The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
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Contents

Acknowledgements ................................................................................................................................... iii
List of papers ........................................................................................................................................ v
1. Introduction ......................................................................................................................................... 1
   1.1 Geographic distribution and developmental biology of Calanus finmarchicus ..................... 3
   1.2 Reproduction, growth and lipid accumulation in C. finmarchicus .................................. 4
   1.3 Feeding ecology .......................................................................................................................... 5
   1.4 Objectives of the thesis ............................................................................................................... 6
2. Results and discussion ....................................................................................................................... 7
   2.1 Reproduction of C. finmarchicus females ............................................................................... 7
   2.2 Somatic growth .......................................................................................................................... 12
   2.3 Lipid dynamics of C. finmarchicus in the Trondheimsfjord .................................................. 16
   2.4 Feeding selectivity ..................................................................................................................... 20
3. Conclusion and future work ............................................................................................................... 25
   3.1 Conclusions ............................................................................................................................... 25
   3.2 Future work .................................................................................................................................. 26
4. References ........................................................................................................................................... 27

Enclosure. Paper I–IV
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Øystein Leiknes
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List of papers

I. Leiknes, Ø., Bergvik, M., Vadstein, O., Olsen, Y. Reproduction in *Calanus finmarchicus* in a central Norwegian fjord, effects from potential food and maternal essential fatty acid content. Submitted.


Contributions

Paper I was initiated by ØL. MB participated in collecting *Calanus finmarchicus* females, the incubations were run by ØL. The analytical work, statistical analysis and writing were performed by ØL with comments from the other authors.

Paper II was the result of cooperation between ØL, SAE and NET. SAE and NET provided data from experiments run in 2007, whereas ØL performed experiments in 2009 and 2011. The analytical work was performed by ØL, MB and SAE. ØL wrote the paper with comments from the other authors.

Paper III was initiated by MB and ØL, partly in cooperation with DA. ØL and MB did the field work and most of the subsequent sorting of live *C. finmarchicus*. DA did some of the analyses. KRD developed a method of lipid analysis and did the major part of the lipid analyses. Advisors contributed to planning of the field sampling. MB did most of the writing of paper III, whereas YO, DA and ØL were involved in the final stages of the paper.

Paper IV was based on three experiments. Experiment (Exp) 1 and 2 was the main part of the master thesis of AS. A third experiment was planned and carried out by NET and OV. YO, OV, US and ØL planned Exp. 1 and 2. ØL developed a method to decrease the density of ciliates enabling a ciliate gradient in Exp. 1 and 2. ØL and AS carried out Exp. 1 and Exp. 2. AS counted the samples in Exp. 1 and 2 and compiled the first submitted version of paper IV, with comments from the other authors. ØL made a major revision of the paper with comments from the other authors.
1. Introduction

Copepods form a group of crustaceans that evolved from benthic ancestors and colonized the pelagic environment some 200–400 million years ago (Bradford-Grieve, 2002). The group typically dominates the zooplankton biomass in all seas of the world (Verity & Smetacek, 1996) and are probably the numerous multicellular organisms on earth (Mauchline, 1998). Their name originates from the Greek words kope: oar and podos: foot. The pelagic copepods are very similar in shape, regardless of a range in total length of 0.25–18 mm (Fosshagen & Iliffe, 1988; Owre & Foyo, 1967). The suggested success factors of pelagic copepods involve: 1) The torpedo-shaped body and sensory armed antennules that makes them very effective at both detecting and escaping predators. 2) The high capability to detect prey reduces the energy needed to remove food particles from the water. 3) The high efficiency of detecting mates allows for sexual reproduction in every generation (Kiørboe, 2011).

The calanoid copepod *Calanus finmarchicus* (Gunnerus 1770) is the dominating copepod species in the North Atlantic. This species was initially described as *Monoculus finmarchicus* by the Norwegian bishop Gunnerus (Figure 1) (Gunnerus, 1770). He was a bishop in Trondheim, mid-Norway and the initiator of the first Norwegian scientific institution: The Royal Norwegian Society of Sciences and Letters. He was a pen pal of Carl von Linne, was the first scientist in Norway to employ the binomial nomenclature, and described a number of marine species. *Monoculus finmarchicus* was later redescribed as *Calanus finmarchicus* by G.O. Sars. The first proper sampling net was developed less than 200 years ago, and the first closing net which allowed studies of vertical migrations was developed by Fridtjof Nansen in the 1890’s. Trondhjem Biological Station was established in 1900, for the purpose of sea ranching of plaice, but also for investigations of oceanography and marine biology (Nordgård, 1926; Sakshaug & Sneli, 2000). Extensive studies on the phytoplankton and zooplankton in the Trondheimsfjord was initiated by professors E. Sakshaug and T. Strømgren in the late 1960’s, and continuous sampling in addition to hydrographical measurements has been conducted until recently (Haug et al., 1973; Sakshaug, 1972; Sakshaug & Myklestad, 1973; Strømgren, 1974).

![Figure 1. The first drawing of Calanus finmarchicus made by Gunnerus (A) and picture of a female Calanus finmarchicus (B).](image)
During the last 50 years, there has been a steady growth in the aquaculture industry and with that an increasing demand for fish feed based on marine resources. At present, 90% of fish stocks are either fully fished or overfished (FAO, 2014). The harvesting yields of so-called forage fish are limited to 30–35 million tons per year and the limited availability of food resources in the aquaculture industry is mitigated by the increased use of agricultural lipids and proteins in fish feed. However, the terrestrial components can only serve as supplement, and especially the long-chain polyunsaturated n-3 fatty acids (LC n-3 PUFAs) like docosahexaenoic acid (C22:6 n-3, DHA) and eicosapentaenoic acid (C20:5 n-3, EPA) must presently be derived from marine sources (Olsen, 2011). Alternative sources of LC n-3 PUFAs are being explored, including Antarctic krill (Euphausia superba) and Calanus finmarchicus (FAO, 2014). The main incentive for choosing zooplankton as a supplement in feed production is that, on average, the zooplankton are one trophic level lower than planktivorous fish. As a general rule, 80–95% of the energy/matter consumed by an animal is lost as CO2 and organic components. The resulting transfer of organic matter from one trophic level to the next has a trophic yield of 5–20% of the consumed food (mean 10%) (Ryther, 1969). The flip side of these calculations is that the production is 5–20 times higher at one trophic level lower in the food chain. In addition to harvesting at lower trophic levels, the use of plants and micro-organisms for feed has also been proposed as solutions to improve the overall efficiency of fish production in aquaculture (Olsen, 2013).

C. finmarchicus builds up rich lipid reserves during spring to survive dormancy during winter. They spawn the subsequent spring, often in dense shoals that may give the sea a reddish hue (Ban et al., 1997; Marshall & Orr, 1955). The annual production of C. finmarchicus in the Norwegian Sea is estimated to 29 million tonnes of carbon with a production to biomass (P/B) ratio of 4.3 (Hjøllo et al., 2012). Harvesting C. finmarchicus has been suggested as a potential source of protein for humans already during World War 2 (Moore, 2011), and as feed for aquaculture purposes during the 1970’s (Omori, 1978; Wiborg, 1976), but the harvesting season was too short to make harvesting economically feasible at that time. In 2011, the world’s first commercial fishery on C. finmarchicus opened in the Norwegian Sea (Hjøllo et al., 2012), and the end products of that fishery are at present oils for human consumption, freeze dried or wet feed for aquaria fish, first feed for fish larvae and shrimps, and additives for pet food or flavour for food industry. The catch is limited to 1000 tonnes wet weight in Norwegian waters and a further increase in the harvest of C. finmarchicus require further knowledge and a science based and sustainable management practice. The Institute of Marine Research are, on behalf of the Directorate of Fisheries, developing a new management plan for commercial harvest of C. finmarchicus in Norwegian waters (fiskeridir.no, 2013).

One of the main challenges in the management of C. finmarchicus as a harvestable resource is its short lifespan and patchy distribution, causing huge fluctuations in time and space (Broms et al., 2009; Melle et al., 2014). An increasingly important tool to assess the biomass fluctuations in C. finmarchicus is reliable ecosystem models. These models rely on input parameters on biological variables like reproductive rates, growth rates, mortality and feeding selectivity (Samuelsen et al., 2009; Slagstad & Tande, 2007; Wassmann et al., 2006). To evaluate the quality of the output of the models, data of temporal and spatial distribution of
the food web compartments studied must be collected. It is obviously an impossible task to collect synoptic data on a basin scale, and the advection makes it difficult to follow single cohorts during time. However, the development of automatized equipment for surveying plankton, like laser optical plankton counter (LOPC), *in situ* fluorometer, and the development of satellite-based mapping of surface chlorophyll *a* has greatly improved the possibility to evaluate model fit, and this has improved the general understanding of the key processes that governs large scale variability in planktonic food webs (Basedow *et al.*, 2006).

### 1.1 Geographic distribution and developmental biology of *Calanus finmarchicus*

*Calanus finmarchicus* has its distribution centre in the North Atlantic gyre (Fleminger & Hulsemann, 1977) and is the dominating species in this area (Planque & Batten, 2000). However, the regional distribution of *C. finmarchicus* has been shown to vary with the North Atlantic Oscillation (Greene & Pershing, 2000) and *C. finmarchicus* has recently been reported to shift its main distribution northwards because of sea warming (Chust *et al.*, 2014).

The Norwegian Coastal Current is slightly influenced by the brackish water from the Baltic Sea and fresh water runoff from Norway (Helland-Hansen & Nansen, 1909). This water mixes with the North Sea water and Atlantic Water and the salinity increases to approximately 31–32 PSU as the current flows northward along the Norwegian Coast (Sætre, 2007). The Trondheimsfjord has a main basin with a coastward sill at 190 meters, has a tidal difference of ~1.9 metres and there are six main rivers entering the fjord (Figure 2). The water masses below sill depth are dominated by Atlantic water (>34 PSU), and is exchanged about twice a year. The Coastal Current Water masses dominates above sill level, and in the surface layers there is a brackish layer fluctuating with the freshwater runoff (Jacobson, 1983).

*C. finmarchicus* is overall the most important copepod species in terms of biomass, both in coastal current waters and in many of the Norwegian fjords (Bagolein *et al.*, 2001; Skreslet *et al.*, 2000; Somme, 1934; Strømgren, 1971; Strømgren, 1974; Tande, 1982; Wiborg, 1954). *Calanus finmarchicus* grows through successive molts from eggs through six naupliar stages (N1–N6) and five copepodite stages (C1–C5) before reaching adulthood as either female or male. It spawns during spring, and produces normally one main generation before descending to deep waters for dormancy, mainly as C5 (Somme, 1934; Strømgren, 1974; Tande, 1982; Wiborg, 1954). Spawning females are present in surface waters from January and through the summer (Marshall & Orr, 1955; Tande, 1982), but the spawning usually peaks in advance of or during the phytoplankton spring bloom. There is, however, some evidence that parts of the spring population that grow into the C5 stage and develop further to adults and thereby undergo a second spawning during summer, instead of descending to deeper waters (Conover, 1988; Lie, 1968).
1.2 Reproduction, growth and lipid accumulation in *C. finmarchicus*

Plankton secondary production is often estimated from growth measurements or from studies of cohort development (Burkill & Kendall, 1982; Runge *et al.*, 1985; Winberg, 1971). An alternative approach is to measure the egg production rate and the carbon content of the eggs and females. When zooplankton has reached maternity, the somatic growth has ceased and the rate of egg production can therefore be regarded as a proxy for secondary production (Kiorboe & Johansen, 1986; Poulet *et al.*, 1995). *C. finmarchicus* and other lipid-rich copepods have shown to reproduce in the absence of food (Marshall & Orr, 1955; Mayor *et al.*, 2009a), concurrent with a decrease in body weight (Hirche & Kattner, 1993). When eggs are produced in the absence of food, the net growth rate must be negative. The reproductive rates of *C. finmarchicus* and the subsequent growth of nauplia are both sensitive to food concentration (Frost, 1972; Hirche *et al.*, 1997; Jonasdottir *et al.*, 2005; Marshall & Orr, 1955; Runge, 1985) and to food quality (Aubert *et al.*, 2013; Hygum *et al.*, 2000c; Mayor *et al.*, 2009a).
The egg production and hatching success of *C. finmarchicus* has been shown to be sensitive to the content of protein (Jonasdottir *et al.*, 2002), specific amino acids (Helland *et al.*, 2003), and essential fatty acids (EFAs) in the food, of whom eicosapentaenoic acid (EPA, C20:6 n-3) and docosahexaenoic acid (DHA, C22:6 n-3) are most important (Jonasdottir *et al.*, 2002; Jonasdottir *et al.*, 2005; Koski *et al.*, 2012; Pond *et al.*, 1996). As the reproduction rates and the mortality of newly hatched nauplia are shown to be highly variable between seasons and geographic regions, these are important issues to be addressed, and there is no general consensus on what factor that predominantly limits zooplankton- and specifically *C. finmarchicus* production in the marine environment.

Because the two first nauplia stages in *C. finmarchicus* are unable to feed, the individual weight of nauplia (N) stages N1 and N2 decreases (Harris *et al.*, 2000; Marshall & Orr, 1955). From stage N3 onwards, the carbon based somatic growth is exponential until they reach copepodite stage 5 (C5). The lipid accumulation is slow during stage N3–C2 and most of the storage lipids are accumulated during stages C3–C5 (Hygum *et al.*, 2000c; Kattner & Krause, 1987). Both the growth and the accumulation of lipids are dependent of the feeding of *C. finmarchicus*. The time between moults decreases and the lipid accumulation accelerates with increasing food availability (Harris *et al.*, 2000; Hygum *et al.*, 2000c). The lipids are stored in an oil sac in the central body cavity, mainly as wax esters (WE) (Miller *et al.*, 1998). In addition, they store a small fraction of triacylglycerides (TAG) that is uses for short-term storage (Hygum *et al.*, 2000c; Sargent & Henderson, 1986).

The metamorphosis to adult copepods, combined with a period of starvation through winter, reduces the average carbon content of the C5 stage of *C. finmarchicus*. The adult males and females are bigger than the C5, but because of less storage lipids, their carbon content is usually similar to or smaller than in that of stage C5 (Sargent & Falk-Petersen, 1988; Tande, 1982).

### 1.3 Feeding ecology

Traditionally, *C. finmarchicus* has been regarded as herbivorous (Graeve *et al.*, 1994; Marshall, 1924; Teegarden *et al.*, 2008). Other studies have either shown a non-selective consumption of ciliates (Levinsen *et al.*, 2000) or a selectivity for ciliates over other food particles by *C. finmarchicus* (Irigoien *et al.*, 1998; Nejstgaard *et al.*, 1997; Nejstgaard *et al.*, 1994). Size might be another important aspect of the feeding ecology of copepods, and some studies indicate that the copepodite graze bigger cells more efficiently than small, flagellated algae (Frost, 1972; Gismervik *et al.*, 1996; Hansen *et al.*, 1994; Hansen *et al.*, 1997) and that ciliates and alternative small food sources are too scarce or too small to contribute to the diet (Irigoien *et al.*, 2003). The degree of omnivorous feeding of *C. finmarchicus* has large implications on the development of realistic ecological models, but so far most of the ecological models developed for the *C. finmarchicus* population assume a pure diatom diet (Hjøllo *et al.*, 2012; Samuelsen *et al.*, 2009; Wassmann *et al.*, 2006). *C. finmarchicus* experience a wide range of food concentrations, and the selectivity seems to be affected by both the absolute and the relative concentration of the potential food sources (Saage, 2006; Saage *et al.*, 2008).
1.4 Objectives of the thesis
An important aspect when assessing the potential effects of zooplankton harvest is the degree of food limitation in \textit{C. finmarchicus}. If the reproduction and subsequent growth of the \textit{C. finmarchicus} population is heavily affected by limited availability of food, we can hypothesize that a limited harvest could result in increased food availability for the remaining population. The main aim of this thesis was to investigate how nutrition impact important life-history traits in \textit{C. finmarchicus}. Oxford Dictionary of English defines nutrition as “the process of providing or obtaining the food necessary for health and growth”. During this study, nutrition includes feeding selectivity, quantity and quality of potential food items and how these affect the reproduction, growth and lipid accumulation. Realistic ecological models rely on the parameterization of these important traits of the life cycle of \textit{C. finmarchicus}. The main objective was to evaluate to what extent nutrition influence the reproduction, growth, lipid accumulation and feeding in \textit{Calanus finmarchicus}.

The reproductive biology of \textit{C. finmarchicus} in the Trondheimsfjord was studied through three consecutive seasons (2009–2011) (Paper I). \textit{C. finmarchicus} females were collected from a field station and were incubated individually. The egg production rates and the share of eggs hatching to nauplia (hatching success) were monitored. Somatic growth of the nauplii of \textit{C. finmarchicus} was studied in 2007, 2009 and 2011 (Paper II). Nauplii were grown in flow-through chambers, and fed natural seston. To evaluate possible effects of food concentration and food quality on the reproduction and somatic growth of \textit{C. finmarchicus}, the food quantity and food quality was surveyed. The food quantity was monitored by measuring chlorophyll \textit{a} (chl\textit{a}), particulate organic carbon (POC) and by microscopy counts, whereas the food quality was evaluated by measuring the content of particulate organic nitrogen (PON), particulate organic phosphorus (POP), and essential long chain n-3 fatty acids.

The C5 stage of \textit{C. finmarchicus} was sampled at different depths from January to June in 2009, 2010 and 2011 (Paper III). The fatty acid composition was analysed in individual copepods and in the seston, and the stage composition and abundance of \textit{C. finmarchicus} was analysed from depth integrated net samples. The fatty acid composition in the copepods was compared with the fatty acid profile of the phytoplankton present.

The feeding selectivity of \textit{C. finmarchicus} copepodites was studied by carrying out three incubation experiments (Paper IV). Two of the feeding experiments were conducted using natural plankton during spring bloom and post-bloom conditions, with a gradient in ciliate concentration. The third experiment was conducted with cultured dinoflagellates and ciliates.
2. Results and discussion

2.1 Reproduction of *C. finmarchicus* females

In the present thesis, the reproductive biology of *C. finmarchicus* was studied by incubation experiments during three successive seasons (2009–2011) (Paper I). The general objective of this study was to investigate the effects of food quantity, food quality and female fatty acid composition on the egg production rate and the hatching success of *C. finmarchicus* in the Trondheimsfjord. Female *C. finmarchicus* were collected with a modified Nansen net (mesh size 200 μm, non-filtering cod end) and incubated individually in petri dishes containing filtered sea water. The food concentration was evaluated by monitoring the microplankton community by microscopy counts, by chlorophyll *a* (chl *a*) measurements and by measuring particulate organic carbon (POC). The food quality was evaluated by measuring the content of particulate organic phosphorus (POP) and nitrogen (PON) and the fatty acid composition of the seston material. We also analysed the fatty acid content of the female *C. finmarchicus* to evaluate the effects of female fatty acid composition on the reproduction rates.

The egg production rate (EPR) was generally low during winter (5.7 to 9.1 eggs fem⁻¹ d⁻¹) and high and variable in the period from mid-March through May, during which the egg production averaged 17.9 ± 1.7 eggs fem⁻¹ d⁻¹ (mean ± SE, range 9.3 to 30.0). This was similar to the patterns observed by previous studies, but our maximum rates (Figure 3A, Paper I) were slightly lower as compared to the maximum rates previously published (Head *et al.*, 2013a; Koski, 2007; Melle & Skjoldal, 1998, and references therein). Other important aspects of the reproduction of *C. finmarchicus* are the hatching success (HS), showing how many of the eggs produced that hatched to viable nauplia (Figure 3B) and spawning frequency (SF), expressing percentage of incubated females that produces eggs (Figure 3C). SF and EPR were strongly correlated, whereas HS showed no correlation with either SF or EPR. The HS did not follow any apparent pattern, and the sampling days with low HS were spread through the seasons, averaging 67.6 ± 1.5% (average ± SE). The SF appeared to follow a similar trend in all years, with few females spawning during January and February (~20%), increasing to a maximum in late March (82%), followed by a period of lower, but varying spawning frequency.

We found significant correlations (P < 0.05) between several of the food concentration variables and EPR (Paper I). The variables that were strongest correlated with the variation in EPR was the biomass of diatoms (Spearman correlation, Rs = 0.76, p = 0.0004). The EPR was also significantly correlated with the biomass of microplankton, when we considered only the food particles within the optimum size spectrum of *C. finmarchicus* (Gifford *et al.*, 1995; Hansen *et al.*, 1994; Hansen *et al.*, 1997), and removed particles <10 μm spherical diameter (Rs = 0.74, p = 0.001) and with the concentration of POC (Rs = 0.66, p = 0.004) (Figure 4). Previous studies on the reproduction in *C. finmarchicus* have shown that the reproductive rates vary both seasonally and regionally, and our average EPRs were less than half of the maximum rates reported elsewhere (Head *et al.*, 2013a; Jonasdottir *et al.*, 2011; Jonasdottir *et al.*, 2008; Marshall & Orr, 1955; Melle & Skjoldal, 1998), which indicate that one or several
factors reduced fecundity during our study. Other studies on *C. finmarchicus* and *C. helgolandicus* have indicated that the food quality and food quantity can affect both the hatching success and the spawning frequency (Jonasdottir et al., 2002; Jonasdottir et al., 2005; Koski et al., 2012; Pond et al., 1996). However, in our study, the HS was not correlated with any of the explanatory variables (Paper I).

We detected spawning females of *C. finmarchicus* at the surface during the pre-bloom phase (January to early March) during all three years in the Trondheimsfjord, well before the spring bloom. During this period the females showed low reproductive rates (EPR 5–12 eggs fem$^{-1}$ d$^{-1}$, 9–18 % spawning frequency, Figure 3). The observed microplankton concentration (1.0–3.6 μg C L$^{-1}$, Paper I) could only support an EPR of approximately 2 eggs fem$^{-1}$ d$^{-1}$, assuming a clearance rate of 0.5 L fem$^{-1}$ d$^{-1}$ (Paffenhöfer, 1971; Saage, 2006), and an efficiency of 0.30 to convert C ingested into C incorporated into eggs (Mayor et al., 2009a) (see Paper I for details regarding the calculations). The observed EPRs had to be fuelled by maternal resources or by other available food items, like detritus particles and cannibalistic feeding of their own newly hatched eggs. Studies of detritus material as food source for *C. finmarchicus* are scarce and the results contradictory (Carlotti & Radach, 1996; Dilling et al., 1998; Paffenhöfer & Strickland, 1970).
Figure 3: Reproductive rates of *Calanus finmarchicus* sampled in 2009–2011. A: Egg production rate (EPR, number of eggs produced female$^{-1}$ day$^{-1}$); B: Hatching success (percent hatching per sampling day, mean ± SE); C: Spawning frequency (% of females spawning). Bars express 1 SE.
A second non-microplankton food source of adult *C. finmarchicus* could be the eggs and newly hatched nauplia. Previous studies have shown cannibalism by female *C. finmarchicus* and *C. helgolandicus* when the concentrations of alternative food particles are low (Basedow & Tande, 2006; Bonnet *et al.*, 2004). This has been put forward as a possible explanation for why there seems to be a synchronized peak of copepodite stages despite the fact that the first spawning takes place well in advance of the spring bloom (Ohman *et al.*, 2004; Ohman & Hirche, 2001). From our data, the first generation after spring spawning (stage C4) peaked around early May each year with a subsequent increase in C5 in deeper waters around May–June (Paper III). With a developmental time of ~50 days (Møller *et al.*, 2012, average temperature 8°C, food concentration 100 μg C L⁻¹) this would imply that most of the new generation originated from the eggs produced during the spring bloom. In January–March, the abundance of females in the upper 50 metres never exceeded 0.025 ind L⁻¹, the highest egg production rate was 15 eggs female⁻¹ day⁻¹, the hatching success was ~80%, and the spawning frequency was <30% (Figure 3A, B and C). The resulting number of eggs released to the upper 50 metres was therefore at best 0.09 eggs L⁻¹ d⁻¹, equal to 0.02 μg C L⁻¹ d⁻¹. Although the consumption of their own newly hatched eggs and nauplia might be an important factor structuring the population of the *C. finmarchicus*, the consumption of their own eggs and nauplia seems inadequate to explain the observed egg production rates during the pre-bloom period.

Other food particles that may be available during periods of low phytoplankton concentrations include ciliates and heterotrophic dinoflagellates. Some previous studies have shown that *C. finmarchicus* has the ability to sustain a high EPR based on the ingestion of ciliates and heterotrophic dinoflagellates in post-bloom conditions (Head *et al.*, 2013b; Ohman & Runge, 1994), whereas others have shown that the biomass of heterotrophic microplankton normally is too low to explain the energetic shortfall in the production of eggs (Irigoien *et al.*, 1998;
Our calculations showed that the consumption of ciliates could at best only account for 36% of the energy requirement for the observed EPRs (Paper I).

During the period from January to May, *C. finmarchicus* females showed a decreasing content of total fatty acids, especially of C20:1n-9 and C22:1n-11. There was also a decrease in the contents of these fatty acids from January to February for *C. finmarchicus* copepodite stage 5 (C5) (Paper III). These fatty acids are regarded as storage fatty acids, originating from degraded wax esters from oxidation of the fatty alcohol moiety of wax esters (Sargent & Falk-Petersen, 1988). Previous studies have shown that the early development of the gonads in *C. finmarchicus* is fuelled by internal reserves (Pasternak *et al.*, 2004; Sargent & Falk-Petersen, 1988; Tande, 1982) and starved *C. finmarchicus* females can maintain some egg production (Marshall & Orr, 1952; Niehoff, 2004) with a subsequent decrease of fatty acids and protein content (Mayor *et al.*, 2009a). The EPR and the spawning frequency in our study were positively correlated with the concentration of EPA and DHA in the females (Figure 5). The EPA and DHA in the seston were highly variable between the sampling dates, and the concentration of EPA and DHA was always lower in the seston than in female *C. finmarchicus*. High tissue content combined with a poor capability for synthesis of DHA and EPA through chain elongation and desaturation of shorter n-3 moieties reflects a high dietary requirement for EPA and DHA.

The contents of EPA and DHA in the food of *C. finmarchicus* has shown to be of special importance for the EPR and hatching success (Jonasdottir *et al.*, 2002; Jonasdottir *et al.*, 2005; Koski *et al.*, 2012; Pond *et al.*, 1996). In our study, EPR increased significantly (*P* < 0.05) with increasing content of total fatty acid (TFA) and the concentration of EPA in the seston.
(Paper I), and with the content of EPA and DHA in the females (Figure 5). The concentration of EPA in the seston is related to the diatom bloom, whereas increasing DHA in the seston was related to the blooms of dinoflagellates and smaller flagellates (Paper III).

When considering the abundance estimates for the different depth intervals (Paper III), we discovered that most of the overwintering C5’s migrated to the upper 100 metres and moulted to adults in the period from January to March. The main spawning event was therefore found to be just in advance of or during the spring bloom. The subsequent peak of next generation copepodite stage 4 (C4) appeared in late April and May, after which we could see an increase of C5’s in the depth strata from 100 metres and down to the seafloor (440 metres). However, it seemed like that a subpopulation moulted to adults, and we detected a high abundance of females and a high EPR through the period from May to August. This has previously been shown for *C. finmarchicus* in the Irminger Sea (Heath *et al.*, 2008) and in the Norwegian Sea (Lie, 1968; Pasternak *et al.*, 2004). When analysed for lipid content, the C5s found in deeper waters had almost three times bigger oil sac volume and twice as high TFA-content per individual than individuals found in the upper 50 metres (Paper III). We therefore suggested that the lipid content of the C5 decides whether it will moult to female or descend to deeper waters. Above a certain level, the energy stored is sufficient to bring the C5 through the overwintering period at deep waters.

To summarize, our study of the reproduction of *C. finmarchicus* showed that the egg production depended on the food concentration, the nutritional quality of the food expressed in terms of the TFA- and EPA-content of the food, and the concentration of the highly unsaturated fatty acids DHA and EPA in the females. Regression analysis revealed that none of the variables could explain more than 55% of the variation in EPR. We therefore propose that the *C. finmarchicus* females experience different factors limiting reproduction during the reproductive season. The food concentration was clearly limiting the reproductive rates in the pre-bloom period, and the females must therefore rely on internal stores of fatty acids and proteins. The indication of a second generation of *C. finmarchicus* within the same year suggested that *C. finmarchicus* can show a flexible reproduction strategy. Overall, there was some unexplained variation in the observed EPRs and the females collected for the incubation could potentially be of two different generations, and hence have a dissimilar feeding history.

### 2.2 Somatic growth

Measuring secondary production in marine zooplankton has been shown to be important to adequately quantify the food transfer from primary producers to higher trophic levels in ecosystem models. The secondary production has normally been estimated by studying cohort development, either by sorting individual nauplii or by creating an artificial cohort by size-fractionation with different plankton mesh sizes (Winberg, 1971). Growth and survival of naupliar stages can be critical for the development for calanoid copepod populations, and high rates of egg production are not always followed by an increase in abundance of copepodes (Jonasdottir *et al.*, 2008). High content of long-chain polyunsaturated n-3 fatty acids (LC n-3 PUFAs) in the feed, particularly EPA (C20:5 n-3) and DHA (C22:6 n-3), can enhance reproductive rates of copepods (Jonasdottir *et al.*, 2002; Jonasdottir *et al.*, 2005; Pond *et al.*, 2007).
The hatching success and growth through the two first nauplii stages have also been shown to be sensitive for maternal effects. Higher hatching success and higher protein content has been found for offspring of females experiencing high food availability and high concentrations of essential fatty acids in the food (Koski et al., 2012).

*Calanus finmarchicus* develops from eggs through the first two nauplii stages without feeding, and the growth measured as individual dry weight or carbon content is therefore negative during these stages (Harris et al., 2000). They accordingly spend most of their egg yolk and some of their lipid droplets during their first moults, but starts accumulating new biomass from nauplii stage 3 and onwards. Growth in *C. finmarchicus* has mainly been studied in laboratory experiments (Campbell et al., 2001; Corkett et al., 1986; Tande, 1988) or in mesocosms (Harris et al., 2000; Hygum et al., 2000a; Hygum et al., 2000b). The growth rate has been shown to be affected by temperature and food availability (Møller et al., 2012), and it appears that the naupliar stages are less sensitive for low food concentrations than copepodites (Hygum et al., 2000a). Although the conversion of storage lipids into eggs and the subsequent development and growth of copepod nauplii has shown to be sensitive for the availability of specific polyunsaturated fatty acids, relatively little has been published on the lipid and fatty acid composition of copepod eggs and early nauplii stages (Kattner et al., 2007).

The growth rates of the nauplii of *C. finmarchicus* were studied in 2007, 2009, and 2011 (Paper II). The aim of the study was to investigate how food quantity and food quality affected the growth rate of the early nauplii stages. Females were collected from the Trondheimsfjord and incubated in petri dishes. The egg production rates and the hatching success were monitored and the possible food available for the female *C. finmarchicus* was monitored (Paper I). The eggs and nauplii were transferred to flow through tubes and incubated at *in situ* temperatures. During a total of 12 growth periods, the nauplii were fed natural seston screened at 55 μm to remove background nauplii and to offer food particles that were assumed to be in the optimum food size for the *C. finmarchicus* nauplii. We also added a separate control treatment by feeding a mix of three different microalgae; *Rhodomonas baltica, Isochrysis galbana* and *Dunaliella tertiolecta* kept at a total concentration of 150 μg C L⁻¹, assumed to be above saturation for food ingestion of *C. finmarchicus* nauplii (Campbell et al., 2001). This mixture has successfully been used to maintain a multi-generation culture of *C. finmarchicus* at NTNU Sealab (Hansen et al., 2007).

One immediate conclusion from our growth experiments was that the growth rates of the nauplii fed cultured algae were significantly higher than those fed natural seston for most of the growth season (P < 0.05, Paper II), except for two growth periods in late May (Figure 6). The nauplii fed natural seston showed an increase in growth rate through the growth season, with growth rates close to zero in early March through average values around 0.08 day⁻¹ in late March to growth rates of 0.12 day⁻¹ in May. The growth rate of nauplii fed cultured microalgae were also significantly positively correlated with the growth in nauplii fed natural seston (P < 0.05).
Contrary to reports from previous growth experiments (Campbell et al., 2001; Corkett et al., 1986; Harris et al., 2000; Hygum et al., 2000a; Hygum et al., 2000b; Tande, 1988), we did not find a significant relationship between specific growth rate and the concentrations of chlorophyll a (chl a) or particulate organic carbon (POC) (P > 0.05). Some of the scatter in our results might be explained by variability in food concentrations over short time (days). The microplankton community is known to fluctuate over periods of only days because of natural population fluctuations and mixing of the water masses (Braarud & Nygaard, 1978; Sakshaug & Tangen, 2000). Our incubations lasted 6–10 days, depending on the temperature, and we analysed the seston material only at the start and the end of the incubation period.

The naupliar growth rate increased with increasing food quality of the seston expressed in terms of the content of highly unsaturated n-3 fatty acids; it increased with increasing contents of EPA and DHA in the food of C. finmarchicus nauplii. Both the effect of EPA and DHA in the food could be described by a saturation hyperbola (EPA: $r^2 = 0.350$, half-saturation constant $(K) = 1.42 \pm 1.28$, p = 0.043, DHA: $r^2 = 0.472$, half-saturation constant $(K) = 0.732 \pm 0.620$, p = 0.014; Figure 7, from paper II). To our knowledge, a positive correlation between
the growth rate and the content of DHA and EPA has not previously been reported for nauplii of *C. finmarchicus*.

![Figure 7](image.png)

**Figure 7.** Growth rates (day$^{-1}$, mean ± SE) of nauplii versus A: the content of EPA and B: the content of DHA in the seston (mg g$^{-1}$ DW). Lines indicate regressions with 95% confidence limits. Figure taken from Paper II.

The content of DHA and EPA in the food has repeatedly been shown to have a positive effect on the rate of egg production of different species of copepods (Evjemo et al., 2008; Jonasdottir et al., 2009). The DHA-concentration of suspended particulate matter (<55 μm) is mainly a result of the species composition of plankton, as diatoms generally have low concentrations of DHA and high concentrations of EPA, dinoflagellates and many smaller flagellated species of algae have high concentrations of DHA and variable concentrations of EPA (Ackman et al., 1968; Hallegraeff et al., 1991; Mansour et al., 1999; Reitan et al., 1994; St. John & Lund, 1996). In addition to the species specific differences, the content of DHA and EPA in microalgae are also sensitive to limitations by inorganic nutrients (Reitan et al 1994).

Although we observed significant effects of the DHA and EPA contents of seston on both the reproduction (via contents of DHA and EPA in the females) and on the growth of *C. finmarchicus* nauplii, none of the variables explained more than 55% of the response in either reproduction or growth (Paper I and Paper II). There can be several possible reasons for this. When we decided to exchange the natural seston fed the nauplii every second day, we are not able to fully control the food available to the individual *C. finmarchicus* nauplii during the incubation period. The food availability fluctuates at time scales shorter than the incubation period for the growth experiments and we did a proper analysis of the seston only at the start and the end of the incubation period.

*C. finmarchicus*, as some of the other marine copepods, use lipids stored in the lipid sack to survive through the diapause and to initiate the first spawning prior to the spring bloom (Paper II, and references therein). The oil sac in female copepods is in close proximity to the
gonads, and the lipid content of the females generally decreases as they are producing eggs (Mayor et al., 2009a). We observed successful spawning prior to the spring bloom, although at low rates. Contrary to previous studies (Gatten et al., 1980; Lee et al., 1972; Ohman & Runge, 1994), we detected wax ester to be the major lipid class in *Calanus* eggs. The eggs were collected during the pre-bloom period, and we propose that the eggs are produced mainly from internal reserves. From our study of reproduction in *C. finmarchicus*, we observed low reproductive rates during the pre-bloom period and the highest reproductive rates during the spring bloom (Paper I). The naupliar growth was also overall low in the pre-bloom period, but there was a huge difference between the nauplii fed surplus food and natural seston. The highest naupliar growth rates were observed during May, under a period with high content of LC n-3 PUFAs in the feed (Figure 1, Paper II) and in the females (Figure 2, Paper I). This suggests that the observed reproductive rates and subsequent naupliar growth is the sum of maternal effects and the food availability for the feeding stages of the nauplii. The maternal effect will subsequently have a larger impact during periods of food scarcity for the nauplii, as they fully depend on their internal reserves to survive until they have sufficient food available. But also, the nauplii can benefit from increased growth through feeding stages during periods of a high quantity and quality of the available food.

Our results suggest that the secondary production is dependant not only on temperature and food concentration, but that food quantity and food quality has major impact on reproductive rates, and subsequent somatic growth. Naupliar somatic growth rates are during large parts of the productive season limited by the food quality and there is not clear connection between the secondary production measured as somatic growth and secondary production estimated from reproductive rates. This indicates that the nauplii utilise different food particles than adult females, or that a different food composition is required for naupliar growth compared to what is required for production of viable eggs.

2.3 Lipid dynamics of *C. finmarchicus* in the Trondheimsfjord

There are several reasons to study the lipid dynamics of *C. finmarchicus*: The storage of lipids is requisite for *C. finmarchicus* to be able to overcome dormancy, undertake vertical migration, moultng and the production of gonads (Jonasdottir, 1999). A threshold of lipid level is among several other factors suggested to be a trigger for vertical migration and dormancy (Irigoien, 2004). As mentioned, *C. finmarchicus* and other zooplankton species store energy as wax esters in the lipid sack to be able to undergo diapause during winter. The fatty acid composition in individual C5 *C. finmarchicus* from different depth intervals was studied through the productive period in the Trondheimsfjord (January–June 2009–2011, Paper III) and the fatty acid composition was compared to the fatty acid composition of potential food sources. The objective of the study was to provide more information on how the variations in lipid content could predict the vertical migration and dormancy of *C. finmarchicus* in the Trondheimsfjord.

In order to obtain a sample big enough for fatty acid analysis of the potential food particles, we used a flow-through centrifuge. The methodology was developed for the experiments is described by Evjemo et al. (2008). In short, a flow-through centrifuge was fed by gravity from
a reservoir of water pre-screened through a plankton net (mesh size 200 μm) pumped from approximately 1.5 metres depth. The species composition of the natural plankton was analysed from additional water samples collected by Niskin bottles, and we have assumed that the material collected by the centrifuge reflected the seston in the water.

The dominating polyunsaturated fatty acid (PUFA) of the seston was C18:4 n-3, EPA, and DHA (Papers I, II and III). The content of the diatom fatty acid C16:1 n-7 showed the same pattern of variation in the spring all three years, with the highest content in the middle of April and the start of June. C18:4 n-3 varied much between years, with a share of 5% in 2010 and 25% in 2009. In general, the concentration of DHA increased throughout the production season, this because of the shift of dominating phytoplankton groups from diatoms to dinoflagellates and small flagellates.

Before the onset of the spring bloom, we were able to obtain samples of *C. finmarchicus* eggs, nauplii and copepodites for fatty acid analysis. The eggs were also analysed for lipid class composition (Paper II). Contrary to previous investigations (Gatten *et al.*, 1980; Lee *et al.*, 1972; Ohman & Runge, 1994), the lipid class analysis of *C. finmarchicus* eggs showed a dominance of wax esters (WE, >80 % of total lipid), some triacylglycerides (TAG, 7–19 % of total lipid) and smaller and more constant amounts of phosphatidylcholine, phosphatidylethanolamine and free fatty acids. One immediate difference between our study and the previously published studies was that we sampled the eggs in February, prior to the onset of the spring bloom, whereas the above mentioned studies were from the summer period. This further suggests that the *C. finmarchicus* females are able to utilize the wax esters stored in the lipid sack for the production of eggs, and that the previously reported predominance of TAG and phospholipids in *C. finmarchicus* eggs were found in females experiencing different nutritional conditions. Jonasdottir *et al.* (2008) have suggested that WE is converted to TAG for reproductive needs, but our results shows that also WE can be transferred and form a main part of the lipids in eggs of *C. finmarchicus*.

As previously shown, both the food concentration and the food quality in terms of specific LC n-3 PUFA content in the food may have an impact on the reproduction and growth of *C. finmarchicus*. The fatty acid content of eggs, nauplii and copepodites was analysed from size-fractionated samples (Paper II). The *C. finmarchicus* eggs showed a variable content of total fatty acids (TFA) between sampling days while the content of TFA was more or less similar in the different nauplii stages. Comparing the different copepodite stages, we could detect an increase of TFA from C2 to C5, in agreement with earlier studies (Evjemo *et al.*, 2003; Hygum *et al.*, 2000c). There was also a far lower content of DHA in N3–4 compared to that of C2–3 and later copepodite stages. The content in N3–4 was 5 mg g⁻¹ DW whereas that of C2–3 was 13 mg g⁻¹ DW. *C. finmarchicus* is not able to synthesize DHA at ecologically relevant rates (Bell *et al.*, 2007; Sargent & Whittle, 1981), and the DHA-content of the seston was generally not very high compared to what has previously been observed for the summer period in the Trondheim fjord (Evjemo *et al.*, 2008). The low content of DHA in the naupliar stages and the increasing growth rate with increasing DHA in the seston suggested that this fatty acid could be a key to the growth limitations in *C. finmarchicus*, as shown for other
copepods (Breteler et al., 2005) and fish larvae, which are also classified as carnivore zooplankton (Ruyter et al., 2000; Tocher et al., 2001).

Figure 8. Average dry weight (μg ind⁻¹) (A), prosome volume (mm³) (B), TFA (μg ind⁻¹) (C), and oil sac volume (mm³) (D) in Calanus finmarchicus C5 at 0–50 m, 50–100 m, 100–300 m and 300–440 m. Lower case letters indicate significant differences, N equals the number of replicates. Figure taken from Paper III.

The results from the study of lipid content in copepodite stage 5 of C. finmarchicus (Paper III) revealed that the fatty acid composition in the copepods was related to the fatty acid profile of potential food sources (Paper III). The fraction of C18:4 n-3 ranged from 0 to 13 % of TFA, the fraction of EPA from 6 to 22 % of TFA and the fraction of DHA from 7 to 33 % of TFA. Sampling at multiple depths throughout the production season revealed that the individual dry weight, body volume, TFA content and volume of the oil sac of C. finmarchicus increased with increasing depth (Figure 8). In May, we could also detect an increase in content of C18:4 n-3, EPA and DHA in C5’s from deeper waters and an increased abundance of C5 in the intermediate and deep waters. This suggests that these C5s were of the new generation that had been feeding on the phytoplankton bloom and further descended for dormancy. However, the number of females in the surface also increased, and we observed spawning of females in August (Paper I). The occurrence of a second spawning in C. finmarchicus has previously been observed (Conover, 1988; Lie, 1968), but the underlying mechanism behind this second spawning has yet to be verified. We therefore hypothesize that C5 with high lipid contents
will descend for dormancy, while C5 with a lower content of lipids after the phytoplankton bloom will moult to females and start a new spawning.

As mentioned in the introduction, this study aimed at improving the knowledge on some of the key variables needed to construct ecologically relevant mathematical models of the population of *C. finmarchicus*. Many ecological models use carbon as the “currency” to build the different compartments or to describe the different life stage variables included in the model (Hjøllo et al., 2012; Samuelsen et al., 2009; Wassmann et al., 2006). A mathematical model is a simplified version of reality used to describe and answer specific properties of the real system. Because there still are limitations in computational power, especially for dynamic 3-D models, it is still important to simplify the biological sub-model (Slagstad & Gjøsæter, 2009). At present, most models do not regard food quality as an important variable, and diatoms are in many models regarded as the only food source for *C. finmarchicus* (Hjøllo et al., 2012; Samuelsen et al., 2009). The above mentioned models include lipid accumulation as a key variable to predict initiation of diapause and to allow for pre-bloom spawning, but there is no dependence of food quality on spawning, egg production rates, survival rates and growth rates.

We have suggested that the content of LC n-3 PUFAs in the potential food of *C. finmarchicus*, especially EPA and DHA, has a positive effect on the reproduction rates (via the EPA- and DHA-content of the females) and the growth rates of *C. finmarchicus* nauplii. Inclusion of food quality variables in ecologically relevant models will likely require prediction of the composition of microalgae. Prediction of food quality in terms of LC n-3 PUFA might thereafter be based on phytoplankton or seston composition, but none of these predictions are trivial, and food selection may make such predictions even more complicated. Wassman et al. (2006) had, for example, difficulties predicting the blooms of the two phytoplankton groups included in the model, and they concluded that the patchy distribution and fluctuating densities of suspended phytoplankton biomass also makes it difficult to sample adequate data for a true validation of the model.

During the last two-three decades, ample evidence has been presented that show zooplankton to be sensitive to imbalances in the feed available as they convert primary production to secondary production. Stoichiometric theory (Sterner & Elser, 2002) has previously been developed to evaluate the potential for limitation by carbon or mineral phosphorus and nitrogen (e.g. Hessen, 1992; Olsen et al., 2011; Olsen et al., 1986). The key assumptions are that substrates are used conservatively for growth and are solely of dietary origin and that predators (including zooplankton) have fixed biochemical ratios in their biomass that determine dietary requirements. Because certain LC n-3 PUFAs are not synthesized by zooplankton at ecologically relevant rates (Bell et al., 2007), these are regarded as essential and the stoichiometric theory has further been developed to include LC n-3 PUFAs like EPA and DHA (Anderson & Pond, 2000; Mayor et al., 2009b; Mayor et al., 2011). These studies show that there is potential for limitation of secondary production, but that the C, N, and LC n-3 PUFA limitation potential varies throughout the season. Some of the key parameters for including LC n-3 PUFAs in stoichiometric models still need further exploration. For instance,
not much is known about the assimilation efficiency and basal turnover of essential LC n-3 PUFAs under varying conditions, and recent findings indicate low assimilation efficiency for DHA in Calanus sp. (Mayor et al., 2011).

A main incentive for a potential harvest of C. finmarchicus and other marine zooplankton is their high content of LC n-3 PUFAs (FAO, 2014; Olsen, 2011). Our study on the lipid dynamics of C. finmarchicus (Paper III) showed that the content of important LC n-3 PUFAs was related to the fatty acid composition of the seston. The content of EPA in C. finmarchicus will be high during the spring bloom, and the content of DHA and C18:4 n-3 will increase later in the spring, when dinoflagellates and smaller flagellates are the main food components in the microplankton community. The concentration of C. finmarchicus at the surface varied greatly between years in the Trondheimsfjord, although the overwintering population was similar between the years studied (Paper III). This indicates that the surface population during spring can be advected out of the fjord because of estuarine circulation or into the fjord by the Norwegian coastal current, consistent with previous investigations (Skreslet et al., 2000; Strømgren, 1974). The fluctuating concentrations of the Calanus in our study indicate that fjords may not be a suitable harvesting area, at least in years with low abundances.

2.4 Feeding selectivity
C. finmarchicus experience a wide range of food concentrations with fluctuating biochemical composition during the time period they use to reproduce, grow and accumulate body mass and lipids (Jonasdottir et al., 2008; Marshall & Orr, 1955). Thus feeding selectivity represents an additional, complicating factor in the development of ecosystem models. The degree of omnivory and shifts in food selection and feeding behaviour has major effects on the trophic linkages and stability of ecosystems, as well as the direct impact on the growth, reproduction and fecundity of C. finmarchicus. Some previous feeding selectivity studies have described C. finmarchicus as herbivorous (Graeve et al., 1994; Koski & Riser, 2006; Teegarden et al., 2001), non-selective consumption of ciliates (Castellani et al., 2008; Levinsen et al., 2000; Mayor et al., 2006), or preference for ciliate prey at high ciliate:phytoplankton ratios (Nejstgaard et al., 1997; Nejstgaard et al., 1994). As mentioned in the introduction, size can be another important aspect of the feeding ecology of copepods (Frost, 1972; Gismervik et al., 1996; Hansen et al., 1994; Hansen et al., 1997), and previous studies has shown that the cascading effects from copepods are dependent on the trophic state of the system. In systems were phytoplankton concentrations are low, ciliates are a more important food source than systems dominated by big phytoplankton in high concentrations (Calbet & Saiz, 2005; Stibor et al., 2004). A stable isotope analysis in the Trondheimsfjord indicated C. finmarchicus to be omnivorous with an average trophic level of 2.4 (Saage et al., 2008). Switching from phytoplankton to ciliate prey often involve an overall decrease in ingestion rate, showing that other factors than food concentration can be of importance (Paper IV). Furthermore, inclusion of feeding on microzooplankton has major implications for the modelled feeding potential for C. finmarchicus (Carlotti & Radach, 1996; Slagstad et al., 1999).

The feeding selectivity of C. finmarchicus was studied by carrying out three incubation experiments; two experiments with natural sea water sampled during spring bloom (Exp. I)
and post-bloom conditions (Exp. 2) and a third experiment with cultured dinoflagellates and ciliates (Exp. 3). The main objective of the study was to investigate how the relative and absolute concentration of ciliates in the available food affected the feeding selectivity. In the two first experiments a gradient in ciliate concentration was created to investigate the potential for prey density dependent selective feeding of *C. finmarchicus* (Paper IV). Exp. 1 was conducted under bloom conditions and Exp. 2 during post-bloom conditions, which involved different starting conditions in terms of biomass and taxonomic composition. The microplankton biomass expressing food concentration in Exp. 1 was around 200 μg C L⁻¹ and almost one order of magnitude higher than during Exp. 2 when the concentration was around 25 μg C L⁻¹. Prior to the incubation of *C. finmarchicus*, the microplankton was divided into two batches. One was not further manipulated, but the other batch was vigorously bubbled by air in order to remove ciliates that are known to be fragile. This is, to our knowledge, new methodology. The treatment reduced the initial abundance of most ciliate species and we were able to create a ciliate gradient for each of the two experiments although not as pronounced in Exp. 2 as in Exp. 1.

To evaluate the effect of using natural seston versus cultured algae and ciliates, we compared the feeding experiments conducted with manipulated, natural seston, with an experiment (Exp. 3) using the dinoflagellate *Karlodinium veneficum* and the ciliate *Pelagostrobilidium spirale*. The phytoplankton was offered at a concentration >120 μg C L⁻¹ (considered to be above saturation) whereas ciliates were added in variable concentrations from 5 to 50 μg C L⁻¹.

Overall, the diet of *C. finmarchicus* consisted mainly of diatoms in Exp. 1 and a mixture of dinoflagellates and ciliates in Exp. 2. To evaluate the feeding, the percentage offered of the different main groups was compared to the percentage eaten (Figure 9). Deviation from the 1:1 line suggests selectivity. Dinoflagellates were generally consumed in the same proportions as offered, following the 1:1 line (Figure 9A). Flagellates were generally consumed in a lower proportion compared to that offered, and constituted generally a small part of the consumed food particles.

Diatoms was generally consumed in fractions according to their availability, and never in a higher proportion compared to what was offered (Figure 9C). In Exp. 1 and 2, *C. finmarchicus* ingested ciliates in the proportion they were offered when the ciliates were low in biomass compared to other food items. Above a certain proportion of around 5 % of total feed, the ciliates were cleared from the water at higher rates compared to the other food items (Figure 9D).
Figure 9. Percentage (mean ± SE) of (A) dinoflagellates (B) ciliates (C) diatoms and (D) flagellates in the diet of C. finmarchicus in relation to the 1:1 line. The data above and below the 1:1 line indicate positive and negative feeding selection, respectively. Figure taken from Paper IV.

The feeding pattern of C. finmarchicus in Exp. 3 showed a similar pattern (Figure 10), but in this case it switched to consume ciliates as almost the only food source when the ciliate concentration exceeded 3 % of the total food concentration. This was despite the fact that phytoplankton concentrations were above saturation level (>120 μg C L⁻¹), and that change in feeding strategy resulted in a reduction of total ingested carbon.
Figure 10. Percentage (mean ± SE, n = 5, from paper IV) offered ciliates eaten by *C. finmarchicus* in the experiment with surplus food and variable ciliate concentration in relation to the 1:1 line. The lack of error bars for 4.3 and 10% ciliates offered was because the ciliates constituted 100% of the consumed food particles in all replicates. Figure taken from Paper IV.

To summarize, the diet composition and the calculated selectivity indices support previous results that have classified *C. finmarchicus* as an omnivorous species (Nejstgaard et al., 1997; Ohman & Runge, 1994; Saage et al., 2008). The feeding selectivity of *C. finmarchicus* is not only influenced by the quantity of available food, but also by the quality. Ciliates seem to be an important supplementary food source for *C. finmarchicus* during bloom conditions, and a major component in the diet during post-bloom conditions. Our experiments showed that *C. finmarchicus* has the ability to switch feeding mode on a short term scale dependent on the absolute and relative concentrations of prey which can be detected by mechanoreception. Overall, *C. finmarchicus* tends to positively select ciliates, and the frequently reported dominance of diatom in the diet seems to be a consequence of their overwhelming dominance in the biomass during bloom conditions.
3. Conclusion and future work

3.1 Conclusions
The main deliverables from this thesis to the research programme “Harvest” was to provide input parameters to ecological models for the *C. finmarchicus* population with main focus on reproduction, somatic growth, lipid accumulation and feeding selectivity.

From the presented work it seems likely that the food concentration and the food quality to a large extent influence many important aspects of the life history traits of *C. finmarchicus*. The reproductive rates can through large periods of the spawning season be primarily limited by the food concentration and there is during parts of the production season a suboptimal content of dietary fatty acids in the food particles available for the *C. finmarchicus* (Paper I). We conclude that *C. finmarchicus* females experience different factors limiting the reproduction throughout the reproductive season. The main reproductive event coincides with the spring bloom, and the positive correlation between EPR and microplankton biomass $>10\ \mu m$ and the content of EPA in the seston point to the importance of the diatom spring bloom. However, we detected pre-bloom spawning and some of the variation in EPR and SF could be explained by maternal effects via the content of LC n-3 PUFAs in the females. We also observed high EPRs during the post-bloom period and a second spawning in August, showing that *C. finmarchicus* show a large degree of flexibility that might explain the dominance of this species in the northern hemisphere.

The naupliar growth was also positively related to the content of EPA and DHA in the seston and we could not detect any significant relationship between the food concentration available for the nauplii and the growth rates. This indicated that growth models, that mainly use temperature and available food expressed in terms of carbon, need to be refined. We also presented lipid class data on *C. finmarchicus* eggs that are different from what is previously published. Our data suggests that *C. finmarchicus* females were able to produce eggs from stored lipids and that they do not necessarily transform the wax esters in their lipid stores to TAG for reproductive needs (Paper II). The absolute and relative content of LC n-3 PUFAs were generally variable in *Calanus* eggs, the nauplii had generally a lower TFA and n-3 PUFA content than copepodites.

The lipid content in C5 generally increased from February to June, and the fatty acid composition was highly dependent on the phytoplankton present during this period. The new generation of C5s descended to deeper waters in May, when they reached a certain lipid content. A certain proportion of the C5s originating from the spring bloom generation stayed high in the water column, moulted to females and started a new generation. We detected successful spawning in August, while a large part of the *C. finmarchicus* population had entered dormancy. Because of a lower lipid content of the copepodites in the surface waters, we have hypothesized that the C5s that were unable to reach a critical lipid level for dormancy moulted to females (Paper III).
The results from the feeding selectivity experiments supported previous studies that classify *C. finmarchicus* as an omnivorous species. Furthermore, we detected large differences in the feeding selectivity response when we used cultures of a dinoflagellate and a ciliate instead of natural seston. When the dinoflagellate was offered in surplus with an increasing share of ciliates, the *C. finmarchicus* switched to a pure ciliate diet when the ciliates constituted more than 3% of the total diet, even though this implied a lower overall ingestion rate. We did detect positive selectivity indices for *Thalassiosira* spp. during spring bloom conditions and positive selectivity for conic ciliates >35 μm when the ciliates constituted more than 3% of the total biomass. We conclude that the feeding selectivity is not only influenced by the quantity of available food, but also on the quality. Ciliates seem to be an important supplementary food source for *C. finmarchicus* during bloom conditions and a major component during post-bloom conditions (Paper IV).

### 3.2 Future work

If you use “*Calanus finmarchicus*” as a search entry on topics in the Web of Science database, you get ~2000 hits (October-2015) of which >450 are from the latest five years. This gives an impression on the importance of *Calanus* spp. in the marine pelagic ecosystems and some of the results from this thesis raised several new questions.

The reproduction and growth of *C. finmarchicus* is likely affected by the content of highly unsaturated fatty acids. However, there are still a lot of unanswered questions regarding the interaction between maternal effects and the direct effect of the food available for the female, for the egg production rates, the hatching success, and for the subsequent growth of the nauplii. Some questions can be answered by undertaking experiments using cultures of *C. finmarchicus* and cultured food.

Because LC n-3 PUFAs have shown to have a major impact on many important life-history traits in *C. finmarchicus*, future basin-scale surveys and time series that seek to describe large-scale production patterns should include food-quality aspects and not just bulk measurements of chla or fluorescence to assess the potential food for zooplankton. This can either be conducted by quantifying the dominating microplankton groups or by taking size-fractionated samples for fatty acid composition.

The feeding experiments show that *C. finmarchicus* displays a highly complex feeding behaviour, and our results indicated an omnivorous feeding selectivity and the experiment with cultured algae and ciliates indicated a shift from herbivorous feeding to feeding on ciliates when the ciliated biomass was 3% of the total biomass. The ultimate factors that make *C. finmarchicus* select ciliate prey over other prey are still debated, some argue that they are purely selecting a certain size, others that the mechanical noise from active swimming makes attracts the copepods, and yet others argue that the ciliates are nutritionally superior to other food particles. There have been several attempts to evaluate the elemental and fatty acid composition of the ciliates, but there are so far very few studies on the nutritional composition of this important functional group.
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Reproduction in *Calanus finmarchicus* in a central Norwegian fjord, effects from potential food and maternal essential fatty acid content

Øystein Leiknes¹*, Maria Bergvik¹, Olav Vadstein², Yngvar Olsen¹

¹NTNU Norwegian University of Science and Technology, Department of Biology, NO-7491 Trondheim, Norway

²NTNU Norwegian University of Science and Technology, Department of Biotechnology, NO-7491 Trondheim, Norway

*Corresponding author:

Øystein Leiknes
NTNU Norwegian University of Science and Technology
Department of Biology
NO-7491 Trondheim
Norway
Telephone: +4793227617
E-mail: oystein.leiknes@ntnu.no

Maria Bergvik
maria.bergvik@ntnu.no

Olav Vadstein
olav.vadstein@ntnu.no

Yngvar Olsen
yngvar.olsen@ntnu.no

Highlights:

- Reproduction in *Calanus finmarchicus* was studied during repeated production seasons in the Trondheimsfjord
- The food quality, food quantity and the content of essential fatty acids in females of *C. finmarchicus* were compared to the reproduction rates
- Egg production rates were dependent on food concentration, the content of total fatty acids and of EPA in the food, and the concentration of EPA and DHA in the females
- Female *C. finmarchicus* experience different factors limiting the reproduction rates throughout the reproductive season

Keywords: *Calanus finmarchicus*, reproductive biology, egg production, fatty acid composition, Chlorophyll a
ABSTRACT

The reproduction of the calanoid copepod *Calanus finmarchicus* from a Central Norwegian fjord (the Trondheimsfjord) was studied in three successive seasons (2009–2011). Possible food (seston <200 μm) was analyzed for particulate organic carbon (POC), nitrogen (PON), phosphorus (POP), chlorophyll *a* (*chl a*), fatty acid contents, and species composition of phytoplankton and ciliates. We also analyzed the fatty acid content of female *C. finmarchicus*. The egg production rate (EPR) was positively correlated with the concentration of POC, PON, biomass of phytoplankton and ciliates >10 μm, to the total fatty acid and the EPA content of the seston, and to the content of EPA and DHA in female *C. finmarchicus*. The main spawning took place during the spring bloom but we observed egg production from January to August. Overall, our results indicate that the EPR was influenced by food concentration, food quality and maternal effects (i.e. the fatty acid content of the females). Spawning frequency was positively correlated with the content of EPA and DHA in the females, whereas the hatching success was not significantly correlated with any of the measured variables of food quality, food quantity or maternal effects.
1. Introduction

Since its discovery, *Calanus finmarchicus* (Gunnerus 1770) has been one of the most studied species of zooplankton, likely because of its very high abundance and production. It occurs frequently in enormous shoals in surface waters during the spring, occasionally giving the sea a reddish hue (Ban et al., 1997). *C. finmarchicus* has a period of dormancy in deeper waters, then ascend to the surface and spawn during late winter and throughout the spring (Diel and Tande, 1992). The success of reproduction and the subsequent growth of the nauplia can be a bottleneck for population growth in *C. finmarchicus* (Campbell et al., 2001; Runge et al., 2006). Some studies have shown that the reproductive rates of *C. finmarchicus* can be reduced by the availability of food, either by low food quantity (Frost, 1972; Jonasdottir et al., 2005; Paffenhofer et al., 2005) or by poor food quality (Aubert et al., 2013; Hygum et al., 2000).

Because adult *C. finmarchicus* do not invest energy into somatic growth, egg production can be viewed as a proxy for secondary production. Carbon can be used as a measure for both energy and biomass. It has been shown that the concentration of food carbon is at times limiting the egg production, both when carbon biomass is derived from chla measurements (Hirche and Bohrer, 1987) and from the number of available phytoplankton cells (Hirche et al., 1997; Runge, 1984). Other studies have shown no significant correlations between the food concentration and fecundity, especially when the food carbon concentration is derived from chla measurements (Irigoin et al., 1998; Niehoff et al., 1999; Plourde and Runge, 1993). Heterotrophic food in the form of ciliates and heterotrophic dinoflagellates have been suggested as complementary food to phytoplankton that can support sustained egg production rates in *C. finmarchicus* under periods of low chla concentrations (Ohman and Runge, 1994). The general view of *C. finmarchicus* as a strict herbivore has recently been challenged, as feeding experiments and studies using stable isotope techniques have revealed omnivorous feeding of *C. finmarchicus* (Irigoin et al., 1998; Leiknes et al., 2014; Levinsen et al., 2000; Nejstgaard et al., 1997; Nejstgaard et al., 1994; Saage et al., 2008). It has been hypothesized that *C. finmarchicus* utilizes lipid reserves to reproduce when the food concentration is low (Irigoin et al., 1998; Jonasdottir et al., 2008; Niehoff et al., 1999; Plourde and Runge, 1993), but the reproduction potential is much higher when food is abundant (Frost, 1972; Marshall and Orr, 1955). However, reproduction in *C. finmarchicus* occurs before, during and after the spring bloom (Mayor et al., 2006; Niehoff et al., 1999; Ohman and Runge, 1994) under periods of varying food concentration and quality.
Generally, heterotrophs have a more stable elemental composition than their autotrophic feed, mainly because autotrophs have different abilities to store excess nutrients and carbon (Sterner and Elser, 2002). This may at times result in nutritional imbalances in the diet and could affect the rate of egg production and the viability of the hatched nauplii. E.g. the egg production rates of *Acartia tonsa* and *Paracalanus parvus* has been shown to increase with increasing nitrogen content of the food (Checkley, 1980; Kjørboe, 1989). Other studies have shown that the egg production rate and hatching success in zooplankton can be influenced by the food quality expressed in terms of protein content (Jonasdottir, 1994; Jonasdottir et al., 1995; Jonasdottir et al., 2002) and of specific essential amino acids (Guisande et al., 2000; Helland et al., 2003; Kleppel et al., 1998).

Copepods generally have a high demand for long-chain polyunsaturated n-3 fatty acids (LC-n-3 PUFAs) such as eicosapentaenoic acid (EPA, C20:5 n-3) and docosahexaenoic acid (DHA, C22:6 n-3) and are probably incapable of synthesizing DHA and EPA at ecologically relevant rates (Bell et al., 2007; Sargent and Whittle, 1981). EPA and DHA are therefore regarded as essential fatty acids (EFA). Egg production rates, hatching success and growth in the early nauplii stages of copepod species are at times limited by low concentrations of EFA in the food (Koski et al., 2012). Other studies have shown a positive effect of the seston content of EPA (Jonasdottir et al., 2002; Jonasdottir et al., 2005; Pond et al., 1996) and DHA (Pond et al., 1996) on the reproductive rates of *C. finmarchicus*. Diatoms are known to have low concentrations of DHA and high concentrations of EPA, whereas dinoflagellates and smaller green algae generally have high concentrations of DHA and variable concentrations of EPA (Ackman et al., 1968; Hallegraeff et al., 1991; Mansour et al., 1999; Reitan et al., 1994; St. John and Lund, 1996). A high tissue content of EFAs in eggs and females of *Calanus* sp. combined with a poor capability of synthesizing EPA and DHA and a varying content of EFAs in the food imply that the content of these fatty acids easily can limit zooplankton production (Anderson and Pond, 2000). Since *Calanus* females can benefit from the internal reserves of EFAs during periods of food scarcity (Mayor et al., 2009a, b), both the effects from EFA-content in food and the effects of maternal reserves of EFAs should be evaluated.

Although some studies have monitored reproduction in *C. finmarchicus* during repeated spawning seasons (Durbin et al., 2003; Head et al., 2013a; Runge et al., 2006), very few studies have studied reproduction in *C. finmarchicus* concurrent with measurements on quantitative and qualitative aspects of food and characterization of essential fatty acids.
(EFAs) in the females (Mayor et al., 2009a). Reproduction in *C. finmarchicus* has been studied in western and northern Norway (Diel and Tande, 1992; Koski and Riser, 2006; Rey et al., 1999; Tande, 1982), but not during repeated spawning seasons. The proximity to a population of *C. finmarchicus* makes the Trondheimsfjord an excellent location for monitoring of reproductive rates throughout the spawning season. The Trondheimsfjord is a relatively deep fjord with a seaward sill of 195 meters; the water masses are dominated by a mixture of Atlantic water, water from the Norwegian Coastal Current and brackish water from riverine outflow (Jacobson, 1983). The varying conditions from year to year and within a spawning season provides an opportunity to investigate how varying proportions of phytoplankton and protozoans affect reproduction in *C. finmarchicus*.

The aim of the present study was to investigate the effects of food quantity, food quality and maternal fatty acid composition for the egg production rate, spawning frequency and hatching success of *Calanus finmarchicus* in the Trondheimsfjord. As proxies for food concentration we used the biomass of the microplankton community by microscopy counts, particulate organic carbon (POC) and phytoplankton biomass calculated from chla measurements. Food quality was evaluated by measuring the content of particulate organic phosphorus (POP) and nitrogen (PON), and the fatty acid composition of the seston. The maternal effect was studied by analyzing the fatty acid content of the females. We hypothesized that the effect of food alone can explain the seasonal variation of the reproductive rates of *Calanus finmarchicus*, either as variations in the quantity and the quality of potential food particles during reproduction or through maternal effects that are mainly the result of what the individual *C. finmarchicus* has accumulated prior to spawning.

2. Material and methods

2.1. Sampling procedure

During three successive seasons (2009, 2010, and 2011) from late January to August, individuals of *Calanus finmarchicus* and the seston (<200 μm) were sampled from station Trollet (N 63°29’, E10°18’), Trondheimsfjorden, Norway, on R/V Gunnerus (NTNU Norwegian University of Science and Technology). The sampling frequency was once per month in 2009 and 2010 and once to twice per month in 2011. Temperature and salinity data were measured with a CTD (Seabird Electronics Inc., USA) (Table I).
Samples for microplankton counts, chl$\alpha$, particulate carbon (POC), nitrogen (PON) and phosphorus (POP) were collected with Niskin bottles (30 L) at depths of 0, 3, and 10 meters. Subsamples for microplankton counts were taken from unscreened water and fixed in 1% acidic Lugols solution. The rest of the water was screened with at 200 $\mu$m plankton net to remove large grazers and stored in darkness in acid washed plastic containers until further processing. Water (2–3 L) from these depths were filtered on pre-combusted (450°C, 4 h), acid-washed (4% H$_2$SO$_4$) GF/F filters and frozen (-18°C) for later analysis. Seston samples for analysis of lipids were obtained from seawater pumped from 1.5 meters depth into a reservoir. The water was screened through a plankton net (mesh size 200 $\mu$m) before feeding into a flow-through centrifuge (5500 rpm) by gravity at a flow rate of 0.65–0.85 L min$^{-1}$. The seston was removed from the centrifugal bowl at intervals and the samples were immediately frozen and stored at $-80^\circ$C under N$_2$.

The copepods used for the experiments on egg production were collected by repeated vertical net hauls at a depth interval from 50 meters to the surface. We used a Nansen net (200 $\mu$m mesh size) with a large, non-filtering, cod end to minimize the damage to the copepods. The copepods were carefully transferred to 10 L tanks with surface water, or water from deeper layers when the surface salinity was low. The tanks were brought to the laboratory and were further processed within one hour after sampling.

2.2. Analytical methods

Particulate carbon (POC) and nitrogen (PON) was analyzed on a CN analyzer (Costech ECS model 44010) and particulate phosphorus (POP) was analyzed according to Grasshoff et al. (Grasshoff et al., 1983). Chl$\alpha$ was extracted in methanol and quantified using a fluorometer (Turner Designs) according to Strickland and Parsons (Strickland and Parsons, 1972). POC, PON, POP and chl$\alpha$ where all measured in duplicate, and the values for the different depths were integrated to the 0–10 meter strata by assuming that the 0, 3, and 10 m values constituted 15, 50 and 35% of the water column, respectively. For counting the ciliates and phytoplankton, we mixed 15, 50, and 35 mL of the 0, 3, and 10 m samples assuming that this represented an integrated sample from the 0–10 m water column. A subsample of 50 mL was counted according to Utermöhl (Utermöhl, 1958) after settling for a minimum of 24 h. At least 100 cells of each taxonomic group were counted, if possible. All samples were counted in phase contrast mode on an inverted microscope (Axiovert 200 M, Carl Zeiss, Jena,
Germany). Depending on the density and size of cells, different areas were counted at different magnifications (ciliates: 200X; phytoplankton: 100, 200, 400X).

For biomass calculations, pictures were taken using the Carl Zeiss AxioCam and AxioVision 4.6.3 software (Carl Zeiss, Jena, Germany). Twenty pictures (fewer for less abundant species/groups) for each group counted were taken at the highest possible magnification.

Linear dimensions were determined with the image processing program ImageJ (Rasband, 1997–2009). Biovolume was calculated from the median of the linear dimensions by applying simple geometric shapes to the organisms (Hillebrand et al., 1999; Kragberg et al., 2010; Olenina et al., 2006). The biomass of aloricate ciliates was converted to carbon by the regressions of Putt and Stoecker (Putt and Stoecker, 1989), the biomass of loricate ciliates according to Verity and Langdon (Verity and Langdon, 1984), and the biomass of diatoms, dinoflagellates, and small flagellates was converted to carbon according to Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000). The methods for determining total lipids and the fatty acid methyl esters (FAME) in the seston and in individual copepods are described in Bergvik et al. (Bergvik et al., 2012). In short, the total lipids of the seston were extracted and determined gravimetrically according to Bligh and Dyer (Bligh and Dyer, 1959) with modifications described by Jakobsen et al. (Jakobsen et al., 2008). Fatty acid methyl esters (FAME) from extracted lipids were prepared according to Metcalfe et al. (Metcalfe et al., 1966). The FAMEs were determined quantitatively by gas chromatography (Perkin Elmer AutoSystem XL) running TotalChrom v.6.3.1 software. During hydrolysis fatty acids are removed from both the wax esters and the glycolipids. This means that the content of these components, in the text referred to as non-fatty acid lipids, contain the remainder of the wax esters and glycolipids.

2.3 Egg production and hatching success

Active, undamaged Calanus females were selected under the stereomicroscope and individually placed in petri dishes (diameter 55 mm) containing 20 mL of seawater screened on 5 μm plankton filter. In total, 30–120 females were picked, dependent on the availability, and incubated in darkness at 15°C. The individual egg production was first monitored after 24 hours. Females that laid eggs after 24 hours were transferred to a new petri dish. The incubation continued for another 24 hours before the females were removed and fixed with ethanol. The egg production rate for each female was calculated by dividing the total number
of eggs laid during the 48 h period with the number of incubation days \((d = 2)\). The fixation of
individual *Calanus* females made it possible to separate *C. finmarchicus* from *C.
* helgolandicus* based on the curvature of the fifth pair of swimming legs (Fleminger and
Hulsemann, 1977). *C. helgolandicus* never constituted more than 10% of the total number of
*Calanus* females incubated. The *C. helgolandicus* females were removed from the
calculations, and they were too few to be included as a separate species in our experiments.
The eggs were incubated for 48 h before the number of nauplii was counted for calculation of
hatching success. Because the main focus of this work was to evaluate the effect of food
concentration and quality on the fecundity of *C. finmarchicus*, we excluded the females that
did not lay eggs.

3. RESULTS

3.1. Physical and biological environment

The Trondheimsfjord has a rather deep sill at the entrance of the fjord (195 m). The water
masses are dominated by the Norwegian Coastal Current (salinity 32–34) and can have a
brackish layer with salinities down to 19 in the surface during flood events. In our data, this
was evident at sampling days from late April onwards, when rain and thawing of snow
increased the freshwater runoff, and average salinities for the upper 10 meters were below 30
(Table I). For most of the sampling dates with low salinities (<30 PSU), there was a
pycnocline at 6–10 meters, above which the water column was well mixed.

The phytoplankton community showed a seasonal succession typical of the Trondheimsfjord
(Sakshaug, 1972), with relatively low chla concentrations during the winter (0.1 to 0.8 μg
chla L\(^{-1}\)) and a spring bloom from late March to early April (Table I). The observed chla
maximum for 2010 was 2.3 μg L\(^{-1}\), whereas the maxima for 2009 and 2011 were 5.0 and 4.7
μg L\(^{-1}\), respectively.

The concentration of POC was low (75–147 μg C L\(^{-1}\)) during January and February and
increased to concentrations of 215–726 μg C L\(^{-1}\) from mid-March to August. PON and POP
followed more or less the same seasonal pattern, but there were some variations in the
PON:POC and POP:POC ratios with 155–223 μg N mg C\(^{-1}\) and 9–21 μg P mg C\(^{-1}\),
respectively.
The microplankton community at the sampling station followed a recurring pattern. Typical winter population sizes were observed during the winter season (Sakshaug, 1972), with average biomass for samples from January to early March of 1.6 μg C L⁻¹. In late March 2009 and early April 2010, the diatoms were dominated by *Thalassiosira* spp. and *Chaetoceros* spp., whereas the high biomass of diatoms observed in May 2011 was mainly *Skeletonema* sp. In both 2009 and in 2011, the phytoplankton community was completely dominated by small flagellates in late April/early May, whereas in 2010 the microplankton community constituted a mix of diatoms, dinoflagellates and ciliates (Table 1). The peak biomass of ciliates was observed the 20th of June 2011 (17.6 μg C L⁻¹).

### 3.2. Fatty acid composition of the seston and of Calanus finmarchicus

The fatty acid composition of the seston < 200 μm (Figure 1) and the fatty acid composition for *C. finmarchicus* females (Figure 2) were pooled by season. The total lipid content of the seston varied between 21 and 164 mg g⁻¹ dry weight (DW) and the fraction of non-fatty acid lipids ranged between 54 and 84% of the total lipid content (Fig. 1A). The non-fatty acid fraction was not analyzed further, but algae normally contain variable amounts of pigments, wax esters (Antia et al., 1970; Guehler et al., 1964; Rosenberg, 1967), sterols (Goodwin, 1973; Patterson, 1971) and glycolipids (Meireles et al., 2003; Zhu et al., 1997). The dominating essential fatty acids (EFA) in the seston samples were eicosapentaenoic acid (EPA, C20:5 n-3) and docosahexaenoic acid (DHA, C22:6 n-3). The sum of EPA and DHA constituted 0.8 to 7.8 mg g⁻¹ DW (Fig. 1B), corresponding to 9–29% of total fatty acids (Fig. 1C), with considerable variation between sampling dates. The ratio between DHA and EPA (DHA:EPA) ranged between 0.09 and 2.2, with most values between 0.25 and 0.94. The content of C18:4 n-3 in seston material was also temporarily rather high (range 5–25% of TFA, peak value 28/4-2009). The only n-6 fatty acid found in significant amounts was linoleic acid (C18:2 n-6). Apart from the n-3 and n-6 EFAs, the seston was dominated by monounsaturated fatty acids (MUFAs) and saturated fatty acids (SFAs), mainly C14:0, C16:0 and C16:1 (Bergvik et al., 2012). The content of saturated and monounsaturated fatty acids varied between 44 and 81% of total fatty acids.

We observed significant differences in the total fatty acid (TFA) contents of *C. finmarchicus* over the seasons (Kruskal-Wallis one-way ANOVA on ranks, $H_{16} = 24.1$, $p<0.001$), with a significantly higher TFA concentration in January and February compared to May and June (Mann-Whitney U-test, $p<0.001$) (Fig. 2). The average TFA content in females decreased...
more or less gradually from 123 mg g\(^{-1}\) DW in January to 44 mg g\(^{-1}\) DW in May (Fig. 2).

C14:0 and C16:0 were the dominant saturated fatty acids (SFAs), whereas C20:1 n-9 and C22:1 n-11 were the dominating monounsaturated fatty acids (MUFAs). The concentration of C20:1 n-9 decreased from 11.2 to 0.1 mg g\(^{-1}\) DW from January to May, while C22:1 n-11 showed a similar decrease from 17.0 to 0.2 mg g\(^{-1}\) DW. Concurrent with the overall decrease in the TFA content, there was an increase in PUFA from relatively low concentrations before the spring bloom (17.3 ± 0.5 mg g\(^{-1}\) DW, mean ± SE) to 27.3 ± 2.6 mg g\(^{-1}\) DW in late April to June. DHA and EPA were the dominant PUFA in *C. finmarchicus*. The absolute content (Fig. 2B) of DHA remained stable at 9.5 ± 0.7 mg g\(^{-1}\) DW from January to the end of April, and increased thereafter steadily to 13.7 ± 0.6 at the 28\(^{th}\) of April. EPA followed the same pattern, but decreased after the peak value at the end of April. Because the TFA concentration decreased during the same period, the percentage PUFA increased to a maximum of 54% on the 18\(^{th}\) of May. The concentration of “Other n-3” also increased in April and May, mainly due to relatively high amounts of C18:4 n-3.

3.3. Egg production and hatching of *Calanus finmarchicus*

The egg production rate (EPR) was generally low during winter (5.7 to 9.1 eggs female\(^{-1}\) d\(^{-1}\)) and high and variable in the period from mid-March through May, during which egg production averaged 17.9 ± 1.7 eggs female\(^{-1}\) d\(^{-1}\) (mean ± SE, range 9.3 to 30.0) (Fig. 3A).

The hatching of viable nauplii did not show the same pattern (Fig. 3B). Apart from the 27\(^{th}\) of April 2009 (no hatching), the hatching success fluctuated between 43 and 92%. We could not detect any apparent pattern, and the sampling dates with low hatching success were spread through the seasons, with an average value for all dates of 67.6±1.5% (average ± SE). The portion of spawning females varied quite strongly, from 5% in February 2011 to 82% in March 2011 (Fig. 3C), with an average value of 34 ± 5.2%. The spawning frequency appeared to follow a similar trend in all years, with few females spawning during January and February (~20%), increasing to a maximum in late March (82%), followed by a period of lower, but varying spawning frequency.

The explanatory variables for reproduction could be grouped into four categories; physical conditions, food concentration, food quality and maternal effects (Table II). Hatching success was not significantly correlated with any of the explanatory variables. EPR increased with increasing spawning frequency (Spearman correlation (Rs) = 0.71, p = 0.0007). There was a positive effect of Julian day (Rs 0.63, p = 0.0035) and a slight effect of *in situ* temperature (Rs...
11

- 0.55, p = 0.014) on EPR, but we could not detect any difference between years. The effects of temperature and Julian day were, however difficult to separate, as these variables were heavily correlated (Rs = 0.92, p < 0.0001). Furthermore, the temperature was positively correlated with many of the food concentration variables. EPR was positively correlated with many of the food concentration variables but the variable that best explained the variation in EPR was the biomass of diatoms (Rs = 0.76, p = 0.0004). The EPR was also significantly correlated with the microplankton, especially when we considered the particles within the optimum size spectrum of C. finmarchicus (Gifford et al., 1995; Hansen et al., 1994; Hansen et al., 1997) and removed particles <10 μm (Rs = 0.74, p = 0.001, Fig. 4 A). The relationship could be described by a two-parameter rectangular hyperbola (EPR\(_{max}\) = 19.1 ± 1.8 eggs female\(^{-1}\) d\(^{-1}\), half saturation constant (K) = 0.44 ± 0.26 μg C L\(^{-1}\), \(r^2 = 0.39, p = 0.008\)). We found a slight effect of food concentration on EPR when chla (Rs = 0.45, p = 0.049) was used as a proxy for food concentration.

EPR was also positively correlated to the concentration of particular organic carbon (POC) (Table II, Rs = 0.66, p = 0.004). Because the ratio C:N and P:C was relatively stable, we found a similar significant pattern for EPR and the concentration of PON (Rs = 0.65, p = 0.005) and POP (Rs = 0.60, p = 0.015). For the latter correlations, we removed the POC, PON and POP data from the 18\(^{th}\) of May 2010. At this date, hydrological measurements from nearby rivers showed discharge rates corresponding to a five-year flood the week before this sampling date, and the POC and PON concentrations were higher than previously recorded during a 10-year monitoring program at the same sampling station. The relationship between EPR and POC could be described by a linear regression (\(r^2 = 0.51, \text{slope} 0.04 ± 0.01, p = 0.001, \) Figure 4B).

The food quality of the seston did not seem to have a large influence on the reproductive rates (Table II). However, when we tested the relation between EPR and food quality variables using regression analysis, we found slight, although significant, relationships between EPR and the total fatty acid content in the seston (\(r^2 = 0.31, \text{slope} 0.30 ± 0.13, p = 0.039, \) Fig. 5A), the total lipid content in the seston (\(r^2 = 0.34, \text{slope} 0.16 ± 0.07, p = 0.047\)) and the concentration of EPA in the seston (\(r^2 = 0.39, \text{slope} 2.93 ± 1.06, p = 0.017, \) Fig. 5B).

Both the spawning frequency and the EPR were significantly correlated with the content of EPA, DHA and the sum of EPA and DHA in the females of C. finmarchicus (Table II).

Regression analysis showed no saturation, the EPR was linearly related to the content EPA
and DHA in female C. finmarchicus (EPA: $r^2 = 0.55$, slope 2.58 ± 0.08, $p = 0.009$, Fig. 6A, DHA: $r^2 = 0.38$, slope 2.62 ± 0.04, $p = 0.044$, Fig. 6B).
4. Discussion

4.1. Seasonal variation in the physical and biological environment

Although we might have missed some bloom events because of the long interval between samplings, the variations in composition of the plankton community appeared to be similar to previous measurements (Table 1). The spring bloom in the Trondheimsfjord is usually initiated by the stabilization of the upper water column and the increasing irradiance, and usually starts in the middle of March and culminates during the first half of April (Sakshaug, 1972). A varying degree of freshwater runoff can affect the timing and magnitude of the spring bloom, and from our data we can suspect that we missed the main spring bloom during two seasons (2009 and 2011), since no diatom bloom was observed. Compared to previously recorded concentrations of chl$_a$ at the sampling station in the period 1996–2005 (unpublished results) and from a previous investigation of fecundity in *Temora longicornis* (Evjemo et al., 2008) the measured chl$_a$ concentrations of our study were in the lower range of what is expected during the spring bloom.

Another factor that may have impacted the phytoplankton biomass was the abundance of *C. finmarchicus* in the surface layers. In the spring of 2009, the abundance of *C. finmarchicus* stage IV, V, males, and females in the upper 50 meters was 0.97 ind L$^{-1}$ (Bergvik et al., 2012). This was four times higher than the highest *C. finmarchicus* abundance found in 2011 and almost 20 times higher than the highest abundance in 2010. Assuming clearance rates on diatoms, dinoflagellates and ciliates of 240 mL ind$^{-1}$ d$^{-1}$ (Koski, 2007; Koski and Riser, 2006), the *C. finmarchicus* population could potentially impact the phytoplankton community during the bloom. Grazing by *C. finmarchicus* have shown to contribute to the termination of the phytoplankton spring bloom, both in the Norwegian sea (Niehoff and Hirche, 2000) and in the Trondheimsfjord (Sakshaug, 1972; Strømgren, 1974). A further indication of copepod grazing is that the microplankton community in 2009 was dominated by small flagellates, assumed to be smaller than the optimal size spectrum of *C. finmarchicus* (Gifford et al., 1995; Hansen et al., 1994; Hansen et al., 1997). In conclusion, the seasonal variations during this three-year study provided the spawning *Calanus finmarchicus* with a wide range of food concentrations and food types, ranging from situations with severe food limitation to high and likely saturating food concentrations.
4.2. Fecundity of *Calanus finmarchicus*

The reproduction seemed to follow the same pattern the three seasons, and we did not detect any significant difference in EPR, hatching, or spawning frequency between the years. The mean egg production rate of *C. finmarchicus* measured at a specific time never exceeded 30 eggs fem\(^{-1}\) d\(^{-1}\), but single specimens showed an EPR as high as 106 eggs fem\(^{-1}\) d\(^{-1}\). Our observed average EPR were, however, less than half the maximum values reported elsewhere (Head et al., 2013a; Jonasdottir et al., 2011; Jonasdottir et al., 2008; Koski, 2007; Marshall and Orr, 1955; Melle and Skjoldal, 1998). This indicates that one or several factors reduced fecundity during our study.

We decided to incubate the females at 15°C because previous studies on the effect of temperature on daily egg production have shown no temperature effect in the range from 6–15°C (Laabir et al., 1995; Runge and Roff, 2000). However, according to our own data, the *in situ* temperature had a slight effect on EPR, although the temperature effect was difficult to separate from the effect of season (Julian day) and food concentration. We used filtered sea water because we wanted to limit the chance of bacterial contamination of the incubated females, the eggs, and the newly hatched nauplia. This should not affect the egg production rates, as the egg production rates do not seem to be negatively affected by the lack of food supply during short-term incubation of *C. finmarchicus* (Plourde and Runge, 1993) or *C. helgolandicus* (Laabir et al., 1995). Other studies have also shown that the EPR of *C. finmarchicus* has a time lag of two days from an increase in food concentration to an increase in the EPR (Jonasdottir et al., 2011). This further indicates that the egg production rates of *C. finmarchicus* in this study were a result of the conditions *in situ*.

An important conclusion of our study was that we did not find EPR and hatching to be related to the food concentration measured as the concentration of chl\(_a\). Some studies have drawn the same conclusion (Evjemo et al., 2008; Jonasdottir et al., 1995; Ohman and Runge, 1994), whereas others have found the EPR to be closely related to the concentration of chl\(_a\) (Head et al., 2013b; Runge et al., 2006). This might not be surprising, as chl\(_a\) and other light harvesting pigments of phytoplankton are known to vary with growth conditions and the species composition (Goericke and Montoya, 1998). As seen from the composition of microplankton calculated from cell counts (Table 1), the microplankton community was dominated by flagellates, mainly small spherical cells with a diameter of ~5 μm, at many sampling dates. Ciliates and dinoflagellates also contributed substantially to the biomass of the microplankton.
Some, but not all of the variation in EPR could be explained by food availability measured as the biomass of microplankton >10 μm (Table 4, Fig. 4A). Similar egg production on dates with a completely different microplankton composition suggests that specific food types are not important for the EPR (Table I). At the four sampling dates with the highest EPR, the microplankton composition was dominated by small flagellates (30/3-09 and 26/4-11), diatoms (30/5-11), and dinoflagellates (22/3-11). The pronounced year-to-year fluctuations in the onset of the spring bloom and the subsequent variations in alternate food particles would suggest that C. finmarchicus needs to be capable of managing such fluctuations.

Some previous studies have shown that C. finmarchicus has the ability to sustain a high EPR based on the ingestion of ciliates and heterotrophic dinoflagellates in post-bloom conditions (Head et al., 2013b; Ohman and Runge, 1994). Other studies have shown that the biomass of heterotrophic microplankton is too low to account for the energetic shortfall in the production of eggs (Irigoien et al., 1998; Mayor et al., 2006; Richardson et al., 1999). In our study, the ciliate biomass never exceeded 17.5 μg C L⁻¹. The eggs of C. finmarchicus contain approximately 0.23 μg C egg⁻¹ (Hirche, 1990). A production of 30 eggs fem⁻¹ d⁻¹ would require that individual C. finmarchicus females incorporate ~7 μg C d⁻¹ into eggs. Assuming an efficiency of 0.30 to convert C ingested to C incorporated into eggs (Mayor et al., 2009a; Peterson, 1988), an ingestion of ~24 μg C fem⁻¹ d⁻¹ could support that egg production rate.

Females of C. finmarchicus have shown maximum clearance rates of 0.5 L fem⁻¹ d⁻¹ (Paffenhöfer, 1971; Saage, 2006) and a minimum food concentration to yield an EPR of 30 eggs fem⁻¹ d⁻¹ should therefore be about 48 μg C. A maximum possible ingestion rate of C. finmarchicus feeding on ciliates would account for only ~9 μg C fem⁻¹ d⁻¹, or about 36% of the energy requirement for the production of 30 eggs d⁻¹.

The observed concentrations of phytoplankton and ciliates (Table I) were in large parts of the season much lower than the abovementioned food concentrations needed for maintaining the maximum EPR in C. finmarchicus. As shown from the above calculations, the minimum standing stock of edible food particles needed to support the highest observed egg production rates of our study was 48 μg C L⁻¹. This is a minimum estimate, as we based the calculation upon clearance rates of 100% retention efficiency. Clearance rates of C. finmarchicus feeding on a mix of diatoms, dinoflagellates, ciliates, and small flagellates are generally found to be in the range between 0.05–0.24 L ind⁻¹ d⁻¹ (Koski and Riser, 2006; Mayor et al., 2009a), essentially lower than the maximum rate of 0.5 L fem⁻¹ d⁻¹ (Paffenhöfer, 1971; Saage, 2006).
However, we observed egg production during the pre-bloom phase (January to early March), on dates with obvious food limitation. This indicates that egg production was fueled by the transfer of maternal energy (see below) (Niehoff et al., 1999; Richardson et al., 1999) and perhaps also the ingestion of detritus. The observed POC concentrations varied by a factor of 6 from the lowest to the highest observations (one date excluded, see above), while the phytoplankton and ciliate concentrations varied by a factor of 260. However, previous work on *C. finmarchicus* feeding on detritus are scarce and the results are contradictory (Carlotti and Radach, 1996; Dilling et al., 1998; Paffenhöfer and Strickland, 1970).

A second non-microplankton food source could be the eggs and newly hatched nauplia of *C. finmarchicus*. Previous studies have shown cannibalism by female *C. finmarchicus* and *C. helgolandicus* when the concentrations of alternative food particles are low (Basedow and Tande, 2006; Bonnet et al., 2004). This has been put forward as a possible explanation for why there seems to be a synchronized peak of copepodite stages despite the fact that the first spawning takes place well in advance of the spring bloom (Ohman et al., 2004; Ohman and Hirche, 2001). From our data, the first generation after spring spawning (stage C4) peaked around early May each year with a subsequent increase in C5 in deeper waters around May–June (Bergvik et al., 2012). With a developmental time of ~50 days (Møller et al., 2012) (average temperature 8°C, food concentration 100 μg C L⁻¹) this would imply that most of the new generation originated from the eggs produced during the spring bloom. In January–March, the abundance of females in the upper 50 meters never exceeded 0.025 ind L⁻¹ (Bergvik et al., 2012), the highest egg production rate was 15 eggs female⁻¹ day⁻¹, the hatching success was ~80%, and the spawning frequency was <30% (Fig. 3A, B and C). The resulting number of eggs released to the upper 50 meters was therefore at best 0.09 eggs L⁻¹ d⁻¹, equal to 0.02 μg C⁻¹ L⁻¹ d⁻¹. Although the consumption of their own newly hatched eggs and nauplia might be an important factor structuring the population of the *C. finmarchicus*, the consumption of their own eggs and nauplia seems inadequate to explain the observed egg production rates during the pre-bloom period.

The females of *C. finmarchicus* showed a decreasing content of total fatty acids from January–February to May–June, and especially the fatty acids C20:1 n-9 and C22:1 n-11 decreased during the same period. These fatty acids are regarded as storage fatty acids, originating from degraded wax esters in copepods (Sargent and Falk-Petersen, 1988). The gradual decrease in these fatty acids combined with the above calculated shortfall of potential food suggests that *C. finmarchicus* females must rely on storage lipids to produce the...
observed number of eggs during the pre-bloom phase. This is in accordance with the conclusions of other studies (Irigoien, 2004; Irigoien et al., 1998; Mayor et al., 2009a; Niehoff, 2004; Niehoff et al., 1999; Plourde and Runge, 1993; Richardson et al., 1999). However, we did not find any significant relationship between EPRs and either the total fatty acid or the total lipid content of the females. If reproduction was solely dependent on stored energy, only the ingested material from the previous productive season would impact the EPR. However, we found a significant positive relationship between food concentration and EPR (Fig. 4 A and B), indicating that the food concentration impacted the EPR. But, as seen from the significant relations from the regression analysis, none of the examined variables explain the entire variation in EPR. This can indicate that different variables can limit the egg production rate at different stages of the reproductive season. Although the timing and extent of the spring bloom differed from year to year in our study, pre-bloom spawning was a recurring event. We therefore propose that the pre-bloom spawning of *C. finmarchicus* is fueled by their lipid stores, and that this spawning might be of importance as a response to year-to-year variations in bloom events.

In several previous studies, EPR and the hatching of viable nauplii have correlated with food quality expressed in terms of the content of certain essential fatty acids in the food, most frequently EPA and DHA (Jonasdottir et al., 1995; Jonasdottir et al., 2002; Jonasdottir et al., 2005; Pond et al., 1996). We also detected a positive relationship between the EPA content in the seston and the EPR, and we detected a positive relationship between the content of TFA in the seston and the EPR, as previously shown for *Calanus helgolandicus* (Pond et al., 1996). We also found a significant positive relationship between the concentration of EPA and DHA in females and the EPR. The content of DHA and EPA was relatively stable during the winter, but increased in April. *C. finmarchicus* is probably incapable of synthesizing LC-n-3 PUFAs like DHA and EPA at ecologically relevant rates (Bell et al., 2007) and will therefore depend on their supply in the diet. The concentration of DHA and EPA in the seston was highly variable between sampling dates and the concentration of DHA and EPA in the seston was always lower than in female *C. finmarchicus*. A high tissue content combined with a poor capability for synthesis reflects a high dietary requirement for EPA and DHA, and EPA and DHA could therefore easily become limiting components for the animal.

To exemplify this, we can evaluate the potential for limitation by comparing the concentration of DHA and EPA in the seston and the female *C. finmarchicus*. During March and April, the average DHA concentration of the seston was 0.5 mg g\(^{-1}\) DW, whereas the DHA content of
the females was 10 mg g\(^{-1}\) DW. Assuming 100\% assimilation efficiency and no net metabolic
losses of DHA (i.e. losses through defecation and metabolic degradation are balancing
synthesis), a simple calculation according to Olsen et al. (Olsen et al., 2011) suggests that
these low DHA levels can only support a carbon growth efficiency of 5\%. Higher efficiencies
will mean that DHA is limiting (growth per ingestion; (Straile, 1997)). During May–June, the
DHA content of the seston was 2.3 mg g\(^{-1}\) DW, while the DHA content of the females had
increased to an average of 12 mg g\(^{-1}\) DW. Using the same assumptions, this seston DHA
content could support a specific growth efficiency of 19\%. The EPA content of the females
showed a similar pattern (8.8 mg g\(^{-1}\) DW during March–April, 10.7 mg g\(^{-1}\) DW during May–
June), but the EPA concentration in the seston was higher than the DHA concentration during
the spring bloom period (1.6 mg g\(^{-1}\) DW during March–April, 2.6 mg g\(^{-1}\) DW during May–
June). Under the same assumptions as above, the EPA content in March–April could
potentially support a specific growth efficiency of 18\%, whereas the EPA content of the
seston could support a specific growth efficiency of 24\% during May–June. Previous studies
have shown that *C. finmarchicus* eggs have a lipid composition similar to that of the seston
available for the females (Koski et al., 2012). We found a significant correlation between the
n-3 LC-PUFA concentration in tissues and EPR, indicating that the females indeed could
benefit from their internal reserves. This further elucidates the complex nature of *C.
finmarchicus* reproduction.

The above calculations assume that the *C. finmarchicus* females are consuming the seston
material in the proportions offered. One way for *C. finmarchicus* to mitigate potential DHA
deficiency will be to graze selectively on food particles that are high in DHA. Dinoflagellates
and smaller flagellates are generally rich in DHA and low or moderate in EPA, whereas
diatoms are rich in EPA and low in DHA (Reitan et al., 1994). We found higher DHA
contents in the seston in May–June, when the microplankton community was dominated by
dinoflagellates, small flagellates, and ciliates (Table I). Previous studies on the trophic
position of *C. finmarchicus* have revealed that it is omnivorous (Saage et al., 2008). Food
selectivity experiments have confirmed these findings, and ciliates are generally consumed in
higher proportions than offered (Leiknes et al., 2014; Nejstgaard et al., 1994). These findings
contradict some previous experiments showing that *C. finmarchicus* females selectively graze
on diatoms (Koski, 2007; Koski and Riser, 2006). Previous results from the study of the
dynamics of the lipid content of copepodite stage V *C. finmarchicus* have also shown that the
fatty acid composition of the copepods is related to the fatty acid composition of potential
food sources (Bergvik et al., 2012). This further indicates that *C. finmarchicus* is able to utilize different food items.

To summarize, this study shows that egg production in *C. finmarchicus* females depends on the food concentration, the nutritional quality of the food measured as the content of EPA or TFA of the microplankton, and the concentration of the polyunsaturated fatty acids DHA and EPA in the females. It is important to keep in mind that only one factor is necessary to limit production during each period. We therefore propose that the female *C. finmarchicus* experiences different factors limiting reproduction during the reproductive season. We observed egg production during the whole period investigated, from January to August. In the pre-bloom period, the concentration of phytoplankton and of alternate food sources, like ciliates and copepod eggs, could not sustain the observed EPR. The females must therefore rely on internal stores of fatty acids and probably proteins to be able to reproduce. The *C. finmarchicus* females showed high reproductive rates during periods of fluctuating microplankton community composition, suggesting the ability to utilize different food particles. The main pattern of spawning was in accordance with earlier observations of high egg production during the spring bloom, but the hatching success appeared to be less sensitive to effects of food concentration, food quality or maternal fatty acid composition. However, the flexibility in fundamental traits as reproductive strategy and the indication of spawning of a second generation within the same year indicate a plasticity that might explain the overwhelming dominance of this species in the northern hemisphere.

**Acknowledgements**

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References


Table I: Sampling dates, temperature, salinity, chlorophyll a (0-10 m), particulate carbon (POC), nitrogen (PON), phosphorus (POP), biomass of important microplankton groups and the composition of microplankton groups (%) in 2009-2011. Nd: no data.

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<th>Temperature °C</th>
<th>Salinity PSU</th>
<th>Chlorophyll a μg chl L⁻¹</th>
<th>POC μg C L⁻¹</th>
<th>PON μg N L⁻¹</th>
<th>POP μg P L⁻¹</th>
<th>Ciliates %</th>
<th>Phytoplankton %</th>
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</table>
Table II. Spearman correlations, Rs (p), between response variables (egg production rate (EPR), hatching success (HS), spawning frequency (SF)) and explanatory variables grouped into abiotic factors, food concentration, food quality and maternal effects. Correlations with Rs >0.6 in bold, the highest correlation within groups is labelled with an asterisk.

<table>
<thead>
<tr>
<th>EPR</th>
<th>HS</th>
<th>SF</th>
<th>Factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Julian day</td>
<td>0.63 (0.004)*</td>
<td>-0.03 (0.872)</td>
<td>0.39 (0.095)</td>
</tr>
<tr>
<td>Year</td>
<td>-0.03 (0.926)</td>
<td>0.04 (0.914)</td>
<td>0.12 (0.095)</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>0.55 (0.014)</td>
<td>-0.15 (0.514)</td>
<td>0.31 (0.195)</td>
</tr>
<tr>
<td>POC (μg C L⁻¹)</td>
<td>0.66 (0.004)</td>
<td>0.02 (0.889)</td>
<td>0.22 (0.390)</td>
</tr>
<tr>
<td>PON (μg N L⁻¹)</td>
<td>0.65 (0.005)</td>
<td>-0.06 (0.863)</td>
<td>0.22 (0.400)</td>
</tr>
<tr>
<td>POP (μg P L⁻¹)</td>
<td>0.60 (0.015)</td>
<td>0.06 (0.846)</td>
<td>0.23 (0.399)</td>
</tr>
<tr>
<td>Chla (μg L⁻¹)</td>
<td>0.45 (0.049)</td>
<td>0.02 (0.920)</td>
<td>0.15 (0.528)</td>
</tr>
<tr>
<td>Microalgae (μg C L⁻¹)</td>
<td>0.62 (0.013)</td>
<td>-0.15 (0.573)</td>
<td>0.15 (0.674)</td>
</tr>
<tr>
<td>Ciliates (μg C L⁻¹)</td>
<td>0.68 (0.002)</td>
<td>-0.13 (0.636)</td>
<td>0.35 (0.528)</td>
</tr>
<tr>
<td>Microplankton (μg C L⁻¹)</td>
<td>0.59 (0.013)</td>
<td>-0.16 (0.557)</td>
<td>0.11 (0.674)</td>
</tr>
<tr>
<td>Microplankton &gt;10 μm (μg C L⁻¹)</td>
<td>0.74 (0.001)</td>
<td>0.04 (0.848)</td>
<td>0.31 (0.228)</td>
</tr>
<tr>
<td>Dinoflagellates (μg C L⁻¹)</td>
<td>0.67 (0.003)</td>
<td>-0.07 (0.808)</td>
<td>0.42 (0.094)</td>
</tr>
<tr>
<td>Flagellates (μg C L⁻¹)</td>
<td>0.40 (0.115)</td>
<td>-0.24 (0.360)</td>
<td>0.13 (0.606)</td>
</tr>
<tr>
<td>Diatoms (μg C L⁻¹)</td>
<td>0.76 (0.0004)*</td>
<td>0.13 (0.567)</td>
<td>0.32 (0.213)</td>
</tr>
<tr>
<td>N:C (mg N g C L⁻¹)</td>
<td>-0.18 (0.483)</td>
<td>-0.08 (0.744)</td>
<td>0.11 (0.651)</td>
</tr>
<tr>
<td>P:C (mg P g C L⁻¹)</td>
<td>0.02 (0.893)</td>
<td>0.23 (0.408)</td>
<td>-0.03 (0.893)</td>
</tr>
<tr>
<td>DHA_{seston} (mg g⁻¹ DW)</td>
<td>-0.33 (0.256)</td>
<td>-0.10 (0.647)</td>
<td>-0.27 (0.342)</td>
</tr>
<tr>
<td>EPA_{seston} (mg g⁻¹ DW)</td>
<td>0.42 (0.139)</td>
<td>-0.29 (0.317)</td>
<td>0.40 (0.159)</td>
</tr>
<tr>
<td>EPA+DHA_{seston} (mg g⁻¹ DW)</td>
<td>0.08 (0.776)</td>
<td>-0.14 (0.599)</td>
<td>0.16 (0.584)</td>
</tr>
<tr>
<td>DHA:EPAseston:EPAseston</td>
<td>-0.58 (0.031)</td>
<td>0.02 (0.970)</td>
<td>-0.39 (0.169)</td>
</tr>
<tr>
<td>Total fatty acid_{seston} (mg g⁻¹ DW)</td>
<td>0.23 (0.422)</td>
<td>-0.27 (0.333)</td>
<td>0.17 (0.553)</td>
</tr>
<tr>
<td>Total lipid_{seston} (mg g⁻¹ DW)</td>
<td>0.13 (0.688)</td>
<td>-0.52 (0.092)</td>
<td>0.27 (0.404)</td>
</tr>
<tr>
<td>EPA_{fem} (mg g⁻¹ DW)</td>
<td>0.69 (0.019)</td>
<td>0.04 (0.916)</td>
<td>0.65 (0.032)</td>
</tr>
<tr>
<td>DHA_{fem} (mg g⁻¹ DW)</td>
<td>0.66 (0.028)</td>
<td>0.00 (1.000)</td>
<td>0.66 (0.026)</td>
</tr>
<tr>
<td>EPA+DHA_{fem} (mg g⁻¹ DW)</td>
<td>0.72 (0.012)*</td>
<td>0.10 (0.770)</td>
<td>0.72 (0.013)*</td>
</tr>
<tr>
<td>Total fatty acid_{fem} (mg g⁻¹ DW)</td>
<td>-0.67 (0.023)</td>
<td>-0.07 (0.832)</td>
<td>-0.64 (0.035)</td>
</tr>
</tbody>
</table>
Table III: Summary of variables which significantly influenced egg production rates (EPR).

<table>
<thead>
<tr>
<th>Linear regression</th>
<th>Variable</th>
<th>n</th>
<th>Slope</th>
<th>$R^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>POC seston</td>
<td>17</td>
<td>0.04 ± 0.01</td>
<td>0.505</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>PON in seston</td>
<td>17</td>
<td>0.44 ± 0.23</td>
<td>0.440</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Total fatty acid in seston</td>
<td>14</td>
<td>0.30 ± 0.13</td>
<td>0.310</td>
<td>0.039</td>
</tr>
<tr>
<td></td>
<td>EPA in seston</td>
<td>14</td>
<td>2.92 ± 1.06</td>
<td>0.339</td>
<td>0.047</td>
</tr>
<tr>
<td></td>
<td>EPA in females</td>
<td>11</td>
<td>2.58 ± 0.08</td>
<td>0.554</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>DHA in females</td>
<td>11</td>
<td>2.62 ± 0.04</td>
<td>0.379</td>
<td>0.044</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Two-parameter hyperbola</th>
<th>Variable</th>
<th>N</th>
<th>EPR$_{\text{max}}$</th>
<th>K</th>
<th>$R^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Protist C &gt;10 μm</td>
<td>16</td>
<td>19.1 ± 1.83</td>
<td>0.44 ± 0.26</td>
<td>0.385</td>
<td>0.008</td>
</tr>
</tbody>
</table>
Fig. 1. Fatty acid profiles of the seston. A: Total content of polyunsaturated (PUFA), monounsaturated (MUFA) and saturated (SFA) fatty acids and the fraction of non-fatty acid lipids (mg g⁻¹ DW). The total height of the bars represents the total lipid content of the samples. B: Quantitative content (mg g⁻¹ DW) of important individual and groups of EFA. C: Relative content of important individual and groups of EFA (% of total fatty acids). All measurements represent the mean of two measurements.
Fig. 2. Fatty acid profiles of female *C. finmarchicus*. A: Fatty acid content of females (mg g$^{-1}$ DW). PUFA: polyunsaturated fatty acids, MUFA: monounsaturated fatty acids, SFA: saturated fatty acids. The total height of the bar represents the total lipid content of the samples. B: Quantitative content (mg g$^{-1}$ DW) of polyunsaturated fatty acids (PUFA). C: Relative content of important polyunsaturated fatty acids (PUFA, % of total fatty acids). All values represent the average of 3–11 measurements.
Fig. 3. Reproductive rates of *Calanus finmarchicus* sampled in 2009-2011. A: Egg production rate (EPR, number of eggs produced female$^{-1}$ day$^{-1}$, mean ± SE). B: Hatching success (percent hatching per sampling day, mean ± SE). C: Spawning frequency (% of females spawning).
Fig. 4. A: EPR of *Calanus finmarchicus* females as a function of food concentration measured as A: Protist C >10 μm and B: Concentrations of POC < 200 μm.
Fig. 5. EPR of *C. finmarchicus* females as a function of food quality measured as A: Total fatty acid content in the seston and B: EPA concentration in the seston.
Fig. 6. EPR of *C. finmarchicus* females as a function of female fatty acid content. A: Concentration of EPA (mg EPA g$^{-1}$ DW). B: Concentration of DHA (mg g$^{-1}$ DW).
The effect of essential fatty acids for the somatic growth in nauplii of *Calanus finmarchicus*

Øystein Leiknes 1*, Siv Anina Etter1, Nils Egil Tokle2, Maria Bergvik1, Olav Vadstein1, Yngvar Olsen1

1Department of Biology, NTNU Norwegian University of Science and Technology, Trondheim, Norway
2Planktonic AS, Trondheim, Norway
3Department of Biotechnology, NTNU Norwegian University of Science and Technology, Trondheim, Norway

*Correspondence:* Øystein Leiknes
Department of Biology, NTNU Norwegian University of Science and Technology, Trondheim, Norway
oystein.leiknes@ntnu.no

Keywords: Secondary production, Growth rate, *Calanus finmarchicus*, DHA, EPA, Food concentration, Zooplankton

Abstract

The growth of *Calanus finmarchicus* nauplii was studied in laboratory experiments using natural seston and a mixture of cultured microalgae as food source. We detected no significant correlation between growth and food concentration measured as Chlorophyll *a* (Chl *a*) or particulate organic carbon (POC), but the growth rate was significantly related to the content of EPA (20:5n-3, *r*² = 0.35, *p* = 0.043) and DHA (22:6n-3, *r*² = 0.472, *p* = 0.014) in the seston. The growth rate was overall higher for nauplii fed cultured microalgae (range 0.06–0.19 d⁻¹) compared to the nauplii fed natural seston (range 0.001–0.11 d⁻¹). Although the nauplii fed algae cultures were fed surplus food, the growth did vary between the growth periods. Furthermore, the growth rate for nauplii fed natural seston and for nauplii fed cultured algae were positively related (*r*² = 0.67, *p* = 0.013), suggesting that the maternal condition and the food quality experienced by the mothers could explain some of the variation in naupliar growth rate.

We present lipid class data on *Calanus finmarchicus* eggs from field samples that, contrary to previous studies, showed a high content of wax esters. Fatty acid analyzes of eggs, nauplii stages and copepodites showed that eggs and nauplii have a similar fatty acid composition and that the main increase in the content and share of DHA and EPA was from nauplii to copepodite.

The secondary production measured as naupliar growth was compared to the secondary production measured as carbon specific female egg production rate. The secondary production measured as egg production was generally higher than the secondary production measured as naupliar growth early in the spring, whereas the opposite situation was observed during post-bloom situations in late spring/early summer.
1 Introduction

*Calanus finmarchicus* is the dominating copepod in the North Atlantic and Barents Sea (Conover, 1988). It is a vital link between primary production and higher trophic levels and an important food source for planktivorous fishes (Dommasnes et al., 2004) and whales (Payne et al., 1990), various gelatinous zooplankton (Blachowiak-Samolyk et al., 2007; Ohman et al., 2008), carnivore zooplankton (Tönnesson et al., 2006; Dalpadado et al., 2008), bottom living animals like sponges (Watling, 2007), and corals (Dodds et al., 2009). Eggs and nauplii stages of copepods are the most important food source of many larval fishes and therefore of great importance for their recruitment (Kane, 1984; Runge, 1988; Planque and Batten, 2000).

Secondary production of marine zooplankton has been shown to be an important variable that needs to be estimated in order to quantify the food transfer from primary producers to higher trophic levels. The secondary production has mainly been estimated by studying cohort development, either by sorting individual nauplii or by creating an artificial cohort by size-fractionation with different plankton mesh sizes (Winberg, 1971). Measurements of egg production can also be used to obtain an estimate of the secondary production, under the assumption that females use all their assimilated energy to create offspring and that the energy incorporated into the eggs produced therefore is a direct measure of the secondary production (Kiørboe and Johansen, 1986; Poulet et al., 1995).

The egg production, hatching success and subsequent growth of naupliar stages are critical stages for development of calanoid copepods, and high rates of egg production are therefore not always followed by an increase in abundance of copepodites (Jonasdottir et al., 2008). Different mechanisms are proposed to explain this, including cannibalism (Bonnet et al., 2004; Basedow and Tande, 2006), predation (Eiane et al., 2002; Ohman et al., 2004; Ohman et al., 2008), food limitation (Koski et al., 2010) and toxic effects from diatoms (Ianora et al., 2003). The nutritional value of the food, and specifically the content of long-chain polyunsaturated n-3 fatty acids in the food, particularly eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3), have been shown to be beneficial for reproductive rates of copepods (Pond et al., 1996; Jonasdottir et al., 2002; Jonasdottir et al., 2005; Evjemo et al., 2008).

The hatching and the growth through the two first nauplii stages are also sensitive for maternal effects. Higher hatching success and higher protein content has been found for offspring of females that have experienced high food availability and high contents of essential fatty acids in their food (Koski et al., 2012). The reproduction rate of *C. finmarchicus* in the Trondheimsfjord was found to be closely linked both to food concentration and to food quality in terms of essential fatty acid content of the food and to the content of specific fatty acids in the females (Leiknes et al. 2015, submitted).

The oil sac in females of copepods is in close proximity to the gonads, and the lipid content of the females generally decreases as they are producing eggs. The eggs are known to have a high number of yolk granules with lipovitellin (peptides, phospholipids and cholesterol), and lipid droplets (wax esters or triacylglycerols) that the embryo utilize for energy and biosynthesis of membranes and hormones (Lee and Walker, 1995). Previous studies on the lipid class composition of the eggs from *Calanus helgolandicus* and of *C. finmarchicus* are however scarce and has shown substantial variability (Lee et al., 1972; Gatten et al., 1980; Ohman and Runge, 1994).

*C. finmarchicus* develops from egg through the first two nauplii stages without feeding, and the growth measured as individual dry weight or carbon content is therefore negative (e.g. Harris et al., 2000). They spend most of their egg yolk and some of their lipid droplets during their first
Somatic growth in *C. finmarchicus* nauplii

mols, but starts to gain weight from nauplii stage III and onwards. The main storage lipid increments take place during the copepodite stages CI–V. The growth of *C. finmarchicus* has mainly been studied in laboratory experiments (Corkett et al., 1986; Tande, 1988; Campbell et al., 2001b) or in mesocosms (Harris et al., 2000; Hygum et al., 2000a; Hygum et al., 2000b). The growth rate has been shown to be affected by temperature and food availability (Møller et al., 2012), although it appears that the naupliar stages are less sensitive to low food concentrations than copepodites (Hygum et al., 2000a). Although the conversion of storage lipids into eggs and the subsequent development and growth of copepod nauplii has shown to be sensitive for the availability of specific polyunsaturated fatty acids, relatively little is published on the lipid and fatty acid composition of copepod eggs and early nauplii stages (Kattner et al., 2007).

The aim of this study was to evaluate the effect of food quantity and food quality on the growth of nauplii of *C. finmarchicus*. We measured growth rates of the first nauplii stages of *C. finmarchicus* during three reproductive seasons using natural seston as food and *in situ* temperatures to mimic *in situ* conditions. The potential food concentration of the nauplii was assessed by measuring Chlorophyll *a* (Chl *a*) and particulate organic carbon (POC). The potential food quality was assessed based on the contents of essential fatty acid and total lipid of the food offered to the nauplii. We present fatty acid profiles for *C. finmarchicus* egg, nauplii and copepodites, and lipid class composition for *C. finmarchicus* eggs. The secondary production measured as somatic growth was compared with the secondary production measured as egg production rate of the female *C. finmarchicus*.

2 Material and methods

*Calanus finmarchicus* females was collected through three spring seasons; 2007, 2009 and 2011, from two different locations in the Trondheimsfjord, northwest of Munkholmen (N 63°27', E 10°20'; 2007) and at sampling station Trollet (N 63°29', E 10°18'; 2009 and 2011). During the cruises in 2007, we used two different plankton nets; a plankton net with mesh size 500 μm (diameter 1.5 m, length 10 m) and a non-filtering cod end and a plankton net with 70 μm mesh size (diameter 1 m, length 7 m). Both nets were hauled horizontally at 10 m depth at low speed. The coarse-meshed net was used to collect female *C. finmarchicus* and the fine-meshed net was used for collecting eggs and naupliar stages. In 2009 and 2011, the females were sampled with repeated vertical net hauls from 50 meters depth to the surface using a modified Nansen net with 200 μm mesh size and a large, non-filtering cod end. In 2007 and 2010 smaller stages of copepods were collected with the above described fine net mesh (70 μm). The females and the juvenile stage nauplii were carefully transferred to 25 L tanks containing surface water, brought to the laboratory and further processed within one hour after sampling.

The various stages of *C. finmarchicus* for lipid analysis were obtained by successive filtration of the material collected with the fine mesh net, using a filtration tower consisting of polyethylene tubes (diameter 10 cm) with 25 different mesh sizes. The sample (> 70 μm) was poured into the successive filtration device at the top and thoroughly washed with 10 μm filtered seawater. The major part of the content in each tube was carefully washed, dried, transferred into plastic bottles (20 mL) and frozen under N2 atmosphere for fatty acid analysis. A subsample from each tube was fixed with acidic Lugol (1 % final concentration) and analyzed in a stereoscopic microscope (Leica MZ6) or an inverted microscope (Leica DM IRB), depending on the particle size.

Analysis of total lipids and fatty acid methyl esters in the seston and in copepods was done according to Bergvik et al. (2012a) and analysis of lipid classes according to Bergvik et al. (2012b). During the sampling in 2010, we were able to obtain an almost pure sample of copepod eggs (Table 1) in quantities sufficient for analysis of both fatty acids and lipid classes.
Somatic growth in *C. finmarchicus* nauplii

For quantification of egg production rates active, undamaged females (*n* = 20–134) were selected under the stereomicroscope and incubated individually in petri dishes (5.5 cm) containing 20 mL GF/F-filtered seawater. Details on the incubation procedure and data on rates of egg production and hatching success are reported elsewhere (Leiknes et al. 2015, submitted). In short, the petri dishes were inspected every 24 hour. To avoid egg cannibalism females were moved to a new petri dish if they had laid eggs. The total incubation time of the females was 48 hours. After the removal of the females, the eggs were incubated for a further 48 hours before the number of nauplii was counted and hatching success was calculated.

For the growth experiments, the nauplii from the petri dishes were poured together in a beaker and transferred in equal numbers to flow-through cage cultures. We used plexiglas-tubes (3 X 21 cm, volume 142 mL) and a multichannel peristaltic pump (Ismatech IPC) to supply water. The nauplii were supplied the food in natural seawater collected from 3 meter depth at the pier at Trondheim Biological Station (N 63° 26', E 10° 20'). Some nauplii cultures were fed cultured microalgae (see below) suspended in filtered sea water. The water with the food was supplied from 10 L Pyrex bottles, and new food prepared every second day.

To remove other eggs and nauplii from the food suspension, the water was reverse filtered with at 55 μm plankton mesh before use. Subsamples of the screened natural seawater were filtered onto GF/F-filters for further analyses of Chla, particulate organic carbon (POC) and nitrogen (PON). Chla was extracted in methanol and quantified using a fluorometer (Turner Designs) according to Strickland and Parsons (Strickland and Parsons, 1972). POC and PON were analyzed on a CN-analyzer (Costech ECS model 44010). We also collected a seston sample (<55 μm) for fatty acid analysis by means of a flow-through centrifuge. A complete description of the sampling method of seston and lipid analyses are described elsewhere (Evjemo et al., 2008;Bergvik et al., 2012a).

During the last two sampling seasons we included a separate treatment where the nauplii were fed a mixture of equal carbon amounts of *Rhodomonas baltica*, *Isochrysis galbana*, and *Dunaliella tertiolecta*. The algae were kept in exponential growth on F/2-medium (Guillard, 1975). The total biomass of the added algal mixture was 150 μg C L⁻¹. This mixture of microalgae was chosen because it is used to maintain a multi-generation culture of *C. finmarchicus* at NTNU Sealab (Hansen et al., 2007).

The growth of the nauplii was calculated by measuring the change in biovolume with time. Incubated nauplii were sedated with carbon dioxide and pictures were taken in an inverted microscope (Leica DM IRB) fitted with a digital camera (Sony DFW-700).The pictures were taken from the dorsal side and we used the length (L) and the width (W) to calculate the biovolume using the standard formula of a half elliptic sphere:

\[
V_0 = \frac{\pi L W^2}{12}
\]

Instantaneous specific growth rates of the nauplii (IGR naup, d⁻¹) were calculated from the average biovolume at the beginning \((V_0)\) and the end \((V_f)\) of the growth periods.

\[
IGR_{naup} (d^{-1}) = \frac{V_f - V_0}{t}
\]

To compare the secondary production measured as somatic growth of nauplii with the secondary production measured by egg production rate, we used data on dry weight of female *C. finmarchicus* from the same sampling dates as the females used for the nauplii studies. To calculate carbon-specific secondary production, we assumed a carbon-content of 45% of dry matter for female *C. finmarchicus* (Båmstedt, 1986), and an average egg carbon content of 0.23 μg C egg⁻¹ (Hirche, 1990). Instantaneous adult growth rates (IGR fem, d⁻¹) were calculated from Hopcroft and Roff (1998):

This is a provisional file, not the final typeset article
Somatic growth in *C. finmarchicus* nauplii

\[
\text{IGR}_\text{fem} (d^{-1}) = \frac{\ln(W_{\text{Egg}} + W_{\text{Female}})}{t}
\]

*W*<sub>Female</sub> and *W*<sub>Egg</sub> are the carbon specific masses of the females and the eggs, respectively and *t* is the incubation time in days.

3 Results

The highest Chl \(a\) concentration were observed during growth period (GP) 1.1, GP 3.3 and GP 3.4, with concentrations of 4.6, 5.4 and 3.9 \(\mu g\) Chl \(a\) \(L^{-1}\), respectively (Table 2). During the remaining growth periods the Chl \(a\) concentration fluctuated between 1.1 and 2.3 \(\mu g\) Chl \(a\) \(L^{-1}\).

The POC concentration showed no correlation to Chl \(a\) (\(P > 0.05\)). The total lipid content (TL) and the total fatty acid (TFA) concentration of seston < 55 \(\mu m\) showed pronounced variations between growth periods (Figure 1(A)). The TL was highest during GP 1.1 and 3.4, and lowest during GP 3.1 and 3.2. The content of TFA followed the same pattern as TL, and the overall average for TFA and TL was 16.0 ± 2.9 and 70.5 ± 8.6 (mg g\(^{-1}\) DW), respectively. The dominating fatty acids of the seston were 14:0, 16:0, 18:0, 16:1n-7, 18:3n-3, 18:4n-4, 20:5n-3 (EPA) and 22:6n-3 (DHA). Some taxonomic group specific fatty acids, like the diatom fatty acid 16:1n-7 varied from 0.26 (GP 1.3) to 13.0 mg g\(^{-1}\) DW (GP 3.4), and the flagellate fatty acid 18:4n-3 varied from 0.22 (GP 3.1) to 2.1 mg g\(^{-1}\) DW (GP 3.4). The highly unsaturated fatty acids EPA and DHA constituted on the average 13.6 and 7.5% of TFA, respectively (Figure 1(B), (C)).

It was difficult to obtain pure samples of eggs and nauplii of *C. finmarchicus* after the onset of the spring bloom, and all lipid and fatty acid data are from GP 1.1. The data for copepodites are from GP 1.2. The TL and TFA of eggs and nauplii differed between the sampling dates. The eggs from 25/2 contained almost twice the amount of TL and TFA as those from 17/2 and 10/3 (Figure 2). The nauplii stages NII – III showed a slightly higher TL- and TFA-content than NIII – IV and copepodite stages CII – III, but the TL- and TFA-content increased in the later stages CIII – IV and CIV – V.

The size fractionation also provided almost pure samples of *Protoperidinium* sp. and *Coscinodiscus* sp. (Table 1). The TL and TFA in these microalgae were similar to that of the eggs and nauplii, but the fatty acid composition was different (Figure 3). *Protoperidinium* sp. showed a lower content of EPA and DHA and a higher content of 14:0 and 18:1n-9 than the different stages of *C. finmarchicus*. *Coscinodiscus* sp. had a FA-composition that was similar to that of the copepods, except for a low DHA-content and a high 14:0-content. The nauplii and eggs showed a variable TFA-content and a variable content of fatty acids. The fatty acid composition of the different nauplii stages was similar to those of the eggs, but both TFA and contents of EPA and DHA were much higher in the copepodite stages. The average content of EPA and DHA in nauplii was 10.2 and 5.7 mg g\(^{-1}\) DW in NII – III, and increased to 18.8 and 13.0 mg g\(^{-1}\) DW in CIV – V.

The lipid class analyses of *C. finmarchicus* eggs showed pronounced differences between the sampling days, with the highest content of most lipid classes in the eggs sampled at the 25/2 (Figure 4). Both samples contained high amounts (Figure 4 (A)) and percentage fractions of WE (Figure 4 (B), >80 % of TL), variable amounts and fractions of TAG and less and more stable amounts and fractions of phosphatidylethanolamine (PE), phosphatidylcholine (PC) and free fatty acids (FFA). The variability was accordingly most pronounced for neutral storage lipids.

The specific growth rate of *C. finmarchicus* nauplii exhibited some variability, but showed an increase through the growth season, with growth rates close to zero in early March, average values around 0.08 day\(^{-1}\) in late March, and 0.12 ± 0.02 day\(^{-1}\) in May (Figure 5). For all the growth periods except GP 2.4 and 3.4, the average growth rate was significantly higher for
nauplii fed cultured microalgae than for nauplii fed natural food only (pairwise T-test, p < 0.05, Figure 5).

Higher contents of green matter was observed in the guts of C. finmarchicus nauplii fed surplus microalgae compared to those fed natural seston. The growth rates in the nauplii fed cultured microalgae in excess were found to be different between growth periods (p < 0.001, one-way ANOVA). Nauplii from GP 3.3 fed surplus food had the highest growth rate (0.19 ± 0.003 d⁻¹), whereas nauplii from GP 2.1 and 3.2 had the lowest growth rates for the nauplii fed surplus food, both with a growth rate of 0.060 d⁻¹. The growth rate of the nauplii fed cultured microalgae increased with increasing growth in nauplii fed natural seawater (r² = 0.670, slope 0.924 ± 0.265, p = 0.013, Figure 6), suggesting that 67% of the variability of the growth rate in nauplii fed cultured microalgae was explained by the recent feeding history of the mothers.

There was a tendency for higher naupliar growth with higher Chl a-concentration (Figure 7), but there were no significant relationships between growth and the concentration of Chla (Pearson coefficient 0.497, p = 0.103) or POC (Pearson coefficient 0.163, p = 0.632). The naupliar growth rate increased both with increasing content of EPA and DHA in the food of C. finmarchicus nauplii. Both the effect of EPA and DHA in the food could be described by a saturation hyperbola (EPA: r² = 0.350, half-saturation constant (K) = 1.42 ± 1.28, p = 0.043, Figure 8 (A), DHA: r² = 0.472, half-saturation constant (K) = 0.732 ± 0.620, p = 0.014, Figure 8 (B)).

The growth rates of the nauplii showed pronounced variability both for low and high female growth rates, and the values deviated from the 1:1 line in many growth periods (Figure 9). The growth rates of mothers and offspring was accordingly not significantly correlated (Pearson correlation coefficient 0.129, p = 0.69). However, if the two lowest nauplii growth rates were removed, the naupliar growth rate significantly decreases with increasing female growth (Pearson correlation coefficient -0.622, p = 0.037).

4 Discussion

One main conclusion from our study was that the quantity of food and/or the food quality limited the instantaneous growth rate of the nauplii fed natural seston (IGRnau, d⁻¹). The IGRnau increased significantly (p < 0.05, Figure 8) with increasing content of DHA and EPA in the food. To our knowledge, this has not been reported for nauplii of C. finmarchicus in previous investigations. The contents of DHA and EPA in the food have repeatedly been shown to have a positive effect on the rate of egg production of later stages of copepods (e.g. Evjemo et al., 2008;Jonasdottir et al., 2009). The DHA- and EPA-contents of suspended particulate matter (<55 μm) is mainly a result of the species composition of plankton, as diatoms generally have low contents of DHA and high contents of EPA, whereas dinoflagellates and smaller pigmented flagellates have high contents of DHA and variable concentrations of EPA (Ackman et al., 1968;Hallegraeff et al., 1991;Reitan et al., 1994;St. John and Lund, 1996;Mansour et al., 1999). In addition to these taxonomically specific differences, the content of DHA and EPA in microalgae is also sensitive to limitations by inorganic nutrients (Reitan et al., 1994).

Another factor, not further evaluated, is the varying concentration and consumption of detritus particles. When comparing measured POC-concentrations with carbon in microalgae calculated from Chla-concentrations (C:Chla conversion factor of 64 µg C:µg Chla, Vadstein et al., 2004), the Chla-containing fraction was varying from 24 to 72 % of the total POC-concentration. There are, to our knowledge, no published papers on C. finmarchicus nauplii feeding on detritus particles and previous reports on Calanus spp. adults feeding on detritus are scarce and the results are contradictory (Paffenbößer and Strickland, 1970;Carlotti and Radach, 1996;Dilling et al., 1998). We therefore suggest that the nauplii grazing selectively on phytoplankton and ciliates...
Somatic growth in *C. finmarchicus* nauplii

(Turner et al., 2001; Irigoien et al., 2003) might have experienced higher DHA- and EPA-concentrations in their actual food than what we measured in the seston samples, because dead matter is likely lower in these fatty acids than live plankton (Suroy et al., 2014). Contrary to other studies (Campbell et al., 2001b) the IGR$_{naup}$ was not significantly correlated with the food concentration measured as Chl$_a$ or POC in the present study, in agreement with the suggestion that the nauplia were mainly DHA- and EPA-limited. Moreover, IGR$_{naup}$ of the nauplii fed cultured algae were throughout higher than those of the nauplli fed natural seston; the IGR$_{naup}$ of nauplii fed cultured algae was typically $12\,–\,493\%$ higher than the IGR$_{naup}$ for nauplii fed natural seston (Figure 5). The mixture of the cultured algae was not analyzed for fatty acids, but contained algae with known and complementary fatty acid composition. *Rhodomonas balticum* has a high amount of EPA, DHA, 18:3-n3 and 18:4-n3 (Olsen et al., 2014), *Isochrysis galbana* has a high content of DHA, 18:2n-6, 18:1 and 16:1 (Custódio et al., 2014), and *Dunaliella tertiolecta* has a high content of 18:3-n3, 16:4-n3, 18:1 and 16:0 (Lee et al., 2014).

We found that the DHA-content was more or less equal in eggs and nauplii NII–III of *C. finmarchicus*, on average $5.4\pm0.20$ (mean $\pm$ SE) mg DHA g$^{-1}$ DW (9.8% of total fatty acids, Figure 3). In copepodites CII–III, the average DHA-content had increased to $13.8\pm0.83$ mg DHA g$^{-1}$ DW (31.8% of total fatty acids, Figure 3), in agreement with earlier results for this stage of *C. finmarchicus* (Evjemo et al., 2003). There was no further increase in quantitative DHA content with increasing developmental stage beyond CII–III, but total lipid and TFA contents were steadily increasing. The fatty acid composition for copepodite stage V and females throughout the reproductive season is reported elsewhere (Bergvik et al., 2012a; Leiknes et al., 2015; submitted). The main pattern of variation in absolute and the relative DHA contents showed an increase in DHA through the reproductive season that was related to the fatty acid composition of the food. DHA and EPA are normally not synthesized in significant rates in *C. finmarchicus* (Sargent and Whittle, 1981; Bell et al., 2007). A low capacity of synthesis combined with a high content of DHA reflects high dietary requirements for DHA, and a variable content of DHA in the food makes it likely for DHA to become a critical essential component for the animal. We therefore suggest that in the present study the availability of DHA in the food of the *C. finmarchicus* nauplii limited the growth rate of the nauplii. This has been shown for other copepods (Breteler et al., 2005) and fish larvae, which are classified as carnivore zooplankton (Ruyter et al., 2000; Tocher et al., 2001).

The treatment that involved use of cultured algae as food for the nauplii was intended to serve as a positive control. The added food was always kept at concentrations assumed to be above saturation for *C. finmarchicus* nauplii (150 $\mu$g C L$^{-1}$, Campbell et al., 2001b). As the temperature did not vary widely between the sampling dates, we expected that IGR$_{naup}$ was similar for the experiments with nauplii fed surplus cultured food. However, the IGR$_{naup}$ was not equal for the different growth periods (Figure 5), and we observed that there was a significant relationship between the IGR$_{naup}$ of nauplii fed cultured algae and those fed natural seston ($r^2 = 0.67$, $p = 0.013$, Figure 6). This suggests that variation in maternal condition and the food quality experienced by the mothers explain some of the variation in naupliar growth rate. Our present results on the lipid class and fatty acid compositions of *C. finmarchicus* eggs suggested that both the content of TL and TFA can vary quite strongly and that this might reflect variable nutritional states of the females. The lipid classes forming lipid droplets in the eggs are wax esters and/or triacylglycerides (Lee et al., 2006). In our study we found both WE and TAG in eggs of *C. finmarchicus*, whereas previous investigations have reported phospholipids (Ohman and Runge, 1994) and TAG (Lee et al., 1972; Gatten et al., 1980) as the main lipid classes. Another study found PL as the main lipid class, and PL is the main lipid class in lipovitellin (Lee and Walker, 1995).
Somatic growth in *C. finmarchicus* nauplii

The high variability in lipid content and storage lipid in the eggs could be a result of different nutritional states of the females. The egg samples from our study were from February and early March before the females had started feeding. The storage lipid of the females must therefore have originated from the previous season in the form of WE (Sargent and Falk-Petersen, 1988). The egg samples in the studies of Gatten et al. (1980), Lee et al. (1972) and Ohman and Runge (1994) were sampled during the summer when the females had been fed satiated food concentrations. It is likely that these females had low WE contents and that they therefore transferred less WE to the eggs.

It has been shown that the WEs are converted to TAG for reproductive needs when the copepods leave diapause (Jonasdottir, 1999; Richardson et al., 1999). This is likely to happen, but our result suggested that WE can also be transferred directly to the eggs, at least before the spring bloom. During this period the females usually have low food availability and high lipid reserves in the form of WE. The WE contents of the eggs may influence the mortality and growth rates through the egg and first nauplii stages. We nevertheless suggest that the high variability of lipid and lipid class composition in eggs could be a critical factor for hatching success and mortality of nauplii and needs to be further studied.

The measured growth rates obtained for *C. finmarchicus* nauplii were in the lower range of what has been reported in previous studies (Hygum et al., 2000a; Campbell et al., 2001b), but were similar to those found for *Centrophages typicus* nauplii (Calbet et al., 2000) and for *C. finmarchicus* copepodites obtained for shipboard incubations (Campbell et al., 2001a). Our relatively low IGR\textsubscript{naup} values may originate from a varying efficiency in ingestion and assimilation of food particles. In earlier feeding selectivity experiments (Turner et al., 2001; Irigoien et al., 2003; Castellani et al., 2008), nauplii of *C. finmarchicus* were found to select among food particles smaller than 55 μm. We therefore assume that we did not remove any potential food particles for the nauplii by screening the water on 55 μm. In a feeding study of nauplii of *C. helgolandicus* (Rey et al., 2001), the ingestion rate was higher for nauplii offered big algae (*Prorocentrum micans*, ESD 26–27 μm) than smaller algae (*Isochrysis galbana*, ESD 4–5 μm), but the growth rate was higher in nauplii fed the smaller algae. Others have shown that *C. finmarchicus* nauplii in stages NIV to NVI can select among diatoms, ciliates and dinoflagellates, depending on the species composition of the microplankton community (Turner et al., 2001; Irigoien et al., 2003; Castellani et al., 2008). Field data from a nearby sampling station show that the microplankton community in general was dominated by diatoms during the spring bloom whereas small flagellates, ciliates and dinoflagellates were dominant during the post bloom period (Leiknes et al., 2015, submitted). This suggests that the nauplii offered natural seston could experience low availability of smaller food particles although the Chlorophyll \textsubscript{a} and the POC-data indicated surplus of food.

The observations of reproductive rates of *C. finmarchicus* females together with the somatic growth of nauplii made it possible to compare the two different methods for estimating secondary production. It was then kept in mind that the start of the somatic growth period was five days after the sampling date of females. There was considerable scatter around the 1:1 line. With two low values removed, the IGR\textsubscript{naup} was found to decrease significantly with increasing IGR\textsubscript{fem} (Figure 9). The secondary production by female *C. finmarchicus* was higher than the naupliar growth early in the production season during the spring bloom, whereas the naupliar growth was higher during post-bloom situations in May. This might suggest that the females utilized different food items than the nauplia, as suggested by other authors (Hansen et al., 1994; Gismervik et al., 1996), and/or that the females were fueling the reproduction by internal lipid stores. It is noticeable that...
the four dates with the highest IGR_{naup} in nauplii fed natural seawater were situations dominated by small flagellates (Leiknes et al., 2015, submitted). It has been shown that juveniles may become satiated at lower concentrations of available food than adults. Campbell et al. (2001b) showed that the carbon specific IGR for *C. finmarchicus* nauplia (NIII–VI) was 90 % of maximum IGR at a food concentration of 71 μg C L^{-1}. The egg production rates are dependent on food availability, and a recent review (Melle et al., 2014) showed that female *C. finmarchicus* reached 95% of maximum egg production rate at a Chl-a concentration of 1.1–4.6, depending on the sea basin studied. These Chl-a-concentrations corresponds to a biomass of microalgae of 70–292 μg C L^{-1}, using a C:Chl-a conversion factor of 64 μg C:μg Chl-a (Vadstein et al., 2004). In summary, the specific growth rate of the nauplii varied during the seasons because of variations in food quality. The contents of EPA and DHA in the seston were the variables that had the strongest effect on the naupliar growth rate in our study, but no variable explained more than 47 % of the variation in naupliar growth rate. The regression analysis indicated that both the EPA-content and the DHA-content in the food reached saturation (Figure 8). The pronounced difference in IGR between the nauplii fed natural seston compared to cultured algae in periods of the productive season indicated periods of food limitation, either by food quantity or food quality. Food availability, measured by Chl-a or POC, could not explain the variability in growth rate. Our lipid class analyses on eggs from the early spawning of *C. finmarchicus* showed high WE contents and differed from earlier reports on lipid class compositions of eggs. We therefore propose that the *C. finmarchicus* females can pass on WE to the eggs directly without converting WE to TAG, contrary to what is previously reported (Lee et al., 1972). We suggest that further studies should try to evaluate to what extent the growth and mortality of *C. finmarchicus* nauplii is affected by such maternal effects, or if the food quality or food quantity of the first feeding nauplii stages is most important. There were at times big differences between the secondary production estimated by egg production measurements and by somatic growth. This suggests that it is not sufficient to use a single approach to assess the state of the entire copepod community, but that both approaches should be applied. In addition, the wide range of growth rates found in a narrow limit of temperature variation (6.5–9.5 °C) suggested that other factors than temperature alone should be applied in production models.

5 Acknowledgements

We thank the Research Council of Norway for funding through the project Harvest (project number 178447). We thank the captain and crew of R/V Gunnerus and Calanus for smooth cruise operations and Kjersti Rennan Dahl for technical assistance.

6 Author Contributions

SAE and NET provided data from experiments run in 2007, whereas ØL performed experiments in 2009 and 2011. The analytical work was performed by ØL, MB and SE. ØL wrote the paper with comments from the other authors. YO and OV also contributed to the planning of the experiments.
Somatic growth in *C. finmarchicus* nauplii

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Somatic growth in *C. finmarchicus* nauplii


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Somatic growth in *C. finmarchicus* nauplii


Somatic growth in *C. finmarchicus* nauplii


Somatic growth in *C. finmarchicus* nauplii


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Somatic growth in *C. finmarchicus* nauplii


### 8 Tables and Figures

**Table 1.** Size fractions and the percent distribution by biovolume for the fractions selected for fatty acid analysis. *Cosc.* is *Coscinodiscus* and *Prot.* is *Protoperidinium*, N is nauplii, C is copepodites and roman numbers indicates stages.

<table>
<thead>
<tr>
<th>Category</th>
<th>Size fraction (μm)</th>
<th>Distribution (% biovolume)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Protoperidinium</em> sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Coscinodiscus</em> sp.</td>
<td>70–80</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>190–200</td>
<td></td>
</tr>
<tr>
<td>Eggs (17.02.2010)</td>
<td>80–150</td>
<td>84.5</td>
</tr>
<tr>
<td>Eggs (28.02.2010)</td>
<td>80–150</td>
<td>86.7</td>
</tr>
<tr>
<td>Eggs (10.03.2007)</td>
<td>140–150</td>
<td>47.7</td>
</tr>
<tr>
<td>NII-NIII</td>
<td>106–110</td>
<td>2.7</td>
</tr>
<tr>
<td>NIII-NIV</td>
<td>200–300</td>
<td>0.2</td>
</tr>
<tr>
<td>CII-CIII</td>
<td>400–600</td>
<td>0.2</td>
</tr>
<tr>
<td>CIII-CIV</td>
<td>600–1300</td>
<td></td>
</tr>
</tbody>
</table>
Somatic growth in *C. finmarchicus* nauplii

**Table 2.** Experimental dates, incubation temperatures (°C) and concentration of Chl *a* (μg L⁻¹), and particulate organic carbon (POC, μg C L⁻¹) for the growth periods.

<table>
<thead>
<tr>
<th>Growth period</th>
<th>Date (start-end)</th>
<th>Temperature</th>
<th>Chl <em>a</em></th>
<th>POC</th>
</tr>
</thead>
<tbody>
<tr>
<td>GP 1.1</td>
<td>25.03 – 03.04.2007</td>
<td>6.5</td>
<td>4.56 ± 0.19</td>
<td>419 ± 18.2</td>
</tr>
<tr>
<td>GP 1.2</td>
<td>18. – 28.04.2007</td>
<td>6.0</td>
<td>1.72 ± 0.42</td>
<td>226 ± 30.6</td>
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<tr>
<td>GP 1.3</td>
<td>26.04 – 06.05.2007</td>
<td>7.0</td>
<td>2.05 ± 0.19</td>
<td>224 ± 31.8</td>
</tr>
<tr>
<td>GP 1.4</td>
<td>14. – 20.05.2007</td>
<td>9.5</td>
<td>2.07 ± 0.83</td>
<td>186 ± 24.1</td>
</tr>
<tr>
<td>GP 2.1</td>
<td>02. – 11.03.2009</td>
<td>6.5</td>
<td>1.07 ± 0.37</td>
<td>225 ± 49.5</td>
</tr>
<tr>
<td>GP 2.2</td>
<td>19. – 28.03.2009</td>
<td>6.5</td>
<td>1.63 ± 0.07</td>
<td>329 ± 5.2</td>
</tr>
<tr>
<td>GP 2.3</td>
<td>06. – 15.04.2009</td>
<td>6.5</td>
<td>1.09 ± 0.10</td>
<td>288 ± 21.2</td>
</tr>
<tr>
<td>GP 2.4</td>
<td>24.05 – 01.06.2009</td>
<td>7.5</td>
<td>1.53 ± 0.20</td>
<td>294 ± 34.9</td>
</tr>
<tr>
<td>GP 3.1</td>
<td>12. – 21.03.2011</td>
<td>7.0</td>
<td>1.12 ± 0.33</td>
<td>227 ± 19.6</td>
</tr>
<tr>
<td>GP 3.2</td>
<td>29.03 – 07.04.2011</td>
<td>7.0</td>
<td>2.32 ± 0.05</td>
<td>222 ± 18.4</td>
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<td>GP 3.3</td>
<td>01. – 10.05.2011</td>
<td>8.5</td>
<td>5.38 ± 0.03</td>
<td>258 ± 7.1</td>
</tr>
<tr>
<td>GP 3.4</td>
<td>16. – 25.05.2011</td>
<td>7.5</td>
<td>3.81 ± 1.11</td>
<td>nd</td>
</tr>
</tbody>
</table>

### 8.1 Figure legends

**Figure 1.** Fatty acid profiles of the seston, <55 μm. (A): Total content of fatty acids and lipids. (B): Quantitative content (mg g⁻¹ DW) of different groups of fatty acids. Important essential fatty acids (EFAs; DHA and EPA) are separated. (C): Relative content of the different groups of fatty acids (% of total fatty acids).

**Figure 2.** Total lipid and total fatty acids content (mg g⁻¹ DW) in eggs, nauplii and copepodites of *C. finmarchicus* and of the microalgae *Coscinodiscus* sp. and *Protoperidinium* sp.

**Figure 3.** Fatty acid profiles of eggs, nauplii and copepodites of *C. finmarchicus* and of the microalgae *Coscinodiscus* sp. and *Protoperidinium* sp. (A): quantitative fatty acid content (mg g⁻¹ DW), (B): relative content (% of total fatty acids). The samples from 17/2 and from 25/2 contained a fraction of unknown fatty acids not included in the figure.

**Figure 4.** Content of the different lipid classes; phosphatidylethanolamine (PE), phosphatidylcholine (PC), wax ester (WE), triacylglycerol (TAG), and free fatty acids (FFA) in *C. finmarchicus* eggs. (A): Quantitative content (mg g⁻¹ DW). (B): Relative content (% of total lipids). Error bars equals standard error (n = 2).

**Figure 5.** Scatterplot of biovolume-specific growth rates (day⁻¹) through three seasons (Mean ± SE). Filled symbols indicate nauplii fed natural seston (< 55 μm), open symbols indicate nauplii fed cultured algae. Asterisk indicates growth periods where there is a difference between growth of nauplii fed natural seston and cultured microalgae (Student T-test, *p* < 0.05).

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**Figure 6.** Growth in nauplii fed natural seston (d⁻¹) versus nauplii fed cultured microalgae (d⁻¹). Dots indicate average, error bars standard error. Lines indicate linear regression line with 95% confidence interval.

**Figure 7.** Biovolume-specific growth rate (day⁻¹) of nauplii of *C. finmarchicus* versus Chl a < 55 µm (Pearson correlation coefficient 0.497, p = 0.103).

**Figure 8.** Scatterplot of growth rates (day⁻¹, mean ± SE) of nauplii versus (A): the content of EPA and (B): the content of DHA in the seston (mg g DW⁻¹). Lines indicate regressions (2-parameter hyperbola) with 95% confidence intervals.
Figure 1
Figure 2

The graph shows the lipid and fatty acid contents (mg g\(^{-1}\) DW) for different species. The x-axis represents the species names, and the y-axis shows the content levels. Black bars represent total lipids, while gray bars represent total fatty acids. The species include Egg 1702, Egg 2502, Egg 1003, NIL-NII, NII-NIV, CIHCIII, CIHCIV, CV-CV, Protoporphyra, and Coscinodiscus.
Figure 3

(A) Fatty acids, mg g⁻¹ DW

(B) Fatty acids, % of total

Legend:
- DHA
- EPA
- Other n-3
- n-6
- MUFA
- SAT
Figure 6
Paper III
Is not included due to copyright
Paper IV
Feeding selectivity of *Calanus finmarchicus* in the Trondheimsfjord

Øystein Leiknes, Anja Striberny, Nils Egil Tokle, Yngvar Olsen, Olav Vadstein, Ulrich Sommer

**ABSTRACT**

The feeding selectivity of *Calanus finmarchicus* was studied by carrying out three incubation experiments; two experiments with natural seawater sampled during spring bloom (Exp. 1) and post-bloom conditions (Exp. 2) and a third experiment with cultured dinoflagellates and ciliates (Exp. 3). In the first two experiments a gradient in ciliate concentration was created to investigate the potential for prey density dependent selective feeding of *C. finmarchicus*. Results of microplankton counts indicated *C. finmarchicus* to be omnivorous. Diatoms contributed chiefly to the diet during spring bloom conditions. Despite the high microphytoplankton biomass during the spring bloom (Exp. 1), ciliates were selected positively by *C. finmarchicus* when the ciliate biomass exceeded 6.5 μg C L⁻¹. A selection in favor of large conic ciliates such as *Laboea* sp. and *Strombidium conicum* was indicated by positive selectivity indices. Ciliates were throughout positively selected by *C. finmarchicus* during Exp. 2, and selectivity indices indicated a negative selection of diatoms. The results from Exp. 3 showed that *C. finmarchicus* has the ability to switch from dinoflagellates to ciliates as sole food source, even if the dinoflagellate was offered in surplus. This suggests that other factors, such as nutrition may be of significance for the feeding selectivity of *C. finmarchicus*.

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1. Introduction

Exploitation by fisheries, climate change, and other impacts caused by humans can result in changes in the marine environment and thus in the configuration of food webs. Thus, a fundamental understanding of the mechanisms behind energy transfer through the marine food web is essential for sustainable management of marine biological resources. *Calanus finmarchicus* is the dominant copepod in the North Atlantic Ocean (Plarque and Batten, 2000) and plays a crucial role in parameterization of important biological mechanisms. One of the reasons for this is the huge biomass variations in time and space call for developing realistic ecological models to obtain a better understanding of their patterns of abundance and ecology (Carlotti and space call for developing realistic ecological models to obtain a better understanding of their patterns of abundance and ecology (Carlotti and Enright, 2011).

*Calanus finmarchicus* is the dominant copepod in the North Atlantic Ocean (Plarque and Batten, 2000) and plays a crucial role in parameterization of important biological mechanisms. One of the reasons for this is the huge biomass variations in time and space call for developing realistic ecological models to obtain a better understanding of their patterns of abundance and ecology (Carlotti and Enright, 2011).
1955). Thus feeding selectivity represents an additional, complicating factor in the development of ecosystem models. The degree of omnivory and shifts in food selection and feeding behavior have major effects on the trophic linkages and stability of ecosystems, as well as a direct impact on the growth, reproduction and fecundity of C. finmarchicus.

Plasticity in food selectivity depending on food availability and competition has previously been studied in incubation experiments or experiments using either cultured autotrophic and heterotrophic microplankton or natural seston or as food in different locations (Koski, 2007) or in repeated experiments at the same locations (Fileman et al., 2010; Irigoien et al., 1998). A number of feeding experiments with food mixtures prepared from cultures have demonstrated a preference of various copepod species for ciliates, even when the biomass of ciliates is low compared to that of phytoplankton. This has been demonstrated for Centropages hamatus (Saage et al., 2009) and for Acartia tonsa (Stoecker and Egloff, 1987).

The present study focuses on the feeding selectivity of C. finmarchicus. Our main objective was to study if and in case how the proportion of ciliates in the food affected the feeding selectivity of C. finmarchicus. We have used an innovative bubbling technique to manipulate the ciliate:phytoplankton ratio in the natural seston during spring bloom and post-bloom situations. The results of the feeding selectivity experiments using natural seston are compared to an experiment where C. finmarchicus were offered cultured dinoflagellates and ciliates.

2. Material and methods

Three different feeding experiments were conducted. Two experiments involved the use of natural seawater sampled during the spring bloom (Exp. 1) and the following post-bloom situation (Exp. 2). During both these experiments, a gradient in the ratio of ciliate to phytoplankton was set up. In a third experiment (Exp. 3), we used cultures of the dinoflagellate Karlodinium veneficum (formerly known as Gymnodinium galatheanum) and the ciliate Pelagodinobdella spirale (formerly known as Strobilidium spirale). The dinoflagellate was offered in constant and excess concentrations while the ciliate was given in varying concentrations.

2.1. Experimental set-up

In Exp. 1 and Exp. 2 the feeding selectivity of individuals of C. finmarchicus was studied by conducting two 24 h incubation experiments at Trondheim Biological Station. Zooplankton was sampled in the Trondheimfjord at the station “Froset” (63° 29' N, 10° 18' E, depth: 450 m) from the research vessel "F/F Gunnerus" using a standard WP 2 net (70 cm opening width, 180 μm mesh size) which was hauled vertically from 100 m depth to the surface. Female and copepodite V individuals of C. finmarchicus were carefully picked with a plastic pipette and stored in Petri dishes filled with filtered seawater until the start of the experiment. The copepods were starved for three days in filtered seawater prior to the start of Exp. 1, and for two days before the start of Exp. 2. Seawater with natural seston was sampled from a 3 m depth at the pier of Trondheim Biological Station at the 10th (Exp. 1) and at the 30th (Exp. 2) of April. The water was screened through a 200 μm (Exp. 1) or 100 μm (Exp. 2) mesh on the starting day of Exp. 1 and one day before the starting day of Exp. 2. The sampled water was divided into two separate containers. One half of the sampled water was not further treated and left at incubation temperature in darkness until the start of the incubation (untreated water). The other half of the seawater was bubbled with air to reduce the biomass of ciliates (treated water). Silicon tubes were placed at the bottom of the container, and heavy air bubbling was provided with a compressor system designed to provide air rift in algae cultures. To establish a gradient of ciliates, treated seawater and untreated seawater were mixed at seven different ratios in acid washed Pyrex bottles with a volume of 10 L. Each of the seven treatments consisted of one control bottle with no added C. finmarchicus and three bottles containing eight to ten individuals of C. finmarchicus (28 bottles in total). Prior to the start of the experiment, the state of health of each individual copepod was examined in a dissecting microscope. Dead animals and those appearing to be in bad condition were removed from the incubation.

The incubation of the bottles lasted for 24 h in darkness at 14 °C. Sedimentation of microalgae was prevented by gently stirring the samples manually every 4 h. Time zero samples (T₀) and samples from the controls and bottles with added C. finmarchicus were taken using a rubber hose. The samples were fixed with acid Lugol's iodine to a final concentration of 1% and stored in brown glass bottles (300 ml) until further analysis. The remaining seawater was poured through a 200 μm sieve to capture the copepods. The condition of each copepod was checked in a dissecting microscope. Dead copepods were excluded from the experiment. The average mortality of C. finmarchicus in Exp. 1 was 20%. In Exp. 2, the mortality was zero in most incubation bottles, but one bottle exhibited 20% mortality.

In Exp. 3, C. finmarchicus stage CV was collected from a landlocked bay (Hovpåvågen) outside the Trondheimfjord using a vertically towed plankton net. The cod end was replaced with a 2 L plastic bag to minimize mechanical damage to the animals. The phytoplankton prey, the dinoflagellate K. veneficum (size 10-12 μm) was maintained in a culture with Guillard's F/2 medium (Guillard and Ryther, 1962).

The culture was held at a maximum growth rate, not limited by essential nutrients, minerals or vitamins. The ciliate prey, P. spirale, was maintained at an exponential growth rate in IMR/2 growth medium (Eppley et al., 1969), and fed the cryptophycean Hemiselmis sp. GF/F filtered seawater and a mixture of ciliates and phytoplankton from stock cultures to a final volume of 200 ml and one individual of C. finmarchicus were added to glass containers (250 ml). Phytoplankton was offered at a high and constant concentration above the copepods' need for maintaining maximum ingestion rate (>120 μL C L⁻¹), whereas the ciliates were offered in a gradient from 5 to 50 μL C L⁻¹. The prey gradients consisted of five different feeding solutions, each replicated three to five times. The incubations lasted for 4–7.5 h at 15 °C. Controls included incubations without copepods.

2.2. Microplankton counts and biomass estimation

The enumeration of ciliates and phytoplankton in all three experiments was undertaken according to Utermöhl (1958) using 50 mL sedimentation chambers and a settling time of at least 24 h. It was aimed to count at least 100 cells of each taxonomic group. However, this was not always possible due to the low abundances of some species. If the sample contained < 100 individuals, the whole sample was counted. In Exp. 1 and 2, phytoplankton and ciliates were identified and categorized systematically. Within each taxonomic group, cells were further classified according to shape and size. All samples were counted in phase contrast mode in an inverted microscope (Axiovert 200 M, Carl Zeiss, Jena, Germany). Depending on the density of cells, different areas were counted at different magnifications (ciliates: 200×; phytoplankton depending on size and density: 100–400×).

For biomass calculations, pictures were taken using the Carl Zeiss AxioCam and processed using the program AxioVision 4.6.3 (Carl Zeiss, Jena, Germany). Twenty pictures (fewer for less abundant species/groups) for each group counted were taken at the highest possible magnification. Linear dimensions were determined with the image processing program ImageJ (Rasband, 1997–2009). Biovolume was calculated from the median of the linear dimensions by applying simple geometric shapes to the organisms (Hillebrand et al., 1999; Kragberg et al., 2010; Olenina et al., 2006).

In Exp. 3, ciliates and phytoplankton were quantified in a Leica (DM IRB) microscope. Phytoplankton was quantified using image...
analysis software (ImageJ). Six random images were obtained (resolution 1024 × 768 pixels) from each sedimented phytoplankton sample using a firewire camera (Sony DFW-X700) connected to the microscope. Each image contained 100 to 1000 individual phytoplankton cells.

The biomass of aloricate ciliates was converted to carbon by the regressions of Pütz and Stockeberg (1989), the biomass of loricate ciliates according to Verity and Langdon (1984), and the biomass of diatoms, dinoflagellates, and small flagellates according to Menden-Deuer and Lessard (2000).

2.3. Calculation of ingestion rates and selectivity indices

The prey biomass (B) in the incubation bottles was calculated as the geometric mean of the microplankton concentration at T0 and Tt. Grazing coefficients, clearance rate (CRt), and ingestion rates (I) were calculated after Frost (1972). For Exp. 3, we used a modified version of Frost’s equation (Lucas, 1982) and calculated the individual clearance rates on phytoplankton (CRphyto) and ciliates (CRcil) as:

$$CR_{\text{phyto}} = \left( \frac{\ln(C_{p1}/C_{p2})}{\ln(C_{p1}/C_{p2})} \right) \times V/n$$

$$CR_{\text{cil}} = \left( \frac{\ln(C_{c1}/C_{c2})}{\ln(C_{c1}/C_{c2})} \right) \times V/n.$$  

$C_{p1}$ and $C_{p2}$ are the phytoplankton concentrations (μg C L$^{-1}$) in the control bottles and in the bottles containing copepods, $C_{c1}$ and $C_{c2}$ are the ciliate concentrations (μg C L$^{-1}$) at the start and termination of the experiments, and $n$ is the number of the microplankton concentration during the incubation.

The ingestion rate (I) was calculated as the product of B and CR, and expressed in terms of μg C L$^{-1}$ day$^{-1}$. The biomass of diatoms (Table 1) was in excess for ciliates, as in Exp. 3. V is the incubation volume of 0.5 mL μg ciliate C h$^{-1}$ was applied when the phytoplankton concentration was in excess for ciliates, as in Exp. 3. $V$ is the incubation volume and $n$ is the number of C.finnarucis. $C_{e}$ is the weighted average ciliates concentration during the incubation.

The ingestion rate (I) was calculated as the product of B and CR, and expressed in terms of μg C L$^{-1}$ day$^{-1}$. Feeding preferences of C.finnarucis were assessed with the selectivity index D calculated after Jacobs (1974).

3. Results

3.1. Composition of the microplankton assemblages during the incubation experiments

Exp. 1 was conducted under bloom conditions and Exp. 2 during post-bloom conditions, which involved different starting conditions in terms of biomass and taxonomic composition. The microplankton biomass in Exp. 1 was around 200 μg C L$^{-1}$ and almost one order of magnitude higher than during Exp. 2 when the concentration was around 25 μg C L$^{-1}$ (Table 1). In both experiments the ciliate concentration was manipulated by bubbling the water with air. The success in removal of ciliates varied between Exp. 1 and 2. In Exp. 1, a gradient in biomass was created for all groups of ciliates, ranging from 1.4 to 12.2 μg C L$^{-1}$ (1.0–5.6% of total microplankton biomass) (Table 1). The reduction of ciliates by bubbling was less efficient in Exp. 2. The numbers of Strombidium conicum were strongly reduced by the bubbling, whereas the abundance of Myrionecta rubrum was not affected. During Exp. 2 the range for ciliate biomass was 3.0 to 12.0 μg C L$^{-1}$ (190–48.1% of total microplankton biomass). The bubbling also affected other groups, especially flagellates and diatoms in Exp. 1. The flagellates in Exp. 1 showed gradually increased biomass from treatments 1 to 7. The diatom biomass was lowest in Exp. 1, but did not show the same gradual increase as the ciliates and the flagellates (Table 1).

The microplankton assemblage of Exp. 1 was dominated by chain forming, centric diatoms such as Chaetoceros spp. and Thalassiosira spp., constituting on average 87% of the total microplankton biomass. Pennate diatoms were mainly represented by Pseudo-nitzschia seriata complex, Pseudo-nitzchia delicatissima complex, Thalassionema spp., and Navicula spp. Thecate dinoflagellates such as Ceratium flumineum, Dinophysis spp., and individuals of the order Peridiniales were observed at low abundance. Athecate dinoflagellates of different shapes and size classes ranging from Gyrodinium sp. >80 μm to individuals of the order Gymnodiales <20 μm were also present. The biomass of di- 

<table>
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<th>Flagellates</th>
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<td>200 (89.8)</td>
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<tr>
<td>7</td>
<td>12.2 (5.0)</td>
<td>10.7 (48.1)</td>
<td>169 (82.5)</td>
<td>3.5 (15.8)</td>
</tr>
</tbody>
</table>
around 5%. The dinoflagellates were in general consumed according to availability, but were consumed more efficiently than they were available for treatments 3 and 5 (Fig. 1c and e). Flagellates contributed 5% to the total microplankton biomass (Fig. 1), and were generally consumed in lower or equal proportions as their availability. Overall, there were very few instances where the proportion of food eaten differed from what was offered during Exp. 1.

Although ciliates had a percentage contribution of less than 5% compared to the total biomass offered to C. finmarchicus throughout the treatments, they were in general represented in the diet. In untreated seawater, the percentage contribution of ciliates to the diet of C. finmarchicus was six times higher than their fraction of the available prey (Fig. 1g).

In untreated fjord water in Exp. 2 (Fig. 2g), ciliates contributed to nearly 50% of the microplankton biomass, but also in the treated seawater ciliates formed a large part of the total biomass (Fig. 2a). Thecate and athecate dinoflagellates had a higher relative abundance in the food available than in Exp. 1, and the diet of C. finmarchicus in Exp. 2 constituted mainly dinoflagellates (around 30% of diet) and ciliates (around 50% of diet). Although not significant for all treatments, the proportion of ciliates consumed by C. finmarchicus were higher than the relative fraction of ciliates offered in their food. Diatoms contributed around 20% in the supplied food offered in Exp. 2, but constituted only around 10% to the consumed food (average of all treatments). Flagellates formed for most of the treatments a smaller part of the consumed food of C. finmarchicus compared to what was offered.

When all the data for Exp. 1 and 2 are plotted in the same scatterplot, it becomes evident that the dinoflagellates were consumed in the same proportions as they were offered in the diet, following the 1:1 line (Fig. 3a). Small flagellates were generally consumed in a lower proportion compared to that offered, and they constituted a generally small part of the consumed food particles (Fig. 3b). Diatoms were generally consumed in fractions according to their availability, and never in a higher proportion compared to what was offered (Fig. 3c).

In Exp. 1 and 2, C. finmarchicus ingested ciliates in the proportion they were offered when the ciliates were low in biomass compared to other food items. Above a certain proportion of around 5% of total feed, the ciliates were cleared at higher rates compared to other possible food items (Figs. 1g, 3d).

The feeding pattern of C. finmarchicus in Exp. 3 showed a similar pattern (Fig. 4), but in this case it switched to consume ciliates as almost the only food source when the ciliate concentration exceeded 3% of the total food concentration. This was despite the fact that phytoplankton concentrations were above saturation level (>120 μg C L⁻¹), and that change in feeding strategy resulted in a reduction of total ingested carbon.

C. finmarchicus showed a preference for big ciliates in all the treatments where the ciliates were selected, i.e. the treatments with more than 5% ciliates of total food offered. Small ciliates of the Strobilidium spp. and M. rubrum and conic ciliates <30 μm were ingested in proportion to their concentration in the environment. In contrast, the big size classes of M. rubrum and especially the conic ciliates >35 μm made a larger contribution to the consumed food; 12% consumed versus 7% in the food offered (average of all the treatments in Exp. 2).

3.3 Selectivity indices

The selectivity indices for the most important groups of prey of C. finmarchicus are given in Table 2. Dinoflagellates and flagellates were not included in Table 2 because the selectivity index was never significantly different from 0 (t-test, P > 0.05). The selectivity index in Exp. 1, in which a high food concentration was offered, varied from 0.56 to 0.20 for diatoms with no selection significantly different from zero. There was no clear influence of the ciliate concentration on the selectivity index for diatoms. However, when we calculated the selectivity index for the diatom Thalassiosira spp. a clear positive selection was found in treatments with low ciliate concentration. The selectivity
Conic ciliates were positively selected by C. fmarchicus during feeding experiment 1, low ciliate biomass with 3 μm showed neutral selection (D = 0.06 in treatment 6, which showed a medium ciliate biomass of 6.4 μg C L⁻¹, to D = 0.61 in treatment 7, which showed the highest ciliate biomass of 12.2 μg C L⁻¹ (Table 1). When the concentration of conic ciliates >35 μm was low, C. fmarchicus did not feed on this particular group.

The selectivity indices for diatoms during Exp. 1 ranged from D = −0.4 in treatment 6, which showed a medium ciliate biomass of 6.4 μg C L⁻¹, to D = 0.61 in treatment 7, which showed the highest ciliate biomass of 12.2 μg C L⁻¹ (Table 1). When the concentration of conic ciliates >35 μm was low, C. fmarchicus did not feed on this particular group.

The selectivity indices for diatoms in Exp. 2 where a low food concentration was offered, showed neutral selection (D = 0.06 in treatment 1, low ciliate biomass with 3 μg C L⁻¹) to significant negative selection (D = −0.07 in treatment 7, with high ciliate biomass and a high fraction of conic ciliates >35 μm) of diatoms by C. fmarchicus. Ciliates were positively selected by C. fmarchicus, although not significantly for all treatments. Large conic ciliates were ingested preferably by C. fmarchicus, as shown by significant positive selection indices for all treatments in Exp. 2 and for the treatment with the highest ciliate biomass in Exp. 1. Overall, C. fmarchicus showed neutral selection for most groups during Exp. 1, but we observed a shift from neutral selection to significant positive selection for conic ciliates >35 μm. This coincided with a switch from positive to negative selection for Thalassiosira spp. During Exp. 2 we observed neutral selection for dinoflagellates and flagellates, positive selection for conic ciliates >35 μm and negative selection for diatoms.

4. Discussion

The differences of the microplankton community composition and biomass between Exp. 1 and Exp. 2 follow a common pattern for the shift from bloom to post-bloom conditions. After the depletion of nutrients, the diatoms vanished, and the total biomass decreased. Heterotrophic dinoflagellates and ciliates remained in the water column. The differences in biomass between Exp. 1 and 2 entail a change from what is considered as saturating for ingestion by copepods in Exp. 1 to conditions of severe food limitation in Exp. 2 (Campbell et al., 2001; Saage, 2006).

The treatment of natural seawater with air bubbles in order to manipulate the ciliate concentration is, to our knowledge, a new method. It is already known that both screening of water and fixation are potential loss factors for ciliate abundance (Atienza et al., 2006; Gifford, 1985; Saiz and Calbet, 2011). The sensitivity of ciliates to mechanical disturbance seemed to differ from species to species. Conic ciliates >35 μm were more sensitive to the disturbance than M. rubrum. Because a larger part of the ciliate biomass consisted of M. rubrum in Exp. 2 than in Exp. 1, it was not possible to create the same ciliate gradient during Exp. 2 as in Exp. 1. On average 43% of the ciliate biomass in Exp. 2 was M. rubrum whereas it was only 0.6% of the ciliate biomass in Exp. 1. To our knowledge, there are so far no previous records on the physical fragility of different ciliate species other than reports on tintinnids being more resistant to sampling by nets due to their protective lorica (Gifford, 1985, 1993).

During Exp. 1 the diatoms were dominating and C. fmarchicus ingested diatoms according to their abundance, as seen from the neutral selectivity indices (Table 2). The neutral selection for diatoms contradicts the findings of Meyer-Harms et al. (1999) who reported a positive selection for diatoms and dinoflagellates by C. fmarchicus in the Norwegian Sea during pre-, bloom, and post-bloom conditions. However, the positive selection reported here for Thalassiosira spp. is in accordance with their results. These results emphasize that the selectivity calculated for low taxonomic levels can lead to erroneous conclusions.

Dinoflagellates were consumed more or less according to availability and constituted an essential part of the diet during Exp. 2, but were of minor importance during Exp. 1. Flagellates were of minor importance during both experiments, and did not contribute to more than 10% of the diet consumed.
the diet. We have not adjusted for ciliate grazing on the flagellates during Exp. 1 and 2, as described in Nejstgaard et al. (1997). This was partly because the flagellate biomass was rather low, and because the ciliate biomass consisted of both heterotrophic and mixotrophic ciliates of different size classes.

A switch in feeding strategy with increasing proportion of ciliates would give a sudden increase in % ciliates eaten compared to what was offered. This was more conspicuous in Exp. 3 than in Exp. 1 and 2. One reason for this might be that Exp. 1 and 2 were 24 hour incubations, while incubation times of 4–7 h were used in Exp. 3. If *C. finmarchicus* selects ciliates over other food items at a certain ciliate fraction in the food, we may have experienced a situation where *C. finmarchicus* initially selected ciliates, but switched back to feeding on phytoplankton when the ciliate abundance became lower than the critical limit.

*C. finmarchicus* showed a positive selection for ciliates in treatment 7, Exp. 1 (= natural seawater, no bubbling, Table 2) and a simultaneous negative selection for diatoms. However, if we include the data from Exp. 2, the % eaten versus % ciliates offered did not level off from the 1:1 line for the experiments using natural seawater (Fig. 3d). The selectivity indices were significantly positive for ciliates only for three of the treatments in Exp. 2. However, we found clear positive selectivity indices for conic ciliates >30 μm, in agreement with previous investigations (Nejstgaard et al., 1997).

Other investigations have shown that *C. finmarchicus* has a positive selection for their own nauplia (Basedow and Tande, 2006; Bonnet et al., 2004), indicating that *C. finmarchicus* has to be able to alter its foraging tactic from suspension feeding mode to predatory feeding mode (Tiselius and Jonsson, 1990). Certain ciliate species have shown lower...
Table 2
Mean selectivity index D for the different treatments of the feeding experiments. The selectivity index is calculated after Jacobs (1974), and ranges from −1 to +1. D = 0 means no selective feeding behavior. D > 0 means a positive selective feeding behavior. SE = standard error. Bold values indicate selectivity indices significantly different from 0 (one-sample t-test, P < 0.05).

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<th>Diatoms</th>
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<td></td>
<td>D ± SE</td>
<td>D ± SE</td>
<td>D ± SE</td>
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Acknowledgments
We thank the Research Council of Norway for funding through the project Harvest (project number 178447). We thank the captain and the crew of R/V Gunnerus for smooth cruise operations.

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Bjørn Åge Tømmerås
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Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction

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Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care

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Breeding strategies in birds: Experiments with the Magpie Pica pica

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Alginate gel media for plant tissue culture

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Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic char: Effect of temperature, salinity and season

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Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (Salmo salar) and brown trout (Salmo trutta): A summary of studies in Norwegian streams

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1993 Morten Bakken Dr. scient Zoology Host adaptations towards brood parasitism by the Cockoo
1993 Arne Moksnes Dr. philos Zoology Growth and nitrogen status in the moss Dicranum majus Sm. as influenced by nitrogen supply
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Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment

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The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania

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Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria x ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*

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Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage

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Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples

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Dynamics of Genetic Polymorphisms

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Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period

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Functional characterisation of olfactory receptor neurone types in heliothine moths

2005 Erlend Kristiansen Dr. scient Biology
Studies on antifreeze proteins

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Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations

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Motor control of the upper trapezius

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Interactions between marine osmo- and phagotrophs in different physicochemical environments

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Implications of mate choice for the management of small populations

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Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia

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Salmonid fishes in a changing climate: The winter challenge

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Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana

2005 Kjartan Østby Dr. scient Biology
The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006 Kari Mette Murvoll ph.d Biology
Levels and effects of persistent organic pollutants (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?

2006 Ivar Herfindal Dr. scient Biology
Life history consequences of environmental variation along ecological gradients in northern ungulates

2006 Nils Egil Tokle ph.d Biology
Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*

2006 Jan Ove Gjershaug Dr. philos Biology
Taxonomy and conservation status of some booted eagles in south-east Asia

2006 Jon Kristian Skei Dr. scient Biology
Conservation biology and acidification problems in the breeding habitat of amphibians in Norway

2006 Johanna Jænegren ph.d Biology
Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
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<td>Camilla Kalvatn Egest</td>
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<td>The Evolvability of Static Allometry: A Case Study</td>
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<td>AHM Raihan Sarker</td>
<td>ph.d Biology</td>
<td>Conflict over the conservation of the Asian elephant (<em>Elephas maximus</em>) in Bangladesh</td>
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<td>Gro Dehl Villanger</td>
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<td>Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals</td>
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<td>Simen Pedersen</td>
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<td>Mohsen Falahati-Anbaran</td>
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<td>Evolutionary consequences of seed banks and seed dispersal in <em>Arabidopsis</em></td>
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<td>Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance</td>
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<td>Irja Ida Ratikainen</td>
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<td>Aleksander Handå</td>
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<td>Reproductive and migratory challenges inflicted on migrant brown trout (<em>Salmo trutta</em> L) in a heavily modified river</td>
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<td>Maria Bergvik</td>
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<td>Bjarte Bye Lofaldi</td>
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<td>Optimal performance in the cold Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs</td>
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<td>Tonje Aronsen</td>
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<td>Demographic, environmental and evolutionary aspects of sexual selection Molecular genetic investigation of cell separation and cell death regulation in <em>Arabidopsis thaliana</em></td>
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<td>Jørgen Rosvold</td>
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<td>Marit Linnerud</td>
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<td>Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (<em>Salmo salar</em>) farming Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia</td>
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<td>Anders Foldvik</td>
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<td>Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night</td>
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<td>Factors influencing African wild dog (<em>Lycaon pictus</em>) habitat selection and ranging behaviour: conservation and management implications</td>
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<td>Michael Puffer</td>
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<td>Håkon Holand</td>
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<td>Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants</td>
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<td>Leila Alipanah</td>
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<td>Magni Olsen Kyrkjæide</td>
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<td>Genetic variation and structure in peatmosses (<em>Sphagnum</em>)</td>
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<td>Phospholipids in Atlantic cod (<em>Gadus morhua</em> L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis</td>
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<td>The role of the copepod <em>Calanus finmarchicus</em> in affecting the fate of marine oil spills</td>
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<td>Evolution by natural selection in age-structured populations in fluctuating environments</td>
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<td>The effect of nutrition on important life-history traits in the marine copepod <em>Calanus finmarchicus</em></td>
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