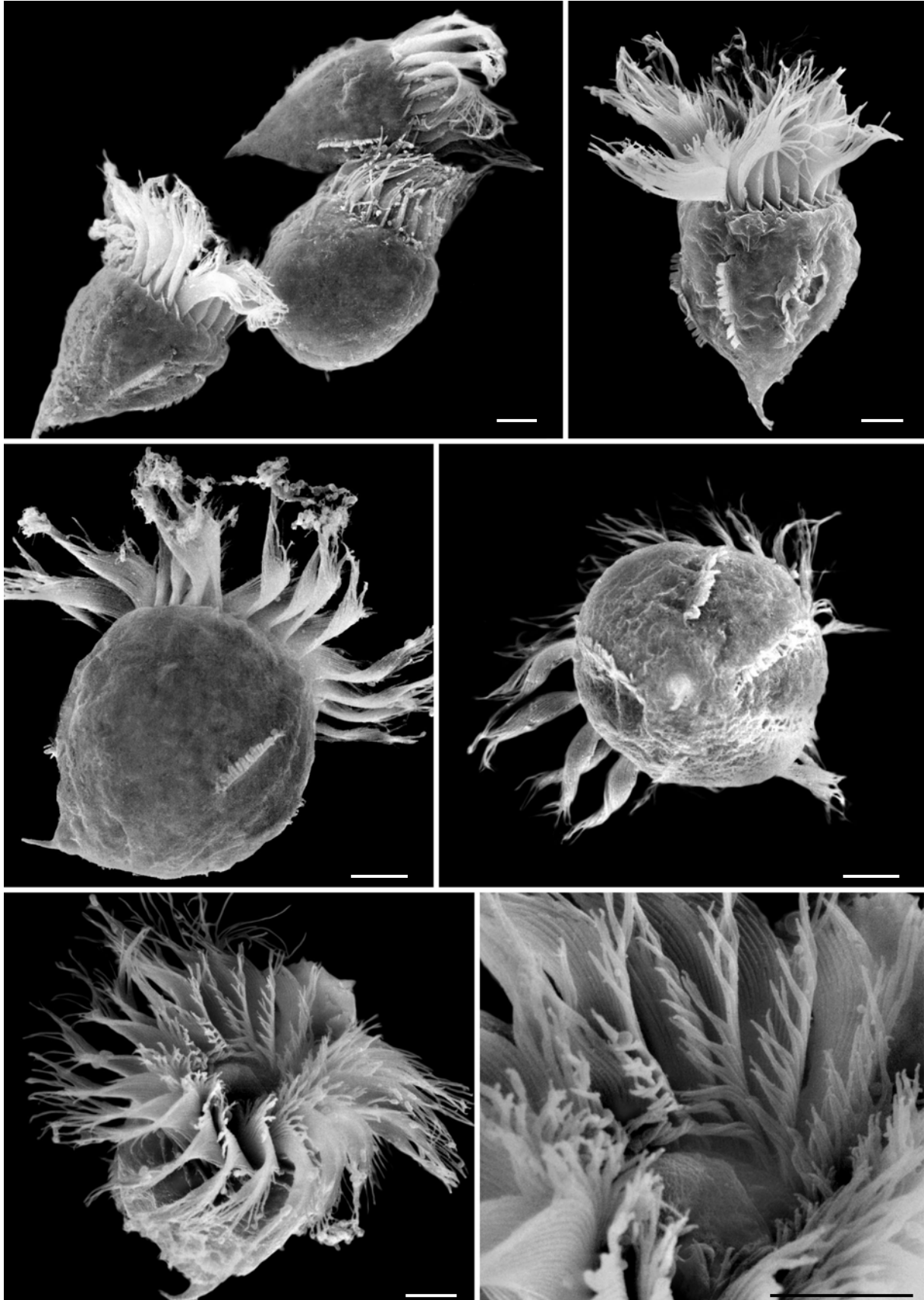


Figure 7 - *Rimostrombidium caudatum*. Images of the ciliate under a scanning electron microscope. Cell size of the living ciliate is 35 - ~50 μm . Scale bar is 5 μm . Photographies by A. Saage, editing by S. Agatha.

2.2 Functional Response Experiments

I performed laboratory experiments to determine the functional responses of *Calanus finmarchicus* and *Centropages hamatus* on different prey organisms. The copepods were incubated in darkness for several hours at different prey concentrations. A plastic pipette was used to transfer single copepods to 100 ml brown glass bottles with filtered, pasteurized seawater. The experiments were started by adding the prey organisms, and stopped by adding acid LUGOL's solution to a final concentration of 1%. The experimental set up included replicates with copepods, controls without copepods, and a start value before incubation. All copepods used in one experiment were the same stage (copepodite CV or adult).

C. finmarchicus was offered an algal and ciliate prey in two laboratory experiments. The first experiment with the dinoflagellate *Gymnodinium galatheanum* as prey was performed in November 2003, and the second with the ciliate *Strombidium* sp. as prey in September 2004. One day prior to the ciliate experiment *C. finmarchicus* was fed the ciliate *Strombidium* sp..

In the first experiment I used ten different concentrations of *G. galatheanum* arranged on a linear scale between 35 and 275 $\mu\text{g C l}^{-1}$ with five replicates of each concentration. To calculate carbon per algal cell I determined cell volume with a particle counter (CASY® Model TTC) assuming 0.14 pg carbon femtolitre⁻¹ (Rocha and Duncan 1985). The particle counter was also used to count the algae at the end of the experiment. Controls without animals were set up for the lowest, the intermediate and the highest concentration with two, one and two replicates, respectively. A start value was measured for the lowest, the intermediate and the highest concentration. The incubation time was four hours. The copepods were copepodite stage V.

In the second experiment ten different concentrations of *Strombidium* sp. between 2 and 170 $\mu\text{g C l}^{-1}$ were arranged in a geometric progression with two replicates of each concentration. The ciliates were measured, and counted at the end of the experiment, using an inverted microscope (Utermöhl 1958), and the carbon content per cell was calculated assuming 0.19 pg carbon μm^{-3} (Putt and Stoecker 1989). Controls without copepods were set up for the concentrations 2, 35 and 170 $\mu\text{g C l}^{-1}$, with two replicates each. Start values were measured for the lowest, the intermediate and the highest concentration. The copepods were adult females.

Table 2 gives an overview of the different experiments performed with *C. finmarchicus*, the prey species that were offered, as well as the characteristics (developmental stage, carbon content, length) of the copepods.

Table 2 - Overview over the experiments (functional response and size selectivity) with description of *Calanus finmarchicus* and the prey species that were used.

Experiment	Prey		<i>Calanus finmarchicus</i>		
	Species	ESD [µm]	Stage	Carbon content ¹ [µg]	Length ² [mm]
Functional response	<i>G. galatheanum</i>	12	C V	147	2.83
Functional response	<i>Strombidium sp.</i>	25	female	142	3.10
Size selectivity	<i>P. patelliferum</i>	6	female	142	3.10
	<i>Tetraselmis sp.</i>	9			
	<i>P. minimum</i>	12			
	<i>S. trochoidea</i>	~20			
	<i>G. aurelium</i>	~22			

ESD: Equivalent spherical diameter; ¹ mean value of copepods that were caught at the same time as those used in the experiments; ² values taken from Marshall and Orr, 1955a

Centropages hamatus was offered two algal and a ciliate prey species in three laboratory experiments. The first experiment with the flagellate *Rhodomonas sp.* as prey was performed in July 2005, the second with the diatom *Thalassiosira weissflogii* as prey in October 2005, and the third with the oligotrich ciliate *Rimostrombidium caudatum* as prey in May 2006. One day prior to the ciliate experiment *C. hamatus* was fed with the ciliate *R. caudatum*.

In the first experiment I used seven different concentrations of *Rhodomonas sp.* arranged on a linear scale between 4.5 and 100 µg C l⁻¹ with two replicates of each concentration. The flagellate cells were measured, and counted at the end of the experiment, using an inverted microscope (Utermöhl 1958), and the carbon content per cell was calculated by measuring the cells with the microscope followed by volume calculation with the help of a simple geometric equation. I assumed a carbon content of 0.14 pg C fl⁻¹ (Rocha and Duncan 1985). Controls without copepods were set up for the lowest, the intermediate and the highest concentrations with two replicates each. Start values were measured for all seven concentrations. The incubation time was six hours, the ambient temperature was 15°C, and the copepods were adult males or females.

In the second experiment ten different concentrations of *T. weissflogii* between 1.5 and 55 µg C l⁻¹ were arranged on a linear scale with two replicates of each concentration. The diatom cells were measured in the same way as described for the flagellate in the first experiment. Controls without copepods were set up for the lowest, the intermediate and the highest concentrations with two replicates each. Start values were measured for all ten concentrations. The incubation time was six hours, the ambient temperature was 15°C, and the copepods were adult males or females.

In the third experiment twelve different concentrations of *R. caudatum*, between 4.5 and 300 $\mu\text{g C l}^{-1}$ were arranged in a geometric progression with two replicates of each concentration. The ciliate cells were counted at the end of the experiment, using an inverted microscope (Utermöhl 1958). Cell Volume was determined as described above for the algae and carbon content per cell was calculated assuming 0.19 $\mu\text{g C } \mu\text{m}^{-3}$ (Putt and Stoecker 1989). For all twelve concentrations controls without copepods were set up, and start values were measured. The incubation time was six hours, the ambient temperature was 10°C, and the copepods were adult males or females.

2.3 Switching Experiment

Centropages hamatus was incubated at 10°C in darkness with a mixture of ciliate and diatom cells as prey. The diatom *Thalassiosira weissflogii* and the oligotrich ciliate *Rimostrombidium caudatum* were offered together to adult male or female *C. hamatus* in varying concentrations. The carbon concentrations for algal and ciliate carbon varied geometrically between 460 to 3.7 $\mu\text{g C l}^{-1}$ and 0.5 to 250 $\mu\text{g C l}^{-1}$, respectively. The total concentration of ciliate and algal prey together was $327 \pm 76 \mu\text{g C l}^{-1}$. A plastic pipette was used to transfer single copepods to 100 ml brown glass bottles with filtered, pasteurized seawater. I added five males or females into one bottle. For each concentration a control without copepods was set up, and a start value was measured. The experiment was started by adding the prey organisms, and stopped after six hours by adding acid LUGOL's solution to a final concentration of 1%.

Table 3 gives an overview of the different experiments performed with *C. hamatus*, the prey species that were offered, as well as the characteristics (developmental stage, carbon content, length) of the copepods.

Table 3 - Overview over the experiments (functional response and switching) with description of *Centropages hamatus* and the prey species that were used.

Experiment	Prey		<i>Centropages hamatus</i>		
	Species	ESD [μm]	Stage	Carbon content ^a [μg]	Length ^b [mm]
Functional response	<i>Rhodomonas</i> sp.	11	male / female	3.21 - 7.44	1.1 - 1.7
Functional response	<i>T. weissflogii</i>	12-27	male / female	3.21 - 7.44	1.1 - 1.7
Functional response	<i>R. caudatum</i>	35-50	male / female	3.21 - 7.44	1.1 - 1.7
Switching	<i>T. weissflogii</i>	12-27	male / female	3.21 - 7.44	1.1 - 1.7
	<i>R. caudatum</i>	35-50			

ESD: Equivalent spherical diameter; ^a mean minimum and maximum values of female *C. hamatus* taken from Hirche 2004; ^b values taken from Sars 1903, Line 1980, and Klekowski and Weslawski 1991

2.4 Size Selectivity Experiments

I studied *Calanus finmarchicus* in two laboratory experiments with two different final concentrations of an algae mixture in February and March 2004 to determine its size selectivity. I used two principles of mixture within the experiments: The algae species were mixed in equal biomass (variation (a)) and equal cell numbers (variation (b)).

In the February experiment the algal mixture was offered in “surplus” concentration and contained the species *Prymnesium patelliferum* (equivalent spherical diameter (ESD): 6 μm), *Tetraselmis* sp. (ESD: 9 μm), *Prorocentrum minimum* (ESD: 15 μm) and *Scrippsiella trochoidea* (ESD: 20 μm). For the dinoflagellate *Gymnodinium galatheanum* (ESD: 12 μm), that was used as food alga for *C. finmarchicus* under maintenance, an algal concentration of 100 $\mu\text{g C l}^{-1}$ corresponded to a cell number of $6.0 \cdot 10^5$ cells l^{-1} . Based on this intermediate sized alga I defined the target values for the “equal biomass” and the “equal cell number” treatments with 25 $\mu\text{g C l}^{-1}$ of each algae species (variation (a)) and $1.5 \cdot 10^5$ cells l^{-1} of each algae species (variation (b)), respectively. The realised total concentration in the experiment was 123 $\mu\text{g C l}^{-1}$. Each variation was replicated fivefold with two controls each, and the start values before incubation were measured.

In the March experiment I used the same algae with one exception: *S. trochoidea* was replaced with *Gyrodinium aurelium* (ESD: 25 μm), and the total algal concentration was kept “limiting”. Once more based on *G. galatheanum* (see above), a theoretical total algal concentration of 20 $\mu\text{g C l}^{-1}$ corresponded to a cell number of $1.2 \cdot 10^5$ cells l^{-1} . Thus 5 $\mu\text{g C l}^{-1}$ of each algal species were mixed for variation (a) (“equal biomass” treatments) and $3.0 \cdot 10^4$ cells l^{-1} of each algae species were mixed for variation (b) (“equal cell number” treatments). The realised total concentration in the experiment was 30 $\mu\text{g C l}^{-1}$. Replication and control bottles were set up, and the start values were measured as in the February experiment.

I used the particle counter (CASY® Model TTC) and the same measurements to calculate carbon per algal cell (assuming 0.14 $\mu\text{g C fl}^{-1}$; Rocha and Duncan 1985) as mentioned above (see 2.2 Functional Response Experiments). The copepods in both experiments were adult females (see table 2 for further details). They were transferred to the experimental bottles (100 ml) the day before the experiments were done. Experiments were initiated by adding a concentrated food mixture and stopped after six hours by adding acid LUGOL’s solution to a final concentration of 1%.

2.5 Trophic Position of *Calanus finmarchicus*

To evaluate the trophic position of *Calanus finmarchicus* in the Trondheim Fjord I took monthly samples. They were analysed for the stable isotope signatures of carbon ($\delta^{13}\text{C}$) and

nitrogen ($\delta^{15}\text{N}$). The same analyses were done for samples of *C. finmarchicus* which were raised for 3 consecutive generations on a pure algal diet in the laboratory. The laboratory raised animals were supplied by Dag Altin, Biotrix, Norway, and were originating from the cultures established as a part of the project “Long-term chronic effects of produced water effluents affecting reproduction in marine crustacean plankton” (170429/S40, Norwegian Research Council).

The wild specimens of *C. finmarchicus* were caught in the Trondheim Fjord (salinity 34 psu) with a 100 μm -plankton-net (Nansen Closing Net, Hydro-Bios Kiel, Germany) with an opening diameter of 70 cm and length of 300 cm. A collecting cylinder (diameter 9.5 cm, length 22 cm) at the bottom end kept the copepods from being damaged. The catching depth varied between 150 and 300 metre depending on the sampling sites.

The laboratory specimens of *C. finmarchicus* were reared in conical polystyrene tanks (280 litres) supplied with running natural seawater at a rate replacing the volume in the tank every second day. The inlet of the supplied seawater is located at 90 m depth outside Trondheim harbour (salinity 34 psu). Before entering the tanks the water was filtered down to a nominal particle size less than 70 micron by initial filtering through sand and to 1 micron by cartridge filters (Cuno, Meriden, Connecticut, USA. Model AP1001). The copepods were fed a mixture of the flagellates *Isochrysis galbana* (IsoT) (ESD: $\sim 5 \mu\text{m}$) and *Dunaliella tertiolecta* (CCAP 19/27) (ESD: $\sim 10 \mu\text{m}$). The mixture was prepared daily on an approximate 1:1 basis on cellular carbon, and were fed continuously into the cultures by a tubing pump (Watson-Marlow, Cheltenham, England. Model 202/U2).

All copepods were separated into the different developmental stages (CIII to adult) under a dissecting microscope, washed in distilled water and put into tin caps. The copepods were then dried at 60°C for 24 hours.

Enteromorpha sp. and *Chorda filum*, two ephemeral algae species, were collected from the littoral zone in the Trondheim fjord when the tide was low to get a trophic position one – baseline. The samples were dried (60°C , 24 hours), pulverised and put into tin caps.

I. galbana and *D. tertiolecta* were grown in autoclaved seawater (121°C for 15 minutes) enriched with Conwy medium (1ml l^{-1} SW, Walne 1974) in aerated semi-batch in 1.5 l PET-bottles culture at $15\pm 1^\circ\text{C}$. The cultures were grown under continuous illumination from one side with fluorescent tubes (Philips TLD 36W, 965) at a nominal intensity of $100\text{--}120 \mu\text{E m}^{-2} \text{s}^{-1}$. To keep the algae in exponential growth approximately 80% of the culture was harvested every third day.

Samples of the algae were harvested from the cultures to determine the baseline of trophic level one (primary production). Aliquots of *D. tertiolecta* were filtered on Whatman GF/C filters (25mm \varnothing) to give nominal $50 \mu\text{g N}$ calculated on basis of cell density. After

gently drying the filters by suction, the filters were dried at 60°C for 24 hours. Due to clogging of the filters before the nominal 50 µg N were deposited, aliquots of *I. galbana* were concentrated by centrifuging at 2000 rpm (Hettich Universal 32R) at 15°C for 10 minutes. After centrifuging the supernatant was discharged, and the algal pellet were resuspended in 1.5 ml seawater, transferred to 2 ml Eppendorf tubes and recentrifuged for 10 minutes at 15°C. After gently discharging the supernatant with a pasteur pipette, the remaining pellets were dried in the tubes at 60°C for 24 hours. A sample of sodiumnitrate (NaNO₃) was put into tin-caps and analysed to determine the δ¹⁵N signature of the nitrogen source in the Conwy-medium.

The dried samples were stored in a dissector until combustion in a CHN-analyser (Fisons, 1500N) connected to a Finnigan Delta Plus mass spectrometer. δ¹⁵N (and δ¹³C) signatures were calculated as

$$\delta^{15}N \text{ or } \delta^{13}C[\text{‰}] = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000, \quad (1)$$

where R is (¹⁴N/¹⁵N) or (¹²C/¹³C). Pure N₂ and CO₂ gas were used as a primary standard and calibrated against IAEA reference standards (N1, N2, N3, NBS22 and USGS24). A laboratory-internal standard (acetanilide) was measured after every sixth sample, encompassing a range of nitrogen comparable to the amount of zooplankton nitrogen. Samples were measured in several runs with a precision of ± 0.2‰ (δ¹⁵N and δ¹³C).

2.6 Calculations

For all experiments the ingestion rate (I) (µg C ind⁻¹ l⁻¹) was calculated as:

$$I = CR \cdot \bar{C} \quad (2)$$

where CR is Clearance rate (ml ind⁻¹ h⁻¹) and \bar{C} is the average food concentration (µg C l⁻¹), calculated as the logarithmic mean (Nejstgaard et al. 1997)

$$\bar{C} = (C_2 - C_0) / [LN(C_2 / C_0)] \quad (3)$$

where C_2 is the final food concentration (µg C l⁻¹) in the replicates and C_0 the food concentration (µg C l⁻¹) at the start of incubation.

For the functional response experiments and the size selectivity experiments CR was calculated as (Lucas 1982):

$$CR = [1/t \cdot LN(C_1 / C_2)] \quad (4)$$

where C_1 is the final food concentration in the controls without copepods and t the incubation time (h). The individual clearance rate (per copepod) was calculated by dividing CR by copepod density (ind ml^{-1}).

For the switching experiment a correction for the ciliate grazing on the diatom was necessary. The clearance rate for the copepod community on diatoms $CR_{com,dia}$ and on ciliates $CR_{com,cil}$ was calculated as (Tokle 2006):

$$CR_{com,dia} = \mu_{dia} - r_{dia} - (CR_{cilcom,dia} \cdot \bar{C}_{cil}) \quad (6)$$

$$CR_{com,cil} = \mu_{cil} - 1/t \cdot [LN(C_{c2} / C_{c1})] \quad (7)$$

where C_{c1} and C_{c2} are the concentrations ($\mu\text{g C l}^{-1}$) of ciliates from the controls without copepods and replicates with copepods, respectively, and t the incubation time. $CR_{cilcom,dia}$ is the clearance rate of the ciliates on the diatoms. A constant value, calculated from the start concentrations before incubation and the controls without copepods (data not shown), of $0.33 \text{ ml } \mu\text{g ciliate C}^{-1} \text{ h}^{-1}$ was applied. \bar{C}_{cil} is the weighted average ciliate concentration during incubation, calculated using equation (3). μ_{dia} and μ_{cil} are factors correcting for growth during incubation of diatoms and ciliates, respectively. μ_{cil} was calculated as:

$$\mu_{cil} = LN(C_{c1} / C_{c0}) / t \quad (8)$$

where C_{c0} and C_{c1} are the concentrations ($\mu\text{g C l}^{-1}$) of ciliates from the start before incubation and the controls without copepods, respectively. An average μ_{cil} of 0.017 h^{-1} ($\pm 0.008 \text{ SE}$) was applied. μ_{dia} is a constant factor of -0.0216 h^{-1} ($\pm 0.0101 \text{ SE}$) and was extrapolated from ciliate grazing on diatoms. r_{dia} is an additional factor to correct for diatom growth during incubation and was calculated as:

$$r_{dia} = 1/t \cdot LN(C_{d2} / C_{d0}) \quad (9)$$

where C_{d0} and C_{d2} are the concentrations ($\mu\text{g C l}^{-1}$) of diatoms from the start before incubation and the replicates with copepods, respectively. To get the individual clearance rates on phytoplankton and ciliates $CR_{com,dia}$ and $CR_{com,cil}$ were divided by copepod density (ind ml^{-1}). The ingestion rates of the copepods on ciliates and diatoms, and therefore the average prey concentrations, were calculated as for the functional response experiments using equation (2) and (3), respectively.

Negative ingestion of diatoms in the switching experiment (due to avoidance by the copepods) was set zero for the calculation of the percentage of ciliates of the total ingestion. Apart from this clearance and ingestion rate values which were negative or obviously outliers were excluded from regressions. In the graphs they are marked with grey symbols and negative values were set zero.

2.7 Statistical Analyses

All statistical analyses were done using SigmaPlot 8.0. The results and the models that were used for the non-linear regressions are listed in the tables 4, 5, and 6.

3 Results

3.1 Functional Response Experiments

The average clearance rate of *Calanus finmarchicus* on *Gymnodinium galatheanum* (Fig. 8A) increased with algal concentration until it reached its maximum of $252 \pm 19 \text{ ml ind}^{-1} \text{ d}^{-1}$ at $136 \mu\text{g C l}^{-1}$. Below $60 \mu\text{g C l}^{-1}$ clearance rate calculation resulted in negative values, which were set zero for illustration. The ingestion rate of *C. finmarchicus* on *G. galatheanum* showed a possible threshold below which no ingestion took place (Fig. 8B) and a linear increase with increasing dinoflagellate concentration. A maximum ingestion rate of $34 \pm 2 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ was observed at a food concentration of $136 \mu\text{g C l}^{-1}$. At concentrations $>200 \mu\text{g C l}^{-1}$ both clearance and ingestion of the dinoflagellate decreased again.

With ciliates as prey organisms the copepods showed increasing clearance rate with increasing prey concentration to a maximum of $503 \pm 151 \text{ ml ind}^{-1} \text{ d}^{-1}$ at a ciliate concentration of $16 \mu\text{g C l}^{-1}$ (Fig. 8A). At the highest ciliate concentration in the experiment ($170 \mu\text{g C l}^{-1}$) the clearance rate declined to $121 \pm 33 \text{ ml ind}^{-1} \text{ d}^{-1}$. The ingestion rates on ciliates demonstrated saturation kinetics (Fig. 8B) and the fitted regression is described by a Holling type III functional response curve. At a concentration of $79 \mu\text{g C l}^{-1}$ *C. finmarchicus* showed maximum ingestion with $24 \pm 11 \mu\text{g C ind}^{-1} \text{ d}^{-1}$.

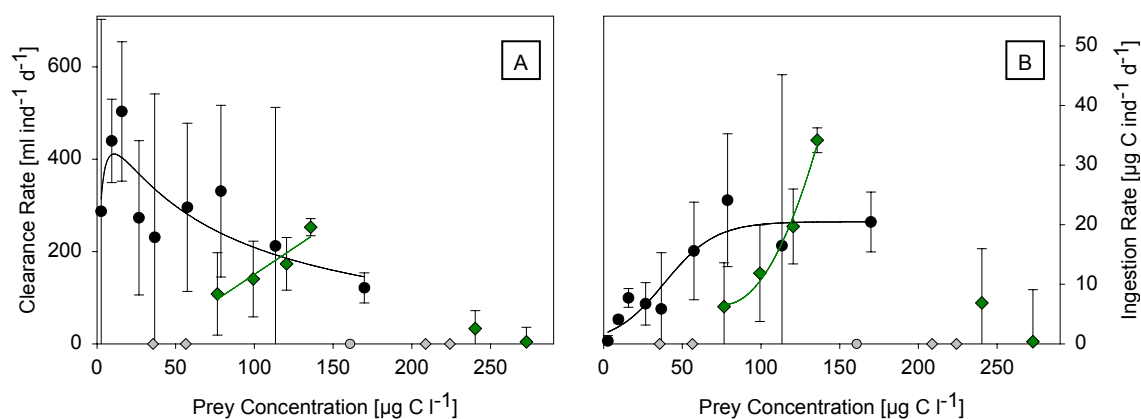


Figure 8 - *Calanus finmarchicus*. Average clearance rates (A) and average ingestion rates (B) of CV stages on the dinoflagellate *Gymnodinium galatheanum* (green diamonds) and of adult females on the oligotrich ciliate *Strombidium sp.* (black circles). Negative values were set zero (grey symbols). Error bars indicate standard error.

Ingestion and clearance rates of the copepod *Centropages hamatus* on the three different prey organisms *Rimostrombidium caudatum*, *Thalassiosira weissflogii* and *Rhodomonas* sp. are shown in figure 9.

Lowest concentration in all three functional response experiments varied between 2.62 and 4.69 $\mu\text{g C l}^{-1}$. The magnitude of clearance rates for adult males and females was similar in the algal experiments. With the ciliate as prey females showed a higher maximum clearance rate than males with $150 \pm 106 \text{ ml ind}^{-1} \text{ d}^{-1}$ and $41 \pm 18 \text{ ml ind}^{-1} \text{ d}^{-1}$, respectively. At ciliate concentrations above 120 $\mu\text{g C l}^{-1}$ no difference could be observed between the sexes (Fig. 9A). With diatoms as prey male *C. hamatus* showed a higher maximum clearance rate than did females with $103 \pm 29 \text{ ml ind}^{-1} \text{ d}^{-1}$ and $59 \pm 9 \text{ ml ind}^{-1} \text{ d}^{-1}$, respectively. No difference between the sexes could be found for diatom concentrations above 20 $\mu\text{g C l}^{-1}$ (Fig. 9C). With the flagellate as prey item clearance rate of female *C. hamatus* was higher than clearance rate of males. Maximum values for females were measured at 54 $\mu\text{g C l}^{-1}$ with $34 \pm 4 \text{ ml ind}^{-1} \text{ d}^{-1}$, and for males at 11 $\mu\text{g C l}^{-1}$ with $23 \pm 2 \text{ ml ind}^{-1} \text{ d}^{-1}$ (Fig. 9E).

Ingestion increased with prey concentration in all three functional response experiments and the fitted regressions are described by Holling type III functional response curves irrespective of prey and sex of the copepods. Male and female *C. hamatus* showed similar values with diatoms as prey. Ingestion of female *C. hamatus* was slightly higher than ingestion of adult males with flagellates or ciliates as prey. Maximum ingestion rates measured for males and females, respectively were: $7 \pm 2.9 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ (at 286 $\mu\text{g C l}^{-1}$) and $11 \pm 0.9 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ (at 246 $\mu\text{g C l}^{-1}$) with ciliates as prey (Fig. 9B), $1.3 \pm 0.1 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ (at 19 $\mu\text{g C l}^{-1}$) and $1.7 \pm 0.8 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ (at 33 $\mu\text{g C l}^{-1}$) with diatoms as prey (Fig. 9D), and $1.3 \pm 0.6 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ (at 77 $\mu\text{g C l}^{-1}$) and $2.2 \pm 0.5 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ (at 98 $\mu\text{g C l}^{-1}$) with flagellates as prey (Fig. 9F).

3.2 Switching Experiment

Clearance and ingestion on ciliates showed no difference between the sexes. The fitted regressions for ingestion follow Holling type III curves. Maximum clearance was $538 \pm 372 \text{ ml ind}^{-1} \text{ d}^{-1}$ at 2.21 $\mu\text{g C l}^{-1}$ and $379 \pm 145 \text{ ml ind}^{-1} \text{ d}^{-1}$ at 0.52 $\mu\text{g C l}^{-1}$ for adult male and female *Centropages hamatus*, respectively (Fig. 10A). Clearance rates decreased with increasing ciliate concentration to $24 \pm 3 \text{ ml ind}^{-1} \text{ d}^{-1}$ at 253 $\mu\text{g C l}^{-1}$ for adult males and to $44 \pm 4 \text{ ml ind}^{-1} \text{ d}^{-1}$ at 227 $\mu\text{g C l}^{-1}$ for adult females. Maximum ingestion for males and females were $8 \pm 1.1 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ and $15 \pm 7.2 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ at ciliate concentrations of 144 $\mu\text{g C l}^{-1}$ and 116 $\mu\text{g C l}^{-1}$, respectively (Fig. 10B). The corresponding diatom concentrations were 144 for the males and 108 $\mu\text{g C l}^{-1}$ for the females (Fig. 10). Ciliates accounted for 100% of total ingestion when ciliate concentration exceeded 5% of the total prey offered (Fig. 11).

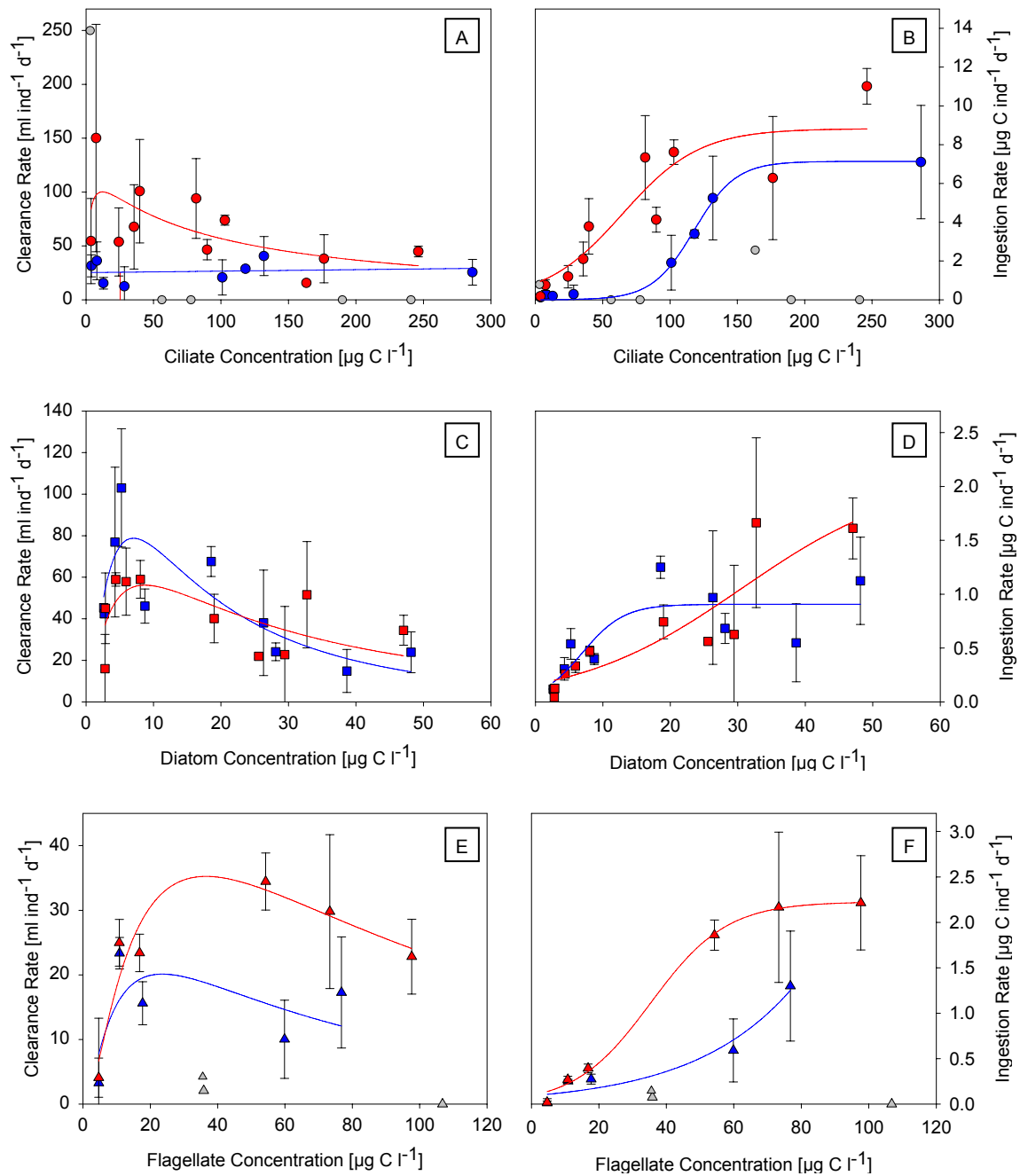


Figure 9 - *Centropages hamatus*. Ingestion and clearance rates of males (blue) and females (red) on the ciliate *Rimostrombidium caudatum*, the diatom *Thalassiosira weissflogii*, and the flagellate *Rhodomonas* sp.. Error bars indicate standard error. Grey symbols are outliers. Note the different scaling of the x- and y-axes.

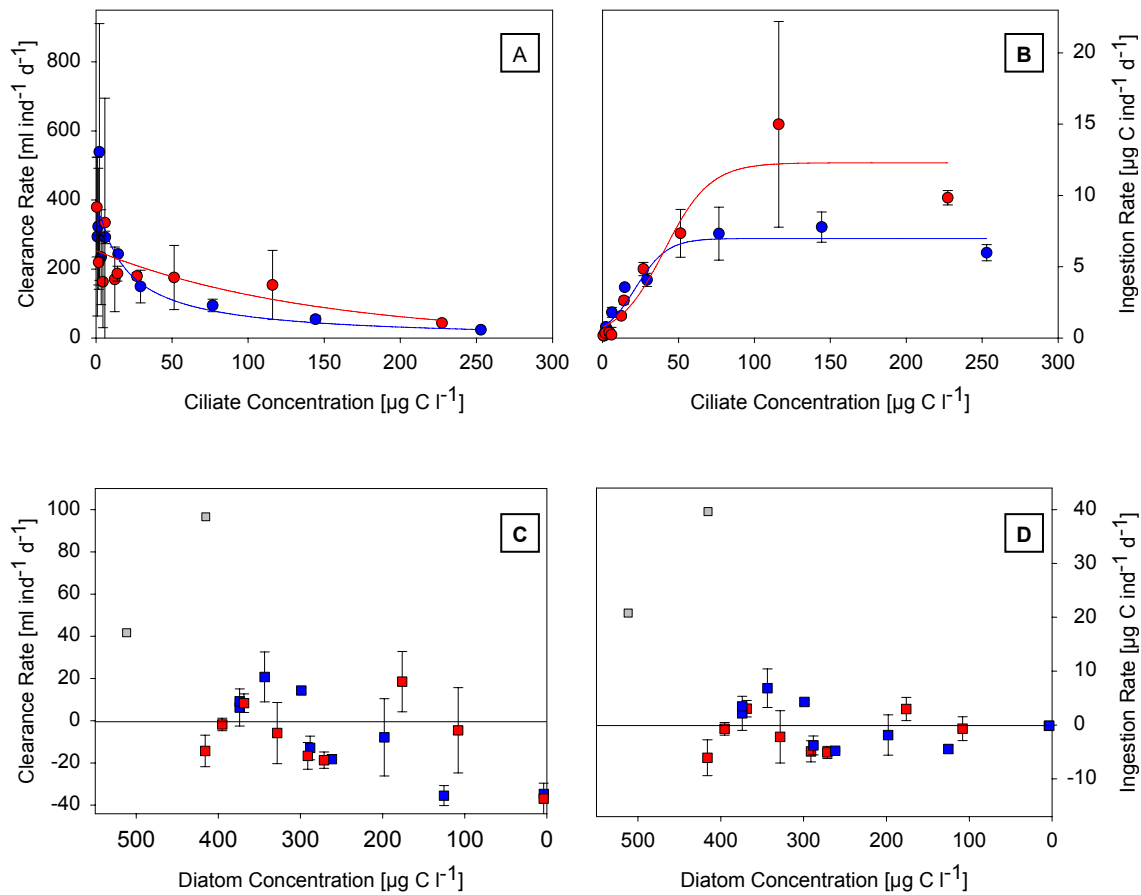


Figure 10 - *Centropages hamatus*. Ingestion and clearance rates of males (blue) and females (red) on a mixture of the ciliate *Rimostrombidium caudatum* (circles) and the diatom *Thalassiosira weissflogii* (squares) (see text for details). Grey symbols are outliers. Error bars indicate standard error. Note the different scaling of the x- and y-axes.

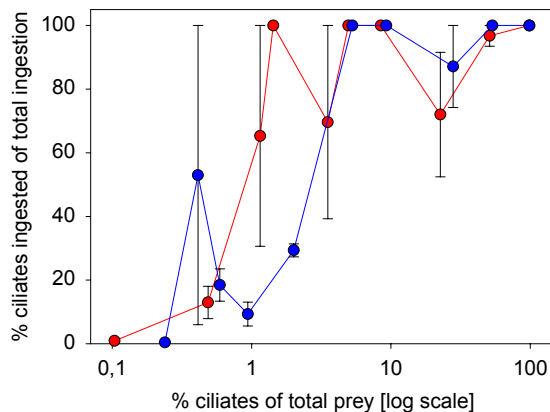


Figure 11 - *Centropages hamatus*. Feeding of males (blue) and females (red) on ciliates when offered a mixture of the ciliate *Rimostrombidium caudatum* and the diatom *Thalassiosira weissflogii* (see text for details). Error bars indicate standard error.

Table 4 - Statistics. R²- and p-values of the fitted regressions.

$$^a y = a \cdot e^{(-0.5 \cdot (\ln(x/x_0)/b)^2)}, ^b y = y_0 + a \cdot x, ^c y = a \cdot e(-b \cdot x), ^d y = a / (1 + e^{-(x-x_0/b)}), ^e y = y_0 + ax \cdot bx^2$$

Clearance rate					
Functional response experiments	Copepod species	Prey species	Developmental stage	R²	P
	<i>C. finmarchicus</i>	<i>Strombidium</i> sp.	CV ^a	0.62	0.0562
	<i>C. finmarchicus</i>	<i>G. galatheanum</i>	female ^b	0.90	0.0525
	<i>C. hamatus</i>	<i>R. caudatum</i>	male ^b	0.02	0.7512
			female ^a	0.40	0.1421
	<i>C. hamatus</i>	<i>T. weissflogii</i>	male ^a	0.65	0.0261
			female ^a	0.33	0.2517
	<i>C. hamatus</i>	<i>Rhodomonas</i> sp.	male ^a	0.41	0.5856
			female ^a	0.89	0.0358
Switching experiment	<i>C. hamatus</i>	<i>R. caudatum</i>	male ^a	0.77	0.0059
			female ^c	0.50	0.0220
Ingestion rate					
Functional response experiments	Copepod species	Prey species	Developmental stage	R²	P
	<i>C. finmarchicus</i>	<i>Strombidium</i> sp.	CV ^d	0.86	0.0027
	<i>C. finmarchicus</i>	<i>G. galatheanum</i>	female ^e	0.99	0.1061
	<i>C. hamatus</i>	<i>R. caudatum</i>	male ^d	0.99	<0.0001
			female ^d	0.82	0.0025
	<i>C. hamatus</i>	<i>T. weissflogii</i>	male ^d	0.69	0.0168
			female ^d	0.80	0.0038
	<i>C. hamatus</i>	<i>Rhodomonas</i> sp.	male ^d	0.95	0.0510
			female ^d	0.99	0.0002
Switching experiment	<i>C. hamatus</i>	<i>R. caudatum</i>	male ^d	0.94	<0.0001
			female ^d	0.92	0.0002

Feeding Behaviour Of Marine Calanoid Copepods

Table 5 - Statistics for the clearance rates. Models of the fitted regressions and their predicted coefficients, standard errors (SE), and significances.

Clearance									
Functional response experiments									
Prey	Copepod	Stage	Model	Variable	Coefficient	SE	T	P	
<i>Strombidium</i> sp.	<i>C. finmarchicus</i>	female	$y = a \cdot e^{(-0.5(LN(x/x_0)/b)^2)}$	a	411.2272	48.3359	8.5077	0.0001	
				b	1.9053	0.4445	4.2863	0.0052	
				x0	10.883	4.1714	2.609	0.0402	
<i>G. galatheanum</i>	<i>C. finmarchicus</i>	CV	$y = y_0 + a \cdot x$	y0	-77.3959	59.9591	-1.2908	0.3259	
				a	2.2791	0.5437	4.1919	0.0525	
<i>R. caudatum</i>	<i>C. hamatus</i>	male	$y = y_0 + a \cdot x$	y0	25.2469	5.1469	4.9053	0.0027	
				a	0.0137	0.0412	0.3319	0.7512	
	female	$y = a \cdot e^{(-0.5(LN(x/x_0)/b)^2)}$	a	100.174	19.1844	5.2216	0.0008		
			b	1.9811	0.7696	2.5744	0.0329		
			x0	12.1571	8.3257	1.4602	0.1824		
			a	78.7821	12.2593	6.4263	0.0004		
<i>T. weissflogii</i>	<i>C. hamatus</i>	male	$y = a \cdot e^{(-0.5(LN(x/x_0)/b)^2)}$	b	1.0461	0.2117	4.9418	0.0017	
				x0	7.0268	1.2863	5.4628	0.0009	
	female	$y = a \cdot e^{(-0.5(LN(x/x_0)/b)^2)}$	a	56.2016	10.168	5.5273	0.0009		
			b	1.2362	0.3661	3.377	0.0118		
			x0	8.7308	1.9952	4.376	0.0033		
			a	20.1142	7.4286	2.7077	0.1136		
<i>Rhodomonas</i> sp.	<i>C. hamatus</i>	male	$y = a \cdot e^{(-0.5(LN(x/x_0)/b)^2)}$	b	1.1695	0.6425	1.8202	0.2103	
				x0	23.5728	9.9748	2.3632	0.1419	
	female	$y = a \cdot e^{(-0.5(LN(x/x_0)/b)^2)}$	a	35.2381	4.3458	8.1085	0.0039		
			b	1.1249	0.2112	5.3262	0.0129		
			x0	36.5922	4.9228	7.4332	0.005		
			a	356,5663	40.8444	8.7299	<0.0001		
<i>R. caudatum</i>	<i>C. hamatus</i>	male	$y = a \cdot e^{(-0.5(LN(x/x_0)/b)^2)}$	b	2.0742	0.6742	3.0766	0.0179	
				x0	2.0901	1.5619	1.3381	0.2227	
				female	$y = a \cdot e^{(-b \cdot x)}$	a	253.1581	31.3534	8.0744
b	0.007	0.0039	1.7968			0.1101			

Switching experiment

Table 6 - Statistics for the ingestion rates. Models of the fitted regressions and their predicted coefficients, standard errors (SE), and significances.

Ingestion

Functional response experiments

Prey	Copepod	Stage	Model	Variable	Coefficient	SE	T	P
<i>Strombidium</i> sp.	<i>C. finmarchicus</i>	female	$y = a / (1 + e^{-(x-x_0/b)})$	a	20.4958	2.3945	8.5597	0.0001
				b	16.1791	6.6944	2.4168	0.0521
				x_0	38.7250	8.5451	4.5319	0.0040
<i>G. galatheanum</i>	<i>C. finmarchicus</i>	CV	$y = y_0 + ax \cdot bx^2$	y_0	52.2242	31.8145	1.6415	0.3483
				a	-1.1869	0.6219	-1.9085	0.3073
				b	0.0077	0.0029	2.6383	0.2306
<i>R. caudatum</i>	<i>C. hamatus</i>	male	$y = a / (1 + e^{-(x-x_0/b)})$	a	7.1380	0.2371	30.1082	<0.0001
				b	15.5456	1.9436	7.9983	0.0005
				x_0	117.7775	1.9107	65.0437	<0.0001
		female	$y = a / (1 + e^{-(x-x_0/b)})$	a	8.8244	1.3127	6.7225	0.0003
				b	28.7006	11.5954	2.4752	0.0425
				x_0	64.5034	16.1426	3.9959	0.0052
<i>T. weissflogii</i>	<i>C. hamatus</i>	male	$y = a / (1 + e^{-(x-x_0/b)})$	a	0.9067	0.1174	7.7216	0.0001
				b	3.0957	2.5319	1.2227	0.2610
				x_0	6.9293	2.5153	2.7549	0.0283
		female	$y = a / (1 + e^{-(x-x_0/b)})$	a	2.1116	1.0118	2.0869	0.0753
				b	12.3635	6.1309	2.0166	0.0835
				x_0	30.6256	14.2415	2.1504	0.0686
<i>Rhodomonas</i> sp.	<i>C. hamatus</i>	male	$y = a / (1 + e^{-(x-x_0/b)})$	a	81.1168	7,404.0909	0.0110	0.9923
				b	29.1546	23.1098	1.2316	0.3343
				x_0	197.9237	2,824.4547	0.0701	0.9505
		female	$y = a / (1 + e^{-(x-x_0/b)})$	a	2.2258	0.0669	33.2876	<0.0001
				b	11.2529	1.1836	9.5075	0.0025
				x_0	35.3547	2.4290	14.5554	0.0007

Switching experiment

<i>R. caudatum</i>	<i>C. hamatus</i>	male	$y = a / (1 + e^{-(x-x_0/b)})$	a	6.9824	0.4884	14.2961	<0.0001
				b	10.3862	2.9569	3.5125	0.0098
				x_0	21.6168	4.1270	5.2379	0.0012
		female	$y = a / (1 + e^{-(x-x_0/b)})$	a	12.2915	1.1834	10.3864	<0.0001
				b	15.0432	4.6751	3.2177	0.0147
				x_0	40.6993	7.3824	5.5130	0.0009

3.3 Size Selectivity Experiments

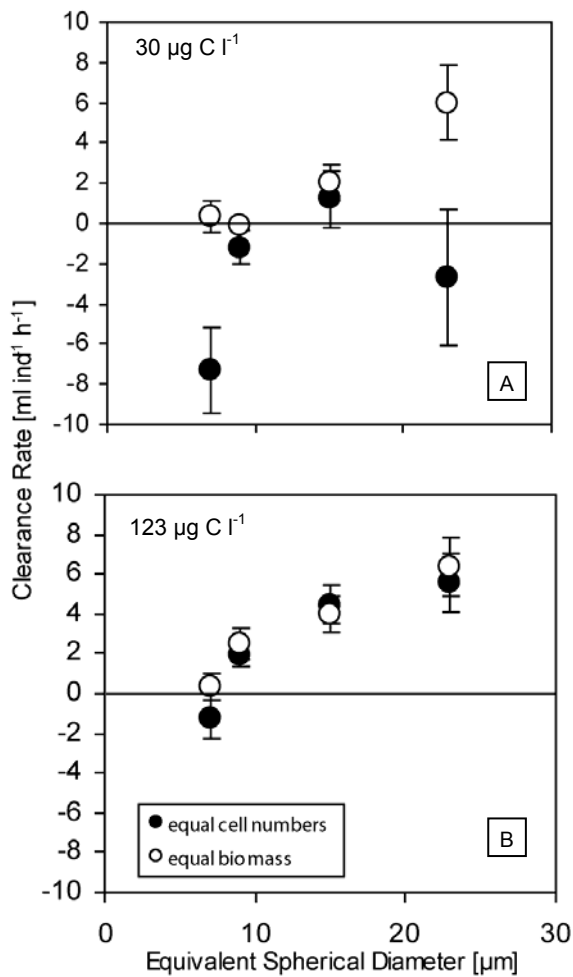


Figure 12 - *Calanus finmarchicus*. Size selectivity of adult females on mixtures of *Prymnesium patelliferum* (ESD: 6 μm), *Tetraselmis* sp. (ESD: 9 μm), *Prorocentrum minimum* (ESD: 15 μm), and *Scrippsiella trochoidea* (ESD: 20 μm) / *Gyrodinium aurelium* (ESD: 25 μm). The algae were offered in different total (30 or 123 μg C l⁻¹) and individual concentrations (see text for details). Error bars indicate standard error.

The experimental set up included equal biovolume (variation (a)) or equal cell numbers (variation (b)) for the four algal species that were fed in the experiments. The theoretical final concentrations were 100 or 20 μg C l⁻¹, to obtain food saturation and food limitation, respectively.

In practice the concentrations in the experiments with the high carbon concentration were 138 μg C l⁻¹ for variation (a) and 108 μg C l⁻¹ for variation (b), and some deviation from equality in biovolume and cell numbers were observed (Table 7). The initial carbon concentrations in variation (a) varied within a factor of 4 and were lowest for the smallest alga *Prymnesium patelliferum*, intermediate for *Tetraselmis* sp. and the biggest species *Scrippsiella trochoidea*, and highest for *Prorocentrum minimum*. The initial cell numbers in variation (b) were approximately equal for *P. patelliferum*, *Tetraselmis* sp. and *P. minimum*, but lower by a factor of 4-5 for *S. trochoidea*.

In the experiment with the low carbon concentration the total concentrations were 33 μg C l⁻¹ for variation (a) and 27 μg C l⁻¹ for variation (b). The initial carbon concentration for the various algae in variation (a) varied within a factor of 3.5 and was lowest for *P.*

patelliferum, whereas *Tetraselmis* sp., *P. minimum* and *G. aurelium* had higher but more similar values. The initial cell numbers in variation (b) varied within a factor of 5 and were similar and highest for *P. patelliferum* and *Tetraselmis* sp., lower for *P. minimum* and lowest for *G. aurelium* (Table 7).

Table 7 - Initial concentrations of the size selectivity experiments of *C. finmarchicus* feeding on a mixture of different sized algae. See text for details regarding variation (a) and (b).

Algae species	High carbon content				Low carbon content			
	Variation (a)		Variation (b)		Variation (a)		Variation (b)	
	$\mu\text{g C l}^{-1}$	$10^5 \text{ cells l}^{-1}$	$\mu\text{g C l}^{-1}$	$10^5 \text{ cells l}^{-1}$	$\mu\text{g C l}^{-1}$	$10^5 \text{ cells l}^{-1}$	$\mu\text{g C l}^{-1}$	$10^5 \text{ cells l}^{-1}$
<i>P. patelliferum</i>	18.2	11.10	21.4	3.38	3.8	2.24	1.3	0.89
<i>Tetraselmis</i> sp.	38.2	9.38	8.4	2.87	10.8	2.14	4.5	0.86
<i>P. minimum</i>	73.6	5.37	36.4	2.66	7.8	0.68	5.4	0.46
<i>S. trochoidea</i> / <i>G. aurelium</i>	35.8	0.37	70.0	0.67	13.7	0.13	19.0	0.19

Calanus finmarchicus prefers the larger prey particles offered over smaller ones and does not seem to eat particles <6-9 μm (Fig. 12). When the four algal species were offered in equal biovolume (variation (a)) the clearance rate was highest on the largest alga (*Scrippsiella trochoidea* or *Gyrodinium aurelium*) and seemed to be independent of the algae concentration. Clearance rate decreased with decreasing cell size. Partly, the same pattern was observed when the algae were fed in equal cell numbers (variation (b)) and the initial carbon concentration was about $125 \mu\text{g C l}^{-1}$ (Fig. 12B). When the initial carbon concentration was low and the algae were offered in equal cell numbers (variation (b)) average clearance rate was negative for all but on species (*P. minimum*) (Fig. 12A). The biggest difference compared to variation (a) was observed for *P. patelliferum* and *G. aurelium*.

3.4 Trophic Position of *Calanus finmarchicus*

The average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *Calanus finmarchicus* (stage CIII to adult male / female) in the Trondheim Fjord varied with time. Highest average values were found in May and February with $\delta^{13}\text{C}$ of $-20.5 \pm 0.1\text{‰}$ and $\delta^{15}\text{N}$ of $8.3 \pm 0.3\text{‰}$, respectively (Table 8). The average values for the $\delta^{13}\text{C}$ signature varied between $-24.8 \pm 0.3\text{‰}$ in August and $-20.7 \pm 0.1\text{‰}$ in May. For $\delta^{15}\text{N}$ the most depleted average signature was observed in April with $5.7 \pm 0.2\text{‰}$, the most enriched average signature in February with $8.2 \pm 0.1\text{‰}$ (Fig. 13). Two generations could be identified between February and August 2004. The overwintering parental generation from 2003 (section I in Fig. 13) and the new generation, which developed in spring / summer 2004 (section II in Fig. 13). In June this new generation descended to deeper water layers for overwintering (section III in Fig. 13).

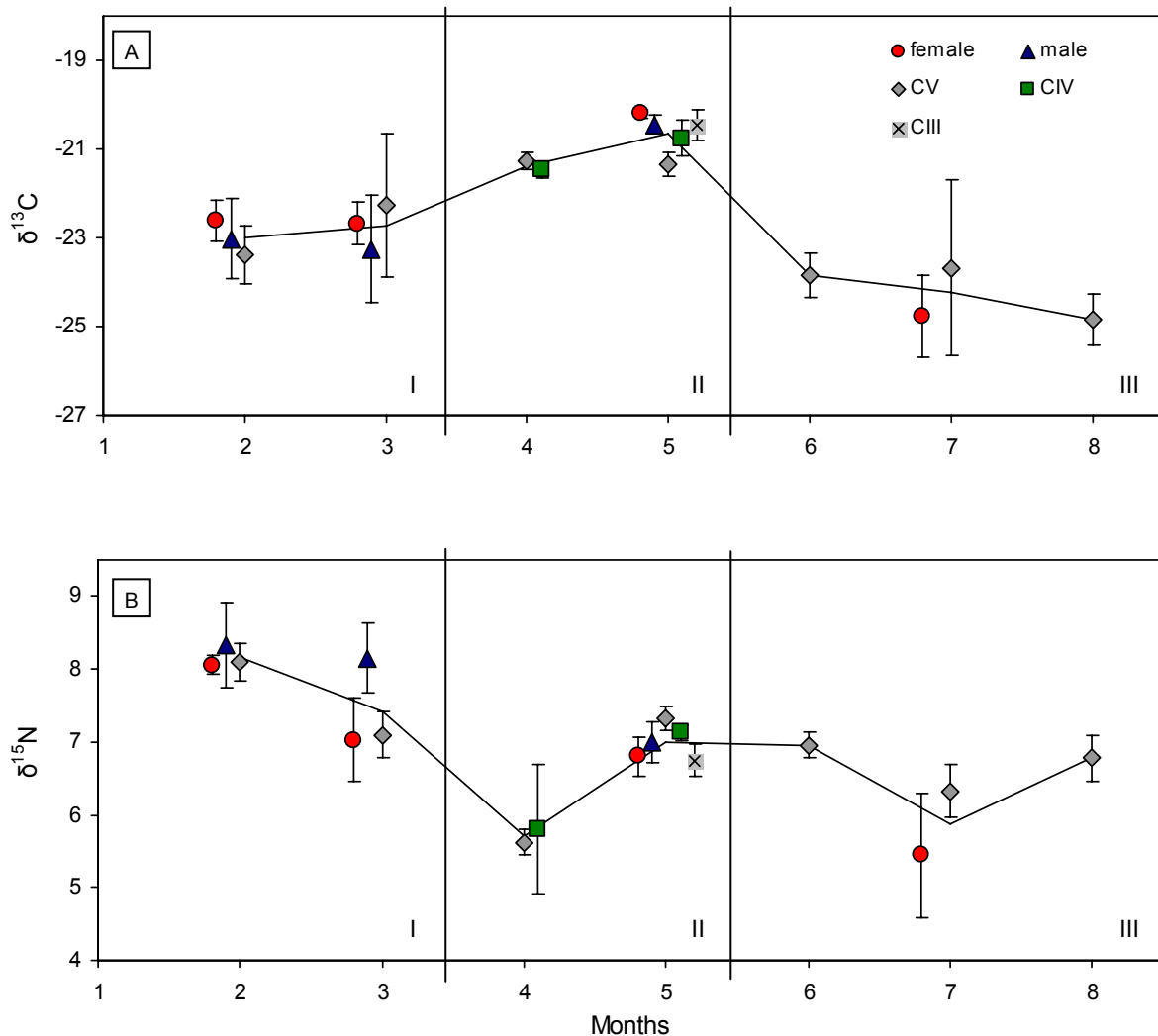


Figure 13 - *Calanus finmarchicus*. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of developmental stages CIII to adult male / female of specimens caught in the Trondheim Fjord (February to August 2004). Error bars indicate standard error.

Feeding Behaviour Of Marine Calanoid Copepods

Table 8 - $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures [‰]. *Calanus finmarchicus* samples were caught in the Trondheim Fjord in 2004 or raised in the laboratory. Samples of *Enteromorpha* sp. and *Chorda filum* were collected from the Trondheim Fjord in summer 2004. *Dunaliella tertiolecta* and *Isochrysis galbana* were used as feeding algae in the laboratory. SE is standard error.

	$\delta^{13}\text{C}$	SE	$\delta^{15}\text{N}$	SE
Trondheim Fjord				
<i>C. finmarchicus</i>				
February				
adult male	-23.0	0.52	8.3	0.34
adult female	-22.6	0.23	8.1	0.06
stage CV	-23.4	0.33	8.1	0.13
mean	-23.0	0.23	8.2	0.07
March				
adult male	-23.3	0.60	8.2	0.24
adult female	-22.7	0.24	7.0	0.29
stage CV	-22.3	0.81	7.1	0.16
mean	-22.7	0.29	7.4	0.38
April				
stage CV	-21.3	0.09	5.6	0.09
stage CIV	-21.5	0.09	5.8	0.44
mean	-21.4	0.10	5.7	0.10
May				
adult male	-20.5	0.15	7.0	0.20
adult female	-20.2	0.06	6.8	0.15
stage CV	-21.4	0.13	7.3	0.09
stage CIV	-20.8	0.20	7.1	0.05
stage CIII	-20.5	0.25	6.8	0.15
mean	-20.7	0.20	7.1	0.09
June				
stage CV	-23.8	0.22	7.0	0.07
mean	-23.8	0.22	7.0	0.07
July				
adult female	-24.8	0.42	5.4	0.38
stage CV	-23.7	0.88	6.3	0.16
mean	-24.3	0.55	5.9	0.45
August				
stage CV	-24.8	0.26	6.8	0.14
mean	-24.8	0.26	6.8	0.14
over all mean	-23.0	0.57	6.9	0.35
<i>Enteromorpha</i> sp.	-18.1	0.09	3.9	0.18
<i>C. filum</i>	-17.2	0.11	2.9	0.14
Laboratory				
<i>C. finmarchicus</i>				
F3 generation				
adult male	-33.5	0.37	2.4	0.22
adult female	-33.9	0.18	1.6	0.09
stage CV	-34.1	0.19	1.9	0.14
mean	-33.8	0.17	2.0	0.23
F4 generation				
adult male	-28.6	only one value	1.6	only one value
stage CIV	-27.9	0.17	1.7	0.16
mean	-28.2	0.35	1.7	0.05
<i>D. tertiolecta</i>	-32.2	0.10	0.2	0.13
<i>I. galbana</i>	-23.9	0.02	9.4	0.04

Both the carbon and the nitrogen content of the overwintering copepods (samples from June, July and August: carbon: average $201.9 \pm 2.04 \mu\text{g copepod}^{-1}$, nitrogen: average $23.0 \pm 0.36 \mu\text{g copepod}^{-1}$) were higher than those of the corresponding stages collected in the months of February to May (exception: males in February). The C:N ratio for the overwintering CV and females sampled from June to August (average C:N: 10.2 ± 0.09), was also higher than in the months before (Fig. 15).

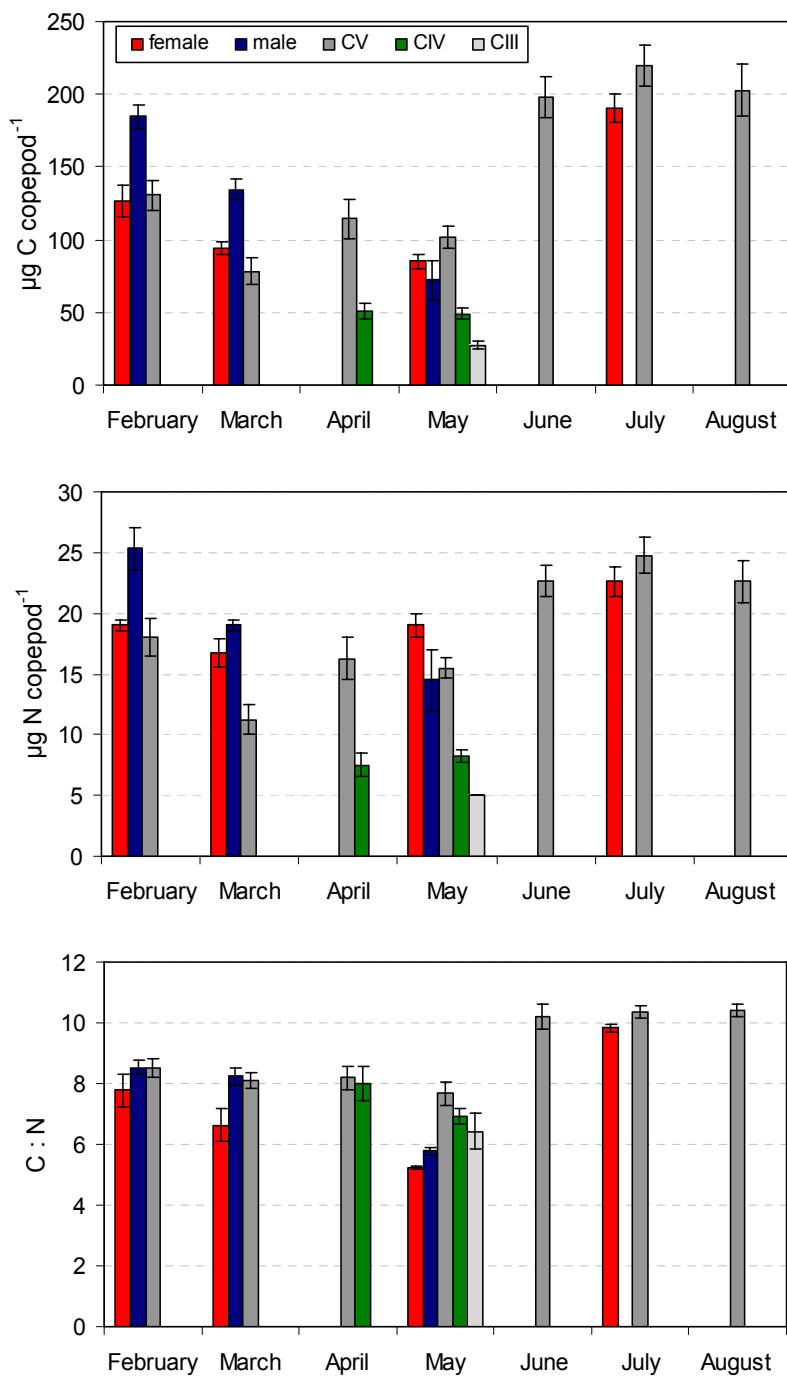


Figure 15 - *Calanus finmarchicus*. Carbon and nitrogen content, and C:N ratio of developmental stages CIII to adult male / female of specimens caught in the Trondheim Fjord from February to August 2004. Error bars indicate standard error.

4 Discussion

4.1 Feeding Behaviour of *Calanus finmarchicus*

4.1.1 The Experiments

The dinoflagellate *Gymnodinium galatheanum* is considered a good maintenance food for *Calanus finmarchicus* (Marshall and Orr 1955a), and indeed eggs and young nauplii were observed when the water in the jars was exchanged once a week. As a motile phytoplankton species *G. galatheanum* does not sink to the bottom but stays in the water column, which makes it more easily available to the copepods. Moreover, I observed considerable faecal pellet production. Therefore I assume that the copepods used in the experiment were in good physiological condition. No acclimatization was necessary for the algal functional response experiment with *C. finmarchicus* because *G. galatheanum* was both the maintenance and the experimental food. One day prior to the ciliate functional response experiment the ciliate was fed to *C. finmarchicus* to give them the opportunity to adapt to this kind of food.

The feeding behaviour of *Calanus finmarchicus* is characterised by prey specific differences in clearance and ingestion rates. *C. finmarchicus* was offered ciliate or algal prey in different concentrations in two functional response experiments. Ingestion of the dinoflagellate *Gymnodinium galatheanum* started above a total algal concentration of $\sim 60 \mu\text{g C l}^{-1}$, whereas *C. finmarchicus* already ingested the offered ciliate prey at concentrations below $3 \mu\text{g C l}^{-1}$. At prey concentrations above $100 \mu\text{g C l}^{-1}$ ingestion of algal and ciliate prey by *C. finmarchicus* was of the same magnitude. In my experiments I could not identify the concentration where ingestion of the dinoflagellate reached saturation or a maximum due to missing data between 136 and $240 \mu\text{g C l}^{-1}$. Ingestion seemed to decline again after a maximum at concentrations $>136 \mu\text{g C l}^{-1}$. This decrease in ingestion contradicts the expected saturation described by Holling functional response curves (Holling 1959), but has been observed in earlier studies on the feeding behaviour of *Calanus* species (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, Mullin 1963). Mullin could not explain this decrease in ingestion at high algal concentrations. Later research revealed that phytoplankton cells, especially diatoms, aggregate at high concentrations (Riebesell 1991, Alldredge et al. 1995). This is either due to their sticky cell surface or because the cells excrete transparent exopolymeric particles (TEP), a sticky substance that may cause other, non-sticky particles to coagulate (Kiørboe and Hansen 1993). These aggregated cells could be less attractive or inedible for copepods. Thus, the low ingestion rates of *G. galatheanum* by *C. finmarchicus* at concentrations $>200 \mu\text{g C l}^{-1}$ in my experiment might not be the result of reduced feeding at higher food availability, but caused by aggregation of the dinoflagellate cells. Aggregates of dinoflagellate cells are less stable, compared to diatoms (Jones et al.

1998), potentially because the gel-like material within dinoflagellate aggregates is not the extremely sticky TEP (Allredge et al. 1998). This might be the reason why I did not find unusual large particles, due to aggregation, when counting *G. galatheanum* with the particle counter. For ciliates maximum ingestion seemed to be reached at concentration of around $80 \mu\text{g C l}^{-1}$. Field observations showed a daily ingestion by *C. finmarchicus* of phytoplankton in bloom situations of 30% body carbon (Irigoien et al. 1998), which corresponds to $\sim 21 \mu\text{g C ind}^{-1} \text{d}^{-1}$ for adult females with a body carbon of $142 \mu\text{g}$ (table 2). The fitted regression could be described by a Holling type III curve and predicted a maximum ingestion of ciliates of $20 \mu\text{g C ind}^{-1} \text{d}^{-1}$ for *C. finmarchicus*. This value seems to be possible (highest individual ingestion observed in the experiment was $45 \mu\text{g C ind}^{-1} \text{d}^{-1}$ at a ciliate concentration of $113 \mu\text{g C l}^{-1}$), but it should be considered with caution. My experimental set-up consisted of two replicates per concentration with only one copepod in each 100 ml bottle. The *C. finmarchicus* used in the ciliate functional response experiment (September 2004) were caught in August 2004 in the Trondheim Fjord. In August *C. finmarchicus* has already descended to deeper water layers and is in a diapause stage, i.e. it is floating motionlessly in the water column to save energy (Hirche 1996). When the copepods (mostly copepodites V) were brought to the laboratory it was possible to “wake them up”. I kept them at 15°C and surplus food supply. After approximately 10 to 14 days the copepods, which formerly were floating at the water surface, started moving through the water column and fed on the offered algae (I observed faecal pellet production). For the ciliate experiment, I used only copepods that were active and had moulted into adult females. Nevertheless, the clearance rates differed strongly between the two replicates per concentration, as can be seen by the large error bars in figure 8. I cannot exclude the possibility that this was due to some feeding deficiencies of some animals caused by interruption of their energy saving stage. On the other hand, the resulting mean values for clearance and ingestion at ciliate concentrations below $30 \mu\text{g C l}^{-1}$ compare well to the rates found by Tokle (2006) with highest clearance at very low concentrations ($<15 \mu\text{g C l}^{-1}$). At concentrations exceeding $100 \mu\text{g C l}^{-1}$, ingestion of algal prey measured as $\mu\text{g C ingested per copepod}$ seems to be higher than on ciliates. This leads to the assumption that *C. finmarchicus* is capable of using different feeding modes for different prey. At low concentrations, ambush feeding results in higher clearance rates (Evjemo et al. 2000), and *C. finmarchicus* showed no clearance on the dinoflagellate, but very high clearance on the ciliate at low concentrations. Both prey types are motile, with the ciliate being the faster one. Swimming velocities for dinoflagellates vary from 0.056 to 0.556 mm s^{-1} (Kamykowski 1995). For spiral swimming ciliates as *Strombidium* sp. swimming velocities between 0.5 and 1.0 mm s^{-1} (*Strombidium reticulatum*, Jonsson and Tiselius 1990) have been reported. When culturing *Strombidium* sp. I observed rapid escape jumps when it was disturbed, e.g. by moving the tissue flask under a dissecting microscope. Performing

such escape jumps ciliates can reach a velocity of up to 8.5 mm s^{-1} (*Mesodinium rubrum*), which exceeds the flow field velocity of a suspension feeding copepod of 8.0 mm s^{-1} direct at the second maxillae, and of about 4.0 mm s^{-1} at a distance of 0.5 mm from the capture area, which was found for the small copepod *Acartia tonsa* (Jonsson and Tiselius 1990). One might argue that a larger copepod as *C. finmarchicus* can create a stronger flow field, and thus capture ciliates when suspension feeding, but this would not explain the ingestion threshold for the dinoflagellate. I therefore propose that *C. finmarchicus* uses ambush feeding on ciliates, whereas small algal prey is ingested by suspension feeding.

Ambush feeding might also be the preferred feeding mode of *C. finmarchicus* on large algal cells which occur in a mixture with smaller algal cells. In the size selectivity experiments clearance of *C. finmarchicus* on the largest algal cells *Scrippsiella trochoidea* (ESD: $20 \mu\text{m}$) and *Gyrodinium aurelium* (ESD: $25 \mu\text{m}$) were highest irrespective of individual or total prey concentration. The total algal concentrations in the size selectivity experiments were defined as “limiting” ($30 \mu\text{g C l}^{-1}$) or “surplus” ($123 \mu\text{g C l}^{-1}$), and at both concentrations the individual algal species were offered in “equal biomass” or “equal cell numbers” (see “2.4 Size Selectivity Experiments” for further explanation).

At limiting total algal concentration clearance of *C. finmarchicus* on cells $<10 \mu\text{m}$ (*Prymnesium patelliferum*, ESD: $6 \mu\text{m}$; *Tetraselmis* sp., ESD: $9 \mu\text{m}$) was negligible, whereas the clearance rate on the largest alga *G. aurelium* was of equal magnitude as on *S. trochoidea*, the largest alga in the “surplus” concentration treatment (Fig. 12). Since the actual individual algal concentrations in terms of biomass of the second smallest alga *Tetraselmis* sp. and the largest alga *G. aurelium* were similar in the “equal biomass” treatment, the higher clearance on the largest algae can only be explained by active selection of *G. aurelium*, most likely due to ambush feeding, as this enhances clearance rates at low concentrations (Evjemo et al. 2000). Suspension feeding copepods can select preferred prey items out of a mixture of similar sized cells due to chemoreception (DeMott 1986, 1988), but here the cells were all edible and selection was most likely due to size differences. Copepods can detect larger non-motile prey because of streamline deformations. These arose in the region between a large object (the copepod) and a smaller object (the phytoplankton cell) approaching each other in a laminar flow at Reynolds number 5, which is characteristic of the fluid regime experienced by foraging copepods. Thus chemoreception is not required for the detection and capture of large phytoplankton cells, and swimming behaviour plays an integral role in prey detection (Bundy et al. 1998).

At surplus total algal concentration *C. finmarchicus* showed no clearance difference on the different algal species between the two variations “equal biomass” and “equal cell numbers”. Clearance on the largest alga was of the same magnitude as at limiting total concentration, but clearance for the intermediate sized cells of *Prorocentrum minimum* (ESD:

15 μm) was twice as high. Also for *Tetraselmis* sp. clearance, though still low, was higher than at a limiting concentration. I have to point out that the actual individual concentrations were not as equal in cell numbers as intended. Cell abundance in both cases (“equal biomass” and “equal cell numbers”) was: largest cell < intermediate cell < smallest cells. Suspension feeding could not explain the higher clearance rate on the less abundant large cells. The very low or negligible clearance of *C. finmarchicus* on *P. patelliferum* and *Tetraselmis* sp. is probably due to the fact that larger algal cells were available to the copepods in the experiment. The suitability of nanophytoplankton for *C. finmarchicus* is controversial. Some studies conclude that algae cells <10 μm are too small for *C. finmarchicus* to feed on them properly (Hansen et al. 1994, Nejstgaard et al. 1997 and 2001a and b), and that prey <5 μm is not suitable at all (Irigoien et al. 1998). Others fed female *C. finmarchicus* with monocultures of nanoplankton algae (*Rhodomonas baltica* (ESD: 8 μm) and *Emiliania huxleyi* (ESD: 4 μm), and observed maximum egg production rates at high concentrations (>800 $\mu\text{g C l}^{-1}$) (Båmstedt et al. 1999). Furthermore, the *C. finmarchicus* from the laboratory which were analysed for their stable isotope signatures in this study were successfully raised over several generations on a diet of *Isochrysis galbana* (ESD: ~5 μm) and *Dunaliella tertiolecta* (ESD: ~10 μm). In my experiments *Tetraselmis* sp. might have been partly ingested because some cells were, due to their high abundances, captured by the feeding appendages together with the preferred and selected larger algal cells of *P. minimum* and *S. trochoidea*. Aggregation of cells at high cell concentrations might be the reason (Riebesell 1991, Alldredge et al. 1995). Higher encounter rates due to the higher total algal concentration might account for the higher clearance on *P. minimum* at surplus algal concentration compared to the limiting concentration experiment. *C. finmarchicus* prefers the largest cells also at high total algal concentration, but still has capacities in its clearance rate before reaching maximum values. At a concentration of ~120-135 $\mu\text{g C l}^{-1}$ of pure ciliate or dinoflagellate prey *C. finmarchicus* showed a mean clearance of ~215-250 $\text{ml ind}^{-1} \text{d}^{-1}$. Clearance on the largest cell in the size selectivity experiments was ~6 $\text{ml ind}^{-1} \text{h}^{-1}$, which corresponds to ~140 $\text{ml ind}^{-1} \text{d}^{-1}$. This still leaves 75-110 $\text{ml ind}^{-1} \text{d}^{-1}$ to the maximum possible clearance rate at this prey concentration. The calculated daily clearance (of ~100 $\text{ml ind}^{-1} \text{d}^{-1}$) on *P. minimum* in the experiments with surplus algal concentration fell in this range.

The results presented here support the hypothesis that the higher clearance on the largest algal cells in a mixture of different sized cells cannot be explained by suspension feeding. I assume that *C. finmarchicus* uses suspension feeding on small “slow” or immotile prey when this is the only food source (as in the dinoflagellate functional response experiment) or when it at least strongly dominates the natural prey assemblage, and is present in high abundances. *Calanus* seems to require a total algal concentration between 27 $\mu\text{g C l}^{-1}$ (*Calanus pacificus* on *Thalassiosira flavutilis*; Frost 1975) and 50-60 $\mu\text{g C l}^{-1}$

(*Calanus finmarchicus* on algae; this study, Marshall and Orr 1955a, Gamble 1978, Daro 1980, Båmstedt et al. 1999) to start ingestion. But on “fast” motile prey (ciliate) or large, preferred algae species, which are a minority in a prey community, *C. finmarchicus* uses ambush feeding, and can thus reach high clearance rates even at low prey abundance (Bundy et al. 1998, Evjemo et al. 2000).

Tokle (2006) showed that *C. finmarchicus* feeds exclusively on ciliates when they contribute with more than 5% to total prey abundance in a mixture with algal prey at surplus concentrations. The fact that ciliates obviously are preferred prey for *C. finmarchicus* can be underlined by the maximum weight specific ingestion rate ($\mu\text{g } C_{\text{Food}} \mu\text{g } C_{\text{Copepod}}^{-1} \text{ d}^{-1}$), which is approximately 80% higher for the ciliate *Strombidium* sp. than that for the dinoflagellate *G. galatheanum* with 0.75 d^{-1} and 0.17 d^{-1} , respectively. But both values are lower than rates of approximately 1 d^{-1} which were found for small copepods, e.g. *Acartia clausi* and *Centropages hamatus* (Tokle et al. 2005a). In my experiments I used adult female *C. finmarchicus* with ciliate prey, whereas the dinoflagellate was offered to copepodites stage V (CV). Thus the higher weight specific ingestion rate on ciliates might be due to the different developmental stages. Mullin (1963) found the grazing rates of adult female *C. finmarchicus* being higher than those of CV. Marshall and Orr (1955b, 1956), on the other hand, reported increasing grazing rates with increasing developmental stage for *C. finmarchicus* from nauplius stage III (NIII) to copepodite stage III (CIII), but found no difference between feeding rates of CV and adult females. Prior to the size selectivity experiments the copepods were fed *G. galatheanum* only. Therefore the results in this case may partly reflect how *C. finmarchicus* reacted to food particles that were smaller or bigger than the one it was acclimatized to. Because of logistic reasons, the copepods were transferred into the experimental bottles the day before the experiments. Thus the rates may be overestimated due to a temporary increase of feeding effort (hunger response (Runge 1980, Hasset and Landry 1988, Huntley 1988)), but the selection between different food items should be the same. All the algae used in the experiment were unknown to the copepods (they were fed *G. galatheanum* before) and there should be no bias of prior acclimatization (Huntley 1988).

The food quality of *Scrippsiella trochoidea* is controversial in the literature. While it was a preferred food item in my experiments and successfully used as copepod food by Nott et al. (1985), other authors have reported rejection because of toxicity (Huntley et al. 1983) or drastically lowered digestive enzyme activity (Hasset 1986). As clearance rate was highest on *S. trochoidea* I assume that there is at least no rejection based on chemical detection (Huntley et al. 1983).

4.1.2 Trophic Position

Stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) are used as a tool to characterize feeding relationships and to follow mass and energy flow in complex food webs (DeNiro and Epstein 1978, 1981, Petersen and Fry 1978). Both the $\delta^{13}\text{C}$ and the $\delta^{15}\text{N}$ signatures of *C. finmarchicus* showed variation over the sampling period from February to August 2004. Sampling was done monthly and the appearance of the different developmental stages of *C. finmarchicus* suggested only one generation in the Trondheim Fjord in 2004. Developmental time of *Calanus* is strongly temperature dependent (Uye 1988). In spring water temperature in the Trondheim Fjord is 3-8°C (Sakshaug 1972), and at a temperature of 4.5°C *C. finmarchicus* requires 38 days for development from nauplius stage NVI to copepodite stage CV (McLaren and Corkett, in Schriever et al. 1986), which suggest approximately two months for development from hatching to reaching adult stage. Thus, if first hatching in the fjord took place in March / April there could have been two months until *C. finmarchicus* descended to deeper water in June, and it is unlikely that a second generation has been missed due to large sampling intervals. In May, I found adult male and female *C. finmarchicus* as well as CIII stages. These differences in the developmental stage of *C. finmarchicus* were most likely due to hatching time and / or environmental differences during their individual development.

$\delta^{15}\text{N}$ signatures (Fig. 13B) suggest the ascent of the overwintering generation from 2003 and the beginning of reproduction in February / March 2004. Samples from April and May already represent the new generation. They are depleted in $\delta^{15}\text{N}$ in April compared to the overwintering generation, due to their feeding on prey which was based on new primary production. The overwintering generation from 2003 lived still on their stored lipids in February and March (Hirche 1996) and did not have the possibility to feed on phytoplankton or microzooplankton, because the phytoplankton spring bloom peak in the Trondheim Fjord does not occur before the beginning of April (Sakshaug and Mykkestad 1973). Therefore, their $\delta^{15}\text{N}$ signatures were representative of their diet in 2003. In May *C. finmarchicus* stages CIII to adult were present in my samples from the fjord. I did not quantify the proportions, but CV clearly dominated the population. Copepods sampled from June to August were almost exclusively CV and already in diapause. This is in accordance with the life cycle of *C. finmarchicus* which at high latitudes descends to deeper water in June (McLaren and Corkett, in Schriever et al. 1986, Hirche 1996). The new overwintering generation showed $\delta^{15}\text{N}$ signatures in the same range as samples from April and May, indicating that they fed on the same prey assemblages as the copepods sampled in spring 2004.

The $\delta^{15}\text{N}$ signature of phytoplankton depends both on the isotopic composition of the nitrogen source and the source itself (nitrate, ammonium or atmospheric nitrogen), and its fractionation during uptake and assimilation (Montoya and McCarthy 1995). Uptake and

assimilation are influenced by the availability of nitrogen and iron, light intensity and temperature (Mariotti et al. 1981, Waser et al. 1998). The nitrogen source before and during the spring bloom is nitrate, but in post bloom situations it is replaced by recycled nitrogen (mainly ammonia) from excretion products (Vargo 1979, Priddle et al. 1995). Because the 'lighter' isotope ^{14}N is preferentially excreted, also the nitrogen source resulting from these excretion products is depleted in $\delta^{15}\text{N}$ (DeNiro and Epstein 1981), and in consequence also the phytoplankton using this nitrogen source will be depleted in $\delta^{15}\text{N}$. Thus, the phytoplankton $\delta^{15}\text{N}$ changes seasonally and regionally with environmental conditions and is not necessarily of the same magnitude in different years. Under the assumption that trophic enrichment of $\delta^{15}\text{N}$ per trophic level is constant (Minagawa and Wada 1984, Post 2002), the $\delta^{15}\text{N}$ of higher trophic levels will depend on the phytoplankton base line (Garton et al. 2005). *C. finmarchicus* raised in the laboratory also showed no difference in fractionation of $\delta^{15}\text{N}$ for the different developmental stages when they were fed the same phytoplankton diet (Table 5). This allows the conclusion that the $\delta^{15}\text{N}$ differences between the overwintering generation from 2003 (samples from February and March) and new generation in 2004 (samples from April to August) in the Trondheim Fjord were caused by diets with different phytoplankton baselines, and that phytoplankton in 2003 probably was enriched in $\delta^{15}\text{N}$ compared to phytoplankton in 2004 (Vanderklift and Ponsard 2003).

It is difficult to isolate natural phytoplankton and measure its $\delta^{15}\text{N}$, because it occurs in assemblage with similar sized microzooplankton as seston. If copepods selectively feed on different seston taxa and these taxa are isotopically distinct, then using seston as bulk fraction in $\delta^{15}\text{N}$ analyses could introduce error into the estimate of copepod trophic position (Matthews and Mazumder 2003). Some studies used filter feeding molluscs as a baseline for trophic level to, when analysing higher trophic levels (e.g. Post 2002). In this study the average $\delta^{15}\text{N}$ of the ephemeral algae *Enteromorpha* sp. and *Chorda filum* was $3.4 \pm 0.5\text{‰}$. The algae were sampled in August and there $\delta^{15}\text{N}$ can be seen as a baseline for primary production, i.e. trophic level one, integrated over the sampling period of *C. finmarchicus*, but it gives no information on temporal or regional fine scale variation in the fjord. The $\delta^{15}\text{N}$ signatures of the new generation of *C. finmarchicus* (samples April to August) are similar and average $6.5 \pm 0.3\text{‰}$. This is an enrichment of 3.1‰ compared to the primary production baseline (3.4‰). A recent literature review found the overall mean $\delta^{15}\text{N}$ enrichment between consumers and their diet to be lower (Vanderklift and Ponsard 2003; $2.54 \pm 0.11\text{‰}$), than previously reported in several other studies (Minagawa and Wada 1984; $3.4 \pm 0.11\text{‰}$, Vander Zanden and Rasmussen 2001; $2.9 \pm 0.30\text{‰}$, Post 2002; $3.4 \pm 0.13\text{‰}$). This would place *C. finmarchicus* at trophic level 2.2, indicating a moderate degree of omnivory. However, the stable isotope analyses from the laboratory cultures of *Dunaliella tertiolecta* and *Isochrysis galbana*, which were grown on the same medium, under the same conditions,

showed that fractionation of $\delta^{15}\text{N}$ is obviously species dependent. The $\delta^{15}\text{N}$ signature of *I. galbana* was even higher than those of the copepods which were feeding on it, and higher than any of the $\delta^{15}\text{N}$ signatures measured for the *C. finmarchicus* sampled in the Trondheim Fjord (Fig. 14). In laboratory experiments lower temperature and nitrogen limitation resulted in enrichment of $\delta^{15}\text{N}$ in the phytoplankton species *Dunaliella* sp., *Rhodomonas salina* and *Thalassiosira weissflogii*. *Acartia tonsa* naupli which were fed these algal species showed the tendency to keep a certain $\delta^{15}\text{N}$ signature independent of $\delta^{15}\text{N}$ signature of their diet (Soyka 2006). The same might be true for *C. finmarchicus* in this study. The copepods raised in the laboratory had an average $\delta^{15}\text{N}$ of 1.8‰, whereas the $\delta^{15}\text{N}$ signature of their prey averaged at 4.8‰. Vanderklift and Ponsard (2003) propose that $\delta^{15}\text{N}$ enrichment of organisms is independent of trophic position (herbivorous, carnivorous, omnivorous, detritivorous), and that $\delta^{15}\text{N}$ enrichment of an organism is determined by the main biochemical form of nitrogenous waste (lower $\delta^{15}\text{N}$ enrichment in organisms which, like copepods, excrete ammonia than in those which excrete urea or urine) and the C:N ratio of the diet (nitrogen-poor diet resulting in lower $\delta^{15}\text{N}$ signatures of the consumer). The performed experiments showed a preference for ciliate prey by *C. finmarchicus*. If the trophic position has no influence on $\delta^{15}\text{N}$ enrichment, than the degree of carnivory for *C. finmarchicus* in the Trondheim Fjord might have been higher than the 20% indicated by the determined trophic level 2.2 (20% carnivory, 80% herbivory). Higher availability of phytoplankton compared to ciliates in the fjord (Sakshaug 1972) might be another explanation for the 80% herbivorous feeding by *C. finmarchicus*.

Also the $\delta^{13}\text{C}$ signature of *C. finmarchicus* sampled in the Trondheim Fjord in 2004 showed temporal variation. Samples from April and May were enriched in $\delta^{13}\text{C}$, compared to samples from June to August of diapausing *C. finmarchicus*, which were $\delta^{13}\text{C}$ depleted (Fig. 14 and 17). Different carbon sources for primary production can cause variation in $\delta^{13}\text{C}$. In stratified aquatic systems primary producers in the upper water column could be depleted in their $\delta^{13}\text{C}$ if they used CO_2 respired by present zooplankton as carbon source, compared to primary producers in deeper water layers where the available CO_2 is of atmospheric origin (Matthews and Mazumder 2003). This possibility might be excluded for *C. finmarchicus* because the copepods from the summer samples did not feed any more but were already in diapause (Hirche 1991, 1996). A better explanation for the variation in the $\delta^{13}\text{C}$ signature of *C. finmarchicus* are the differences in lipid content of the different developmental stages. Lipids have a high C:N ratio and, because the incorporated carbon is biased towards ^{12}C , they are depleted in their $\delta^{13}\text{C}$ signatures compared to proteins and carbohydrates (Kurle and Worthy 2002). Thus lipid rich copepods have high C:N ratios and depleted $\delta^{13}\text{C}$ signatures, as found for *C. finmarchicus* in the Trondheim Fjord in 2004. By applying the equation $\delta^{13}\text{C}' = \delta^{13}\text{C} + D \cdot [-0.2068 + 3.90 / (1 + 287.1 / L)]$ (with

$L = 93/[1 + 1/(0.246 \cdot C/N - 0.775)]$ being the parameterised lipid factor) introduced by McConnaughey and McRoy (1979) to normalize the $\delta^{13}\text{C}$ signatures for lipid content, I could show that the depletion in $\delta^{13}\text{C}$ of the *C. finmarchicus* stage CV is due to its higher lipid content (Fig. 16).

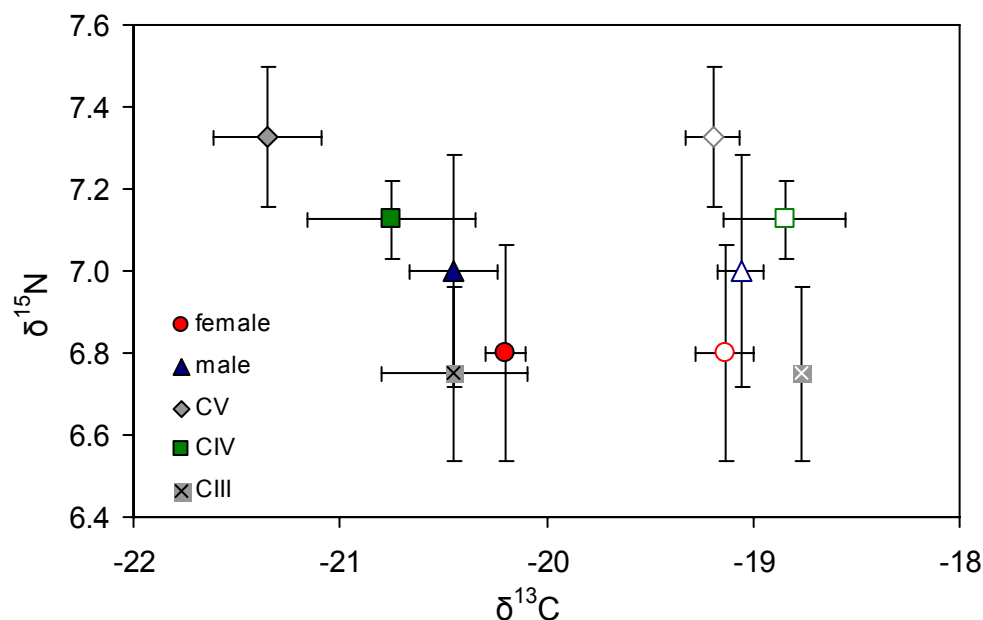


Figure 16 - *Calanus finmarchicus*. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures [‰] of developmental stages CIII to adult male / female of specimens caught in the Trondheim Fjord in May 2004. This month was selected for the demonstration because all stages (CIII to adult) were present in the sample. Open symbols are 'normalized' for lipid contents (McConnaughey and McRoy 1979). Error bars indicate standard error.

The factor D in this equation describes the isotopic difference between lipids and the bulk organism. In my calculations for the May samples of *C. finmarchicus* I used an average D of 6‰ as suggested by McConnaughey and McRoy (1979). This might be inappropriate as this isotopic difference can be highly variable (0.5-15‰, Parker 1964). Matthews and Mazumder (2005) state that normalisation of $\delta^{13}\text{C}$ signatures due to lipid content should not be used if lipids are dietary as is true for most zooplankton, and if the proportion of dietary acquisition and storage of lipids are questions to be answered. Furthermore, the authors suggest that temporal variation in $\delta^{13}\text{C}$ of an animal can be better explained and predicted by its C:N ratio than by the $\delta^{13}\text{C}$ of its diet. The $\delta^{13}\text{C}$ of the two freshwater copepods *Hesperodiaptomus franciscanus* and *Leptodiaptomus tyrelli* was negatively correlated to their C:N ratio. *L. tyrelli* is, like the marine *C. finmarchicus*, a copepod with large variation of lipid content throughout the year. *C. finmarchicus* showed a maximum difference in $\delta^{13}\text{C}$ of ~5‰, with highest signatures found in May and lowest in August as shown in figure 17. The C:N ratio of the developing population in April and May is lower than the C:N ratio of the overwintering population sampled from June to August. *C. finmarchicus* overwinters mainly

as CV, but also overwintering adult males and females have been found (Hirche 1991, 1996). Already in April and May the stage CV had the highest C:N ratio which further increased with time, due to accumulation of more lipids in the oil sac for energy storage during the following winter diapause (Hirche 1996). With this increase in C:N ratios due to increasing lipid content the $\delta^{13}\text{C}$ of the overwintering copepods decreased, which is in agreement with Matthews and Mazumder (2005). This could also explain the higher $\delta^{13}\text{C}$ of the overwintering generation from 2003 sampled in February and March (Fig. 17). These copepods might have had a similar lipid content, and hence C:N ratio in summer 2003 before their descent to deeper waters, as the copepods sampled in summer 2004. They survived the winter by living on their stored lipids (Hopkins et al. 1984, Hirche 1996), which resulted in a temporal change of the C:N ratio to lower values. Thus, at the end of the winter diapause these copepods would be enriched in $\delta^{13}\text{C}$ because of the lower lipid content. In February / March the C:N ratio of CV and adult males was higher than the C:N ratio of adult females. This is probably due to the onset of egg production, which uses energy from the stored lipids (Hirche 1996). And assuming that some of the *C. finmarchicus* which were stage CV in February had moulted into adult females by March their lower C:N ratio is in agreement with the concurrent increase in $\delta^{13}\text{C}$.

The two different generations of *C. finmarchicus* from the laboratory set-up differed markedly ($\sim 6\text{‰}$) in their $\delta^{13}\text{C}$ signatures. Furthermore, they were depleted in $\delta^{13}\text{C}$ compared to the specimens sampled from the fjord (Fig. 14 and 18). But also here a negative correlation between $\delta^{13}\text{C}$ and C:N ratio can be seen. The statement that seasonal variation in $\delta^{13}\text{C}$ signatures of zooplankton mainly can be explained by its C:N ratio (Matthews and Mazumder 2005) is supported by laboratory results which showed that the $\delta^{13}\text{C}$ of *A. tonsa* did not vary when it was fed several species of algae which differed in their $\delta^{13}\text{C}$ (Soyka 2006). But as my data also show, there are differences in the absolute $\delta^{13}\text{C}$ signature between different generations and populations. The mean $\delta^{13}\text{C}$ of the *C. finmarchicus* raised in the laboratory differed by about $\sim 6\text{‰}$ between generations, and the mean $\delta^{13}\text{C}$ of specimens from the fjord differed by $\sim 5\text{-}11\text{‰}$ from the laboratory means. I therefore suggest that the $\delta^{13}\text{C}$ signature of the diet and of the parental generation have an influence on a copepods $\delta^{13}\text{C}$. The C:N ratio might be the main influence on the temporal variation in a given range of the $\delta^{13}\text{C}$ signature of a population (Matthews and Mazumder 2005), but the absolute magnitude of this range of variation is probably caused by the $\delta^{13}\text{C}$ of the diet. This dietary effect on the magnitude of the $\delta^{13}\text{C}$ signatures seems to be passed on from one generation to the next. The *C. finmarchicus* in the laboratory were fed the same diet and the F4-generation was enriched in $\delta^{13}\text{C}$ compared to the F3-generation. The more negative $\delta^{13}\text{C}$ signatures of the *C. finmarchicus* from the laboratory, compared to the wild copepods from the fjord might also indicate their different diet. The copepods from the laboratory were raised

on a pure algal diet, whereas *C. finmarchicus* from the fjord was additionally feeding on microzooplankton.

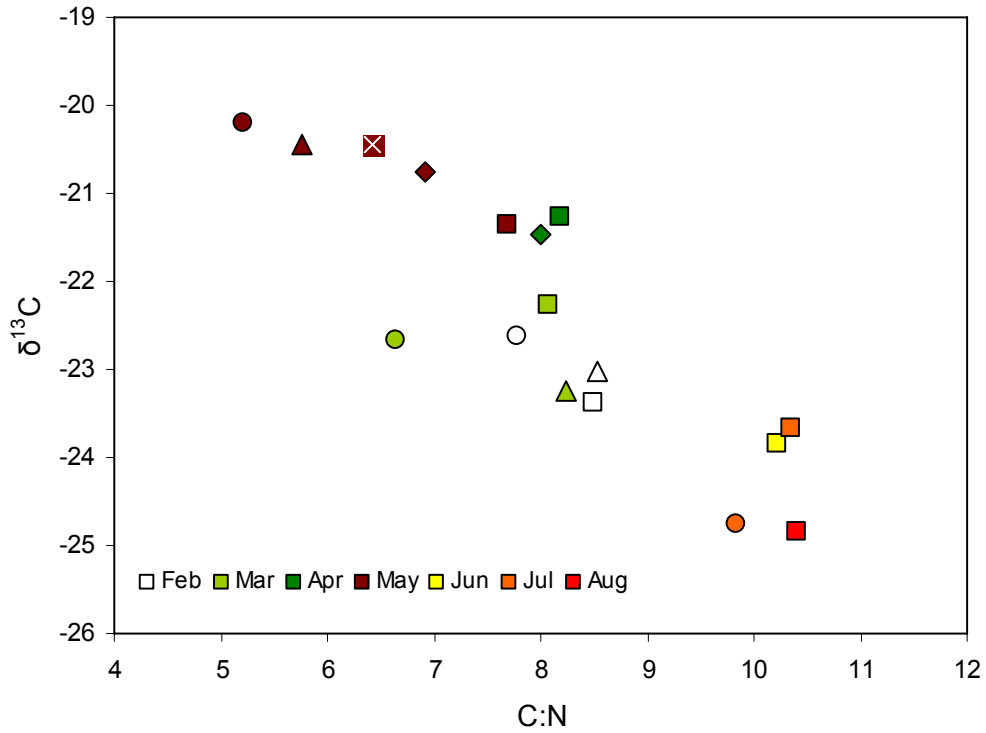


Figure 17 - *Calanus finmarchicus*. Relationship between $\delta^{13}\text{C}$ signatures [‰] and C:N ratio of specimens sampled from the Trondheim Fjord from February until August 2004. Different symbols indicate the developmental stages with: circle-female, triangle-male, square-CV, diamond-CIV, and cross-CIII. Different colours represent the months as given in the legend.

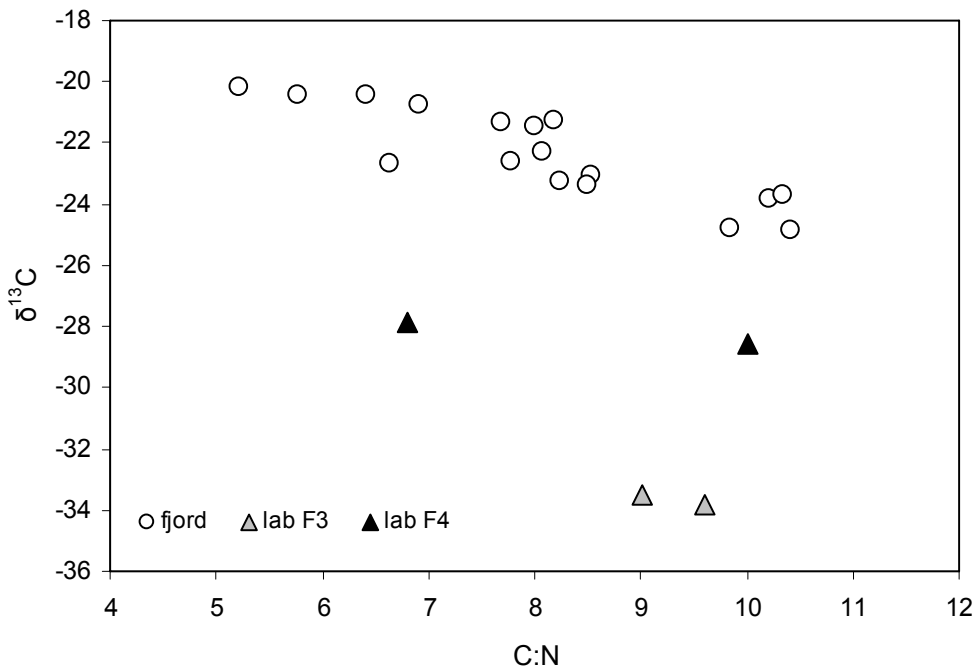


Figure 18 - *Calanus finmarchicus*. Relationship between $\delta^{13}\text{C}$ signatures [‰] and C:N ratio of specimens sampled in the Trondheim Fjord from February until August 2004 (circles) and of specimens raised in laboratory (triangles). F3 and F4 indicate the different generations from the laboratory.

4.2 Feeding behaviour of *Centropages hamatus*

4.2.1 The Experiments

Adult male and female *Centropages hamatus* were exposed in short time laboratory experiments to several prey organisms: the oligotrich ciliate *Rimostrombidium caudatum*, the diatom *Thalassiosira weissflogii*, and the flagellate *Rhodomonas* sp..

Highest clearance rates were not found at the lowest prey concentrations but at slightly higher values, and ingestion followed a Holling type III curve irrespective of type of prey and sex of the copepods. The increasing clearance with increasing prey concentration suggests a feeding threshold for *C. hamatus* at $<5 \mu\text{g C l}^{-1}$, which seems to be similar for algal and ciliate prey. At concentrations $<15 \mu\text{g C l}^{-1}$ highest clearance was observed on ciliates followed by clearance on diatoms and clearance on flagellates. Maximum diatom concentration in the experiment was $\sim 50 \mu\text{g C l}^{-1}$. A comparison of the clearance rates on all three prey species at $\sim 50 \mu\text{g C l}^{-1}$ reveals no difference for clearance on diatoms and flagellates, whereas clearance on ciliates was twice as high as on the algal prey. A similar pattern was found for ingestion, with ingestion of ciliates being 2.5 times higher than ingestion of diatoms and flagellates at $\sim 50 \mu\text{g C l}^{-1}$. This trend continued with further increasing prey concentrations. Ingestion on ciliates was up to three times higher than ingestion on algal prey (*Rhodomonas* sp.). Exceptions from the more general feeding pattern were found for male *C. hamatus*. They showed a more or less constant low clearance on ciliate prey. This resulted in lower ingestion compared to females at lower ciliate concentrations. This constant clearance rate of the males might be explained by suspension feeding, whereas the females used ambush feeding, which results in higher clearance at low prey concentrations (Evjemo et al. 2000). In the switching experiment on the other hand, there was no such difference between the sexes in clearance of ciliates at low concentrations. Here the males showed higher maximum clearance than females (Fig. 10A). Thus the lower clearance by male *C. hamatus* in the functional response experiment might have been a result of the nutritional status of the copepods causing individual variability associated with feeding behaviour (Hwang et al. 1994). Furthermore, the speed of the feeding current of *C. hamatus* is only 0.79 mm s^{-1} at a distance of 1 mm from the antennules (Hwang and Strickler 2001). The prey ciliate in my experiments was *R. caudatum* which swims in spirals, but can perform rapid escape jumps when disturbed (personal observation). Spiral swimming ciliates have swimming velocities between 0.5 and 1.0 mm s^{-1} (*Strombidium reticulatum*, Jonsson and Tiselius 1990), and for escape jumps a velocity of up to 8.5 mm s^{-1} has been reported (*Mesodinium rubrum*, Jonsson and Tiselius 1990). Hence, *C. hamatus* could not capture an escaping ciliate within its feeding current, and in conclusion must have actively selected the ciliate prey, i.e. used ambush feeding.

Comparison of the 95% confidence intervals of the fitted non-linear regressions showed that there is no difference in ingestion rates between the sexes at prey concentrations $<50 \mu\text{g C l}^{-1}$. With further increase in prey concentration ingestion by adult females was twice as high as ingestion by adult males. This difference might suggest a trend because the 95% confidence intervals of the regression lines of male and female *C. hamatus* do not overlap with ciliate prey (*R. caudatum*: $\sim 50\text{--}125 \mu\text{g C l}^{-1}$). Figure 9F might suggest a difference in ingestion between the sexes also for flagellate prey at concentrations $>50 \mu\text{g C l}^{-1}$. The overlap of the 95% confidence intervals of the regression lines of adult males and females with the flagellate *Rhodomonas* sp. as prey (males: $-14,430.90$ to $14,593.13 \mu\text{g C ind}^{-1} \text{ d}^{-1}$; females: 2.09 to $2.36 \mu\text{g C ind}^{-1} \text{ d}^{-1}$) is most likely due to the very high predicted maximum ingestion for the males ($81.12 \mu\text{g C ind}^{-1} \text{ d}^{-1}$). Otherwise, comparison of the predicted maximum ingestion, where the plateau is reached, showed no significant difference between the sexes in the functional response experiments for all prey types. With ciliates as prey the predicted maximum ingestion of $7.14 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ for males and $8.82 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ for females fell within reasonable values (95% confidence interval: males: 6.67 to $7.60 \mu\text{g C ind}^{-1} \text{ d}^{-1}$; females: 6.25 to $11.40 \mu\text{g C ind}^{-1} \text{ d}^{-1}$). *C. hamatus* has an average body carbon content of $\sim 8 \mu\text{g C ind}^{-1}$ (Halsband-Lenk et al. 2001). Copepods can ingest up to 148% of their own body carbon (Durbin et al. 1990). For *C. hamatus* 148% body carbon would equal $\sim 12 \mu\text{g C ind}^{-1} \text{ d}^{-1}$. In the switching experiment a trend was found that maximum ingestion by males on ciliates is lower than by females (95% confidence interval: males: 6.03 to $7.94 \mu\text{g C ind}^{-1} \text{ d}^{-1}$; females: 9.97 to $14.61 \mu\text{g C ind}^{-1} \text{ d}^{-1}$). Naturally occurring ciliate abundances do not exceed $35 \mu\text{g C l}^{-1}$ (Archer et al. 2000, Jensen and Hansen 2000), and at this concentration *C. hamatus* reached an ingestion of $\sim 2 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ and $\sim 4 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ in the functional response experiment and switching experiment, respectively. These rates equal 25 to 50% of body carbon. The ingestion of ciliates by males, and also females, in the switching experiment might show a more realistic pattern, because saturation of the regression curves seemed to start at ciliate concentrations of $\sim 50 \mu\text{g C l}^{-1}$ (Fig. 10B). Under natural conditions feeding of copepods is influenced by factors of disturbance and ingestion rates are lower than found in laboratory studies where disturbing factors usually are excluded. The above mentioned ingestion of 148% body carbon has been observed for *A. tonsa* on high *T. weissflogii* concentrations in a laboratory, but maximum ingestion of the same copepod species in a mesocosm with natural food was only 74% body carbon (Durbin et al. 1990).

When ciliates and diatoms were offered together in the switching experiment highest clearance of ciliates was observed for both sexes at very low ciliate concentrations. Here male *C. hamatus* showed even higher clearance on ciliates than females. Compared to the functional response experiment with ciliate prey the maximum average clearance rates for both male and female *C. hamatus* were reached at lower ciliate concentrations in the

switching experiment, with $\sim 540 \text{ ml ind}^{-1} \text{ d}^{-1}$ at $2.2 \mu\text{g C l}^{-1}$ and $\sim 380 \text{ ml ind}^{-1} \text{ d}^{-1}$ at $0.5 \mu\text{g C l}^{-1}$, respectively. Ingestion of ciliates increased with increasing ciliate concentration, to similar maximum values as in the ciliate functional response experiment. Clearance and ingestion of diatoms was very irregular and did not follow a trend. The very high values for the replicates with lowest ciliate / highest diatom concentration are considered to be outliers (Fig. 10C and 10D). *C. hamatus* is very efficient in capturing ciliates (Sommer et al. 2005). In four cases with ciliate start concentrations between ~ 2 to $\sim 7 \mu\text{g C l}^{-1}$ (34-125 ciliates per bottle) the five copepods per replicate cleared the ciliates completely, in three other replicates only two ciliates were left in 100 ml after six hours of incubation (data not shown). The copepods then probably started to feed on diatoms when no more ciliates were left in the treatment with lowest ciliate concentration and incubation continued, thus resulting in these very high clearance and ingestion rates for diatoms. These values were nevertheless categorized as outliers because of the unrealistic high ingestion of 40 and $20 \mu\text{g C ind}^{-1} \text{ d}^{-1}$ by male and female *C. hamatus*, respectively. For the switching experiment a Holling type II regression was fitted to the clearance rate of adult females because here the values did not show the increase to a peak at low concentrations with following decline. But this is due to high variability in clearance by the female *C. hamatus* at low concentrations in this experiment, and does not indicate a change in feeding behaviour. The ingestion could be described by a Holling type III functional response ($r^2 = 0.92$, $p = 0.0002$).

C. hamatus showed a preference for ciliate prey. Ciliates were ingested at very low concentrations irrespective of the fact if they were offered as the only prey in the functional response experiment, or together with diatoms in the switching experiment. In the latter case ciliates contributed with 100% to the total ingestion of male and female *C. hamatus* when their abundance exceeded 5% of total prey abundance. This threshold might even be as low as 1% for the females (Fig. 11). Tokle (2006) found similar values for female *C. hamatus* when ciliates were offered in varying concentrations together with algal prey in a constant surplus concentration.

None or little feeding by adult males was reported in earlier studies for the larger *Calanus* spp. (Marshall and Orr 1955b, Mullin 1963). In the present study adult males of the small copepod species *C. hamatus* reached $\sim 50\%$ of female clearance and ingestion, similar to rates found for male individuals of the similar sized *Acartia tonsa* (Conover 1956). Reduced energy demand compared to females, which require much energy for egg production (Halsband and Hirche 2001), or the smaller body size itself might be reasons for lower feeding rates of male copepods (Conover 1956, Marshall and Orr 1956).

Temperature is a factor influencing feeding rates of copepods, with higher temperatures resulting in higher grazing rates (Conover 1956). *R. caudatum* was isolated from the Kiel Fjord in March where the water temperature at the surface was around 3°C .

The ciliate cultures were kept in a climate chamber and the temperature was slowly increased to 10°C. Ciliates are sensitive to several environmental factors (Gray 1974, Martin-Cereceda et al. 2002) and cultivating them is not always easy. *R. caudatum* was growing well at 10°C and I therefore decided not to increase the temperature further, and to perform the experiments with *R. caudatum* as prey at 10°C, whereas the temperature was 15°C in the previous experiments with algal prey. Thus, assuming increasing feeding rates with increasing temperature the ingestion shown by *C. hamatus* on ciliates in the experiments at 10°C could be even higher at 15°C. But this does not change the conclusion that ciliates, when present, are preferred prey for *C. hamatus*.

4.3 Conclusion

The feeding behaviour of both *Calanus finmarchicus* and *Centropages hamatus* can be characterised as omnivorous with the ability of selective feeding.

C. finmarchicus is able to select preferred larger prey items from a mixture independently of relative or total concentration. Small unialgal prey above a threshold concentration of $\sim 60 \mu\text{g C l}^{-1}$ is ingested by *C. finmarchicus* using suspension feeding mode, whereas ciliate prey and large algal cells offered in a mixture or at limiting concentrations are captured by ambush feeding.

Feeding by *C. hamatus* on phytoplankton and ciliates starts at similar low concentrations, but the maximum ingestion of ciliates is higher compared to maximum ingestion of algal prey. *C. hamatus* preys preferably on ciliate when they are offered together with diatoms. Ingestion by males is lower at high prey concentrations but reaches $\sim 50\%$ of ingestion by females.

In spring bloom situations it is possible that one algal species dominates the phytoplankton community with up to 98% of total carbon, and very high concentrations of $\sim 900 \mu\text{g C l}^{-1}$ can be reached (Peperzak et al. 1998). In such a situation suspension feeding copepods can ingest the algal prey most efficiently, and build up biomass (Runge 1988, Turner 1984, Mann 1993). Ciliate biomass peaks shortly after the phytoplankton in spring (Johansson et al. 2004). Maximum microzooplankton biomass reported for natural systems range from only $10 \mu\text{g C l}^{-1}$ when dominated by naked ciliates (*Strombidium* spp., *Strobilidium* spp.), over $34 \mu\text{g C l}^{-1}$ (tintinnids, athecate and thecate dinoflegglates) (both in arctic systems, Jensen and Hansen 2000), to $72\text{-}80 \mu\text{g C l}^{-1}$ (nanoflagellates, dinoflagellates, ciliates, split evenly with $24\text{-}26 \mu\text{g C l}^{-1}$ each) (northern Norwegian fjords, Archer et al. 2000). In terms of abundance ciliates do not exceed ~ 7 ciliates ml^{-1} under natural conditions (Irigoien et al. 1998, Tokle et al. 2005b), which for my experiment with *C. finmarchicus* is equivalent to a ciliate concentration of $\sim 17 \mu\text{g C l}^{-1}$, ten times less than the maximum ciliate concentration. Copepods which can ambush feed on ciliates can switch from feeding on

phytoplankton to the nutritional more valuable ciliates (reviewed in Stoecker and Capuzzo 1990, reviewed in Sanders and Wickham 1993, Ohman and Runge 1994), and thus upgrade the quality of their food with essential fatty acids, which are required for metabolic processes, e.g. reproduction (Murray and Marcus 2002). And because ambush feeding results in higher clearance at low prey concentration (Evjemo et al. 2000), copepods able to use this feeding mode can feed sufficiently on the natural occurring ciliate abundances. Thus, copepods which can feed on phytoplankton and ciliate blooms with the same efficiency regarding ingestion, extend the period of good food supply compared to copepods which are restricted to a single feeding behaviour.

All rates of the functional response and switching experiments presented in this study are given in “rate per individual per day”. These daily rates should be considered with caution, because they are extrapolated from laboratory experiments with incubation times of between four to six hours. The results of laboratory experiments on feeding rates given “per day” might be overestimated. Under natural conditions copepods show a diurnal feeding rhythm (e.g. Head and Harris 1987, Perueva 1992). During night they ascend to the surface to feed on phyto- and microzooplankton which are abundant there, and descend to deeper water layers at daytime to avoid visual predation by planktivorous fish or fish larvae (Ghan et al. 1998, Jamieson 2005, Sanvicente-Anorve 2006). For my experiments I assume the copepods fed continuously during incubation, at a rate they would use during night under natural conditions. Since the experiments were stopped after a few hours, daily rates were calculated by multiplying “rates per hour” with the factor 24. But this implies a continuous feeding over the whole day, which is not true for natural copepod communities. Therefore, laboratory feeding rates give rather an indication of theoretical possible maximum rates, but not for the realised rates which are reached in the wild. Beside the already mentioned diurnal feeding rhythm, other factors influencing the clearance and ingestion of wild copepods are food availability, predation, temperature, and turbulence (e.g. Conover 1956, Melle et al. 1994, Saiz and Kiørboe 1995, Hwang and Strickler 2001, Kozlowsky-Suzuki et al. 2006, Pfaffenhoefer et al. 2006, Sanvicente-Anorve et al. 2006). Therefore natural feeding rates of copepods should be lower than those from laboratory experiments were these factors mostly are excluded.

Copepods are part of very complex interactions in the plankton community, which are influenced by many biotic and abiotic factors, and caution is required regarding too much generalisation of their feeding behaviour.

Acknowledgements / Danksagung

My thanks go to Ulrich Sommer who acted as my supervisor. He introduced me to the plankton world and gave me the opportunity to do my research in his department. His critical view on the data helped to improve the results.

I thank Olav Vadstein who supervised my research in Norway. He provided both professional and personal guidance when I was exploring unknown countries, also over long distances.

I am grateful to Ingrid Gismervik who introduced me to ciliate culturing, Dag Altin who provided the laboratory samples of *C. finmarchicus*, Kjersti Andresen who offered her help with laboratory work and equipment, Runar Eggen who helped performing the first experiment, and Nils Togle who involved me in constructive talks about copepod feeding. Thanks to Alexandra Neyts for her administrative care during my stay in Trondheim. Og tusen takk til lunsjbordet som ikke bare holdt kroppen min i livet men også føret ånden min.

I thank Thomas Hansen for analysing the stable isotope samples, Rolf Schmahljohann for introduction and help using the scanning electron microscope, and Sabine Agatha for identifying the ciliate *R. caudatum* and processing the electron microscope images. I am grateful to the staff members of the Experimental Ecology, especially to Cristian Agurto, Gabriele Barth, Jamileh Javidpour, Christine Rautenstrauch, Marcel Sandow, and Cordula Stielau.

A special thank you goes to Birte Schönborn and Stefanie Ismar, who read early versions of the manuscript and added helpful questions and comments.

Meiner Familie danke ich für ihr Vertrauen und ihre uneingeschränkte Unterstützung. Mag die physische Entfernung auch noch so groß sein, bin ich doch immer ganz nah.

Andrea

This research has been supported by a Marie Curie Fellowship of the European Community programme IMPROVING HUMAN RESEARCH POTENTIAL AND THE SOCIO-ECONOMIC KNOWLEDGE BASE under contract number HPMT-CT-2001-00424, the Norwegian Research Council (contract 143184/140 - the Calanus strategic research programme at NTNU), and the Deutsche Forschungsgemeinschaft (contract SO 145 / 25-1).

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Erklärung (Statement)

Hiermit erkläre ich, dass die vorliegende Dissertation, abgesehen von der Beratung meiner Betreuer, selbständig von mir angefertigt wurde und dass sie nach Form und Inhalt meine eigene Arbeit ist. Sie wurde keiner anderen Stelle in Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Biologische Meereskunde erfolgen. Des weiteren erkläre ich, dass ich Zuhörer bei der Disputaion zulasse.