ISBN 978-82-326-1446-2 (printed ver.)
ISBN 978-82-326-1447-9 (electronic ver.)
ISSN 1503-8181

Øystein Leiknes
Doctoral thesis

Doctoral theses at NTNU, 2016:54

Øystein Leiknes

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

Doctoral theses at NTNU, 2016:54

NTNU
Norwegian University of
Science and Technology
Thesis for the Degree of
Philosophiae Doctor
Faculty of Natural Sciences and Technology
Department of Biology

NTNU

NTNU
Norwegian University of
Science and Technology

NTNU
Norwegian University of
Science and Technology

Øystein Leiknes

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

Thesis for the Degree of Philosophiae Doctor

Trondheim, March 2016

Norwegian University of Science and Technology
Faculty of Natural Sciences and Technology
Department of Biology

NTNU
Norwegian University of
Science and Technology

NTNU
Norwegian University of Science and Technology

Thesis for the Degree of Philosophiae Doctor

Faculty of Natural Sciences and Technology
Department of Biology

ISBN 978-82-326-1446-2 (printed ver.)
ISBN 978-82-326-1447-9 (electronic ver.)
ISSN 1503-8181

IMT-report 2016:54

Doctoral theses at NTNU, 2016:54

Printed by NTNU Grafisk senter

Contents

Acknowledgements

This work was carried out at the Department of Biology of the University of Science and Technology (NTNU). Financial support was provided by the Research Council of Norway through the project Harvest (project number 178447). I first of all would like to thank my supervisors; professors Yngvar Olsen and Olav Vadstein. They have provided me with great advice during planning of experiments and field work, and with crucial input to papers. Without their patience this thesis would not have been possible to finalise.

I would like to thank all the co-authors for the collaboration during field and laboratory work and for input to the compilation of papers: Dr Maria Bergvik for joining me on field work conditions spanning from extreme cold and windy days to sampling in bright sun with subsequent picking of *Calanus* for lipid analyses and egg production experiments. I thank Anja Striberny for collaboration during feeding experiments, for excellently taking care of microplankton counts and for fruitful discussions during data processing and writing of the feeding selectivity paper. Dr Nils Egil Tokle provided data to complete this paper and also helped with planning of the project Harvest and my field work. Siv Anina Etter provided data and advice to the paper on growth on *Calanus finmarchicus* and also helped during some of the sampling.

The analytical part of the work was performed both at NTNU and SINTEF Fisheries and Aquaculture. I am grateful for the help from Siv Anina Etter, Kjersti Andresen, Marte Schei and Kjersti Rennan Dahl for help with chemical analyses. The captain and crew of R/V Gunnerus were always helpful and tried their best to help executing the sampling according to plans. The staff and students at Trondhjem Biological Station (TBS) have provided me with a superb working environment.

Finally, I would like to thank my family and friends for being there for me during the ups and downs that comes with being a PhD candidate. My kids, Stine, Lars, Randi and Even have shown great patience during my travels, late evenings at the lab and the occasional absent-mindedness during the writing process. You give me balance in life at times where the welfare of the *Calanus* population seems to be the centre of the universe. Last, but not least, thank you to my beloved wife Irene for always loving and supporting me. Without your support, I don't know how I could have managed to finish my thesis. I love you.

Øystein Leiknes
Trondheim, November, 2015

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.

II. Leiknes Ø., Etter, S.A., Tokle, N.E., Bergvik, M., Vadstein, O., Olsen, Y. The effect of essential fatty acids for the somatic growth in nauplii of *Calanus finmarchicus*. Submitted.

III. Bergvik, M., Leiknes, Ø., Altin, D., Dahl, K.R., Olsen, Y. (2012) Dynamics of the Lipid Content and Biomass of *Calanus finmarchicus* (copepodite V) in a Norwegian Fjord. Lipids, 47:881–895.

IV. Leiknes, Ø., Striberny, A., Tokle, N.E., Olsen, Y., Vadstein, O., Sommer, U. (2014) Feeding selectivity of *Calanus finmarchicus* in the Trondheimsfjord. Journal of Sea Research, 85:292–299.

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 most 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).

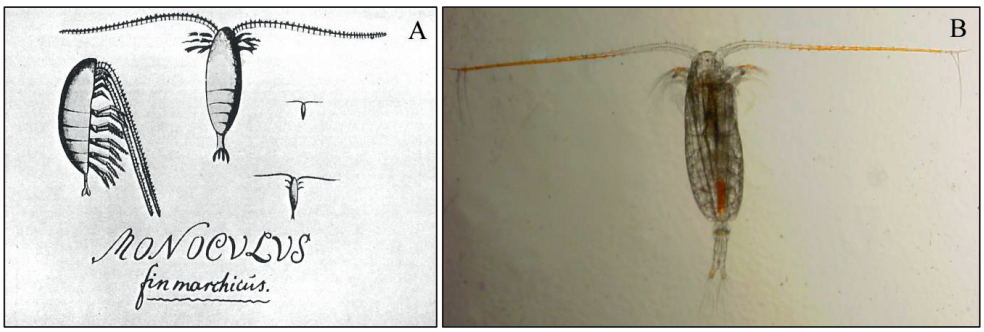


Figure 1. The first drawing of *Calanus finmarchicus* made by Gunnerus (A) and picture of a female *Calanus finmarchicus* (B).

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 CO_2 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 (Bagoien *et al.*, 2001; Skreslet *et al.*, 2000; Sømme, 1934; Strømgren, 1971; Strømgren, 1974; Tande, 1982; Wiborg, 1954). *Calanus finmarchicus* grows through successive moults 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 (Sømme, 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).

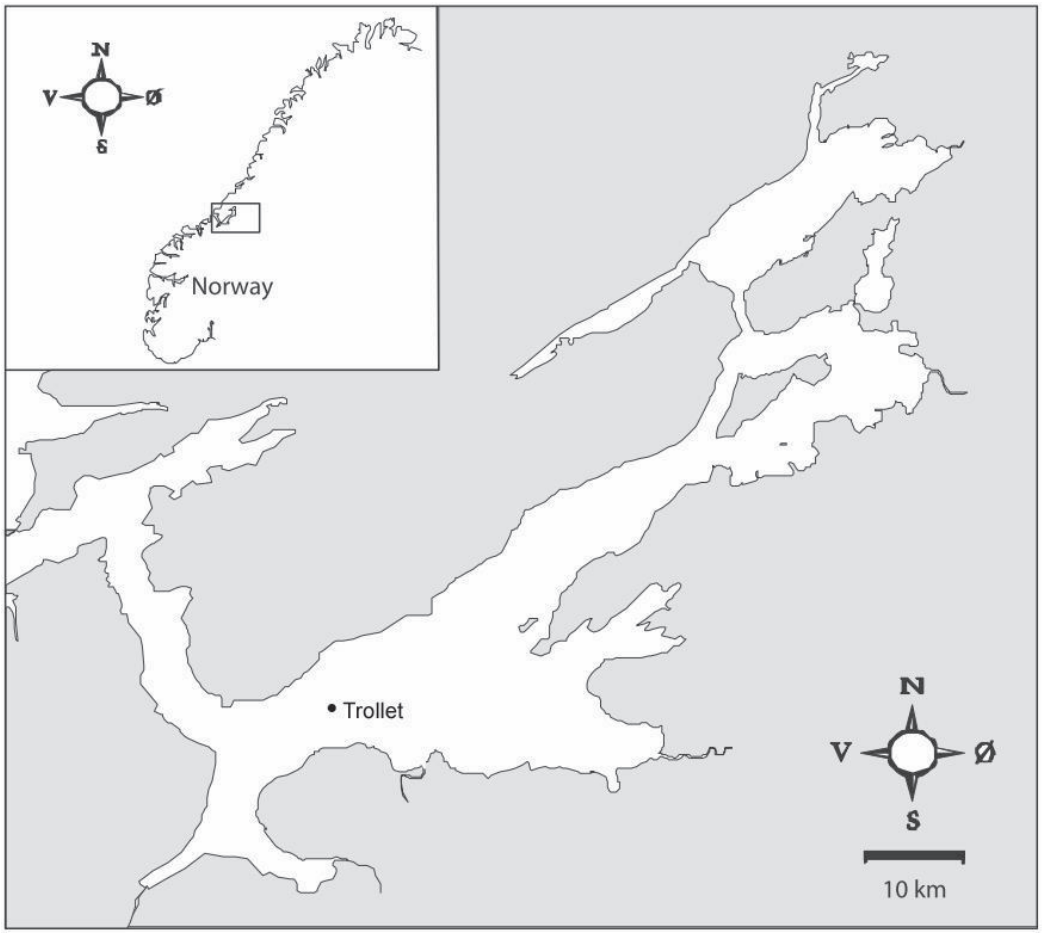


Figure 2: Map of the Trondheimsfjord. Sampling station "Trollet" (63°29'N, 10°18'E) is situated in the middle of the main fjord basin. The depth at "Trollet" is 400 metres.

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 (Kiørboe & 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.*,

2006). 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 *C. finmarchicus*. If the reproduction and subsequent growth of the *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 *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 *C. finmarchicus*. The main objective was to evaluate to what extent nutrition influence the reproduction, growth, lipid accumulation and feeding in *Calanus finmarchicus*.

The reproductive biology of *C. finmarchicus* in the Trondheimsfjord was studied through three consecutive seasons (2009–2011) (Paper I). *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 *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 *C. finmarchicus*, the food quantity and food quality was surveyed. The food quantity was monitored by measuring chlorophyll *a* (chl*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 *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 *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 *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).

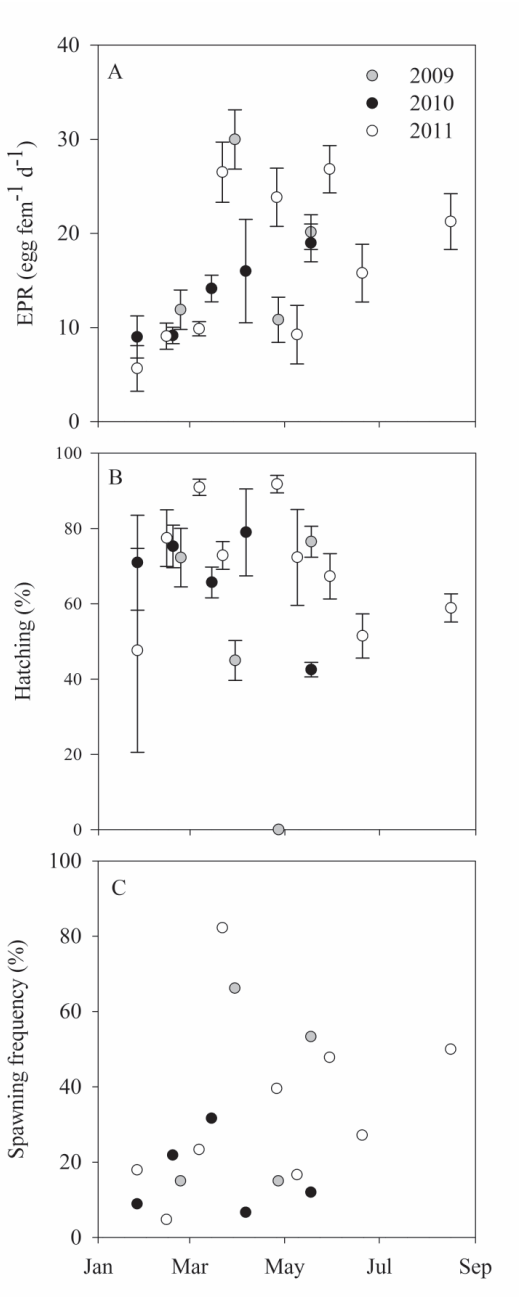


Figure 3: Reproductive rates of *Calanus finmarchicus* sampled in 2009–2011. A: Egg production rate (EPR, number of eggs produced female^{-1} day^{-1}); B: Hatching success (percent hatching per sampling day, mean ± SE); C: Spawning frequency (% of females spawning). Bars express 1 SE.

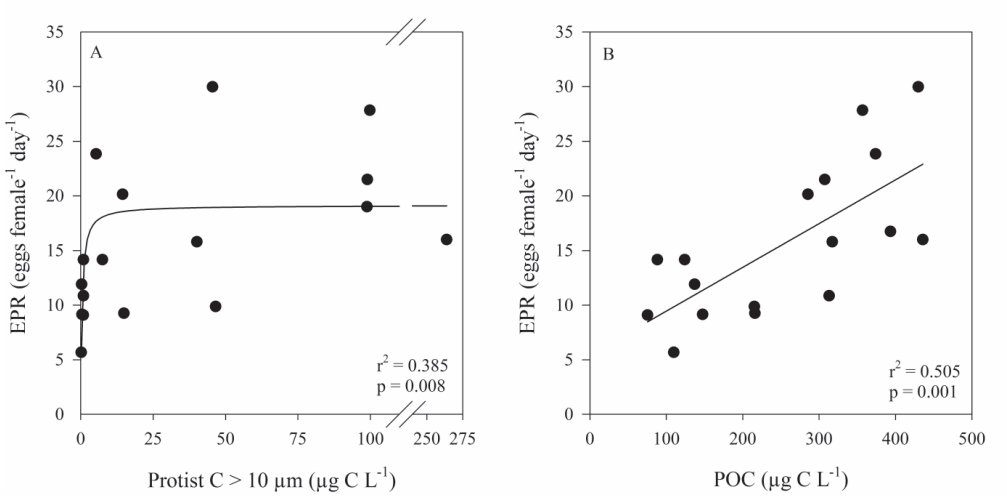


Figure 4. A: EPR of *Calanus finmarchicus* females as a function of food concentration measured as A: Protist C >10 µm and B: Concentrations of POC < 200 µm. Figure taken from Paper I.

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 $^{-1}$ 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.

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;

Mayor *et al.*, 2006; Richardson *et al.*, 1999). 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.

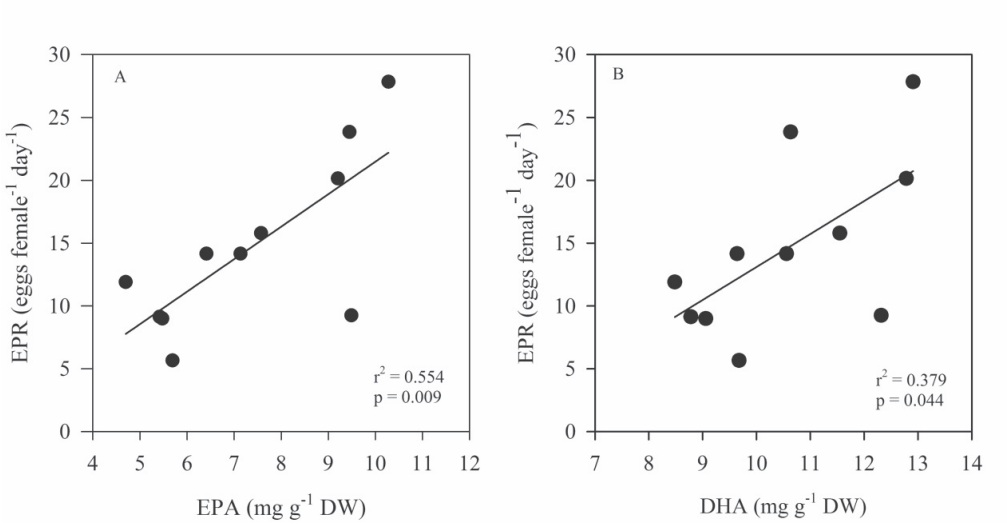


Figure 5. EPR of *C. finmarchicus* females as a function of female fatty acid content. A: Concentration of EPA (mg EPA g^{-1} DW). B: Concentration of DHA (mg g^{-1} DW). Figure taken from Paper I.

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 copepodites (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.*,

1996). 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).

C. 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 ($P < 0.05$).

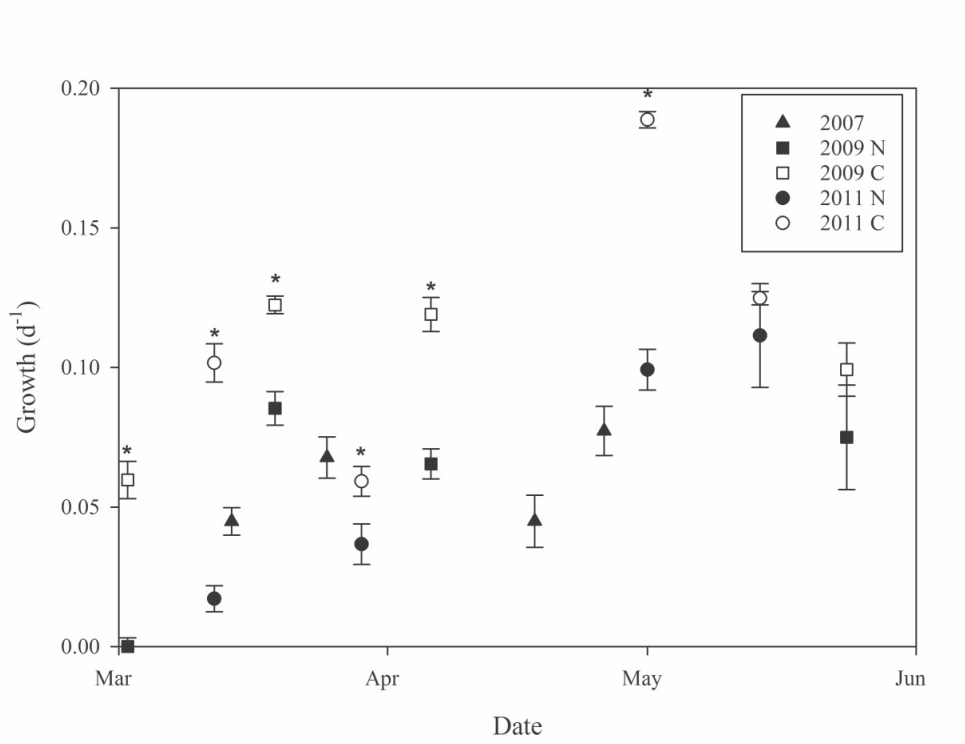


Figure 6. Biovolume-specific growth rates (day^{-1}) of *C. finmarchicus* nauplii through specified seasons in 2007–11 (Mean ± SE). Filled symbols indicate nauplii fed natural seston (< 55 µm), open symbols indicate nauplii fed cultured algae (Labelled N and C, respectively). Asterisk indicates growth periods where there was a significant difference between growth of nauplii fed natural seston and cultured microalgae (Student T-test, $p < 0.05$). Figure taken from Paper II.

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 ± 1.28, $p = 0.043$, DHA: $r^2 = 0.472$, half-saturation constant (K) = 0.732 ± 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*.

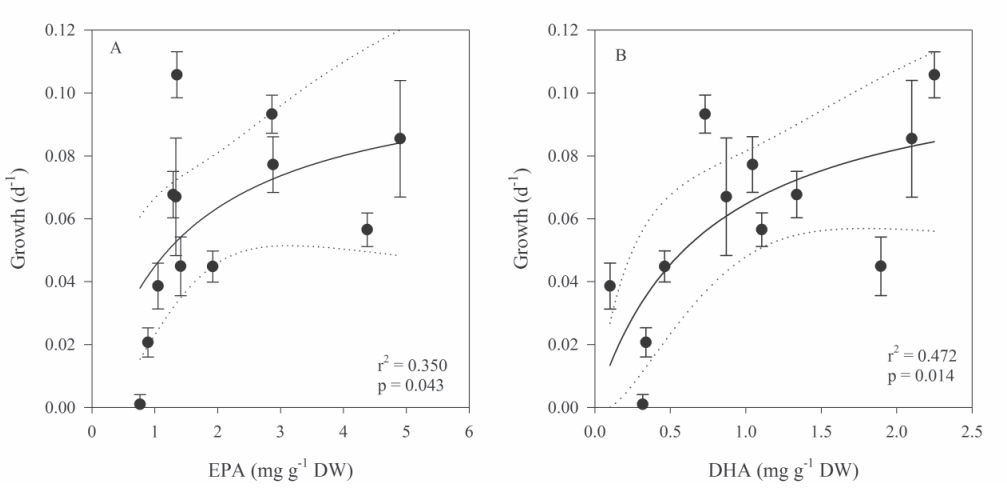


Figure 7. Growth rates (day^{-1}, mean ± SE) of nauplii *versus* A: the content of EPA and B: the content of DHA in the seston (mg g^{-1} DW). Lines indicate regressions with 95% confidence limits. Figure taken from Paper II.

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, moulting 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).

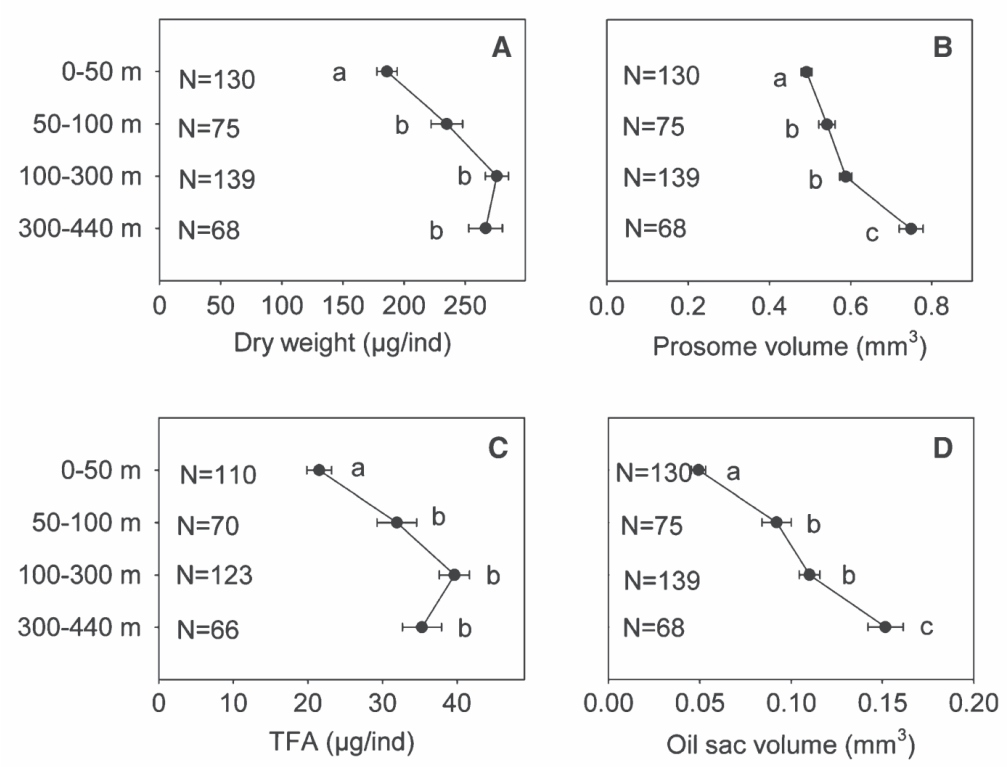


Figure 8. Average dry weight (µg ind^{-1}) (A), prosome volume (mm^3) (B), TFA (µg ind^{-1}) (C), and oil sac volume (mm^3) (D) in *Calanus finmarchicus* C5 at 0–50 m, 50–100 m, 100–300 m and 300–440 m. Lower case letters indicate significant differences, N equals the number of replicates. Figure taken 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 uses 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. 1)

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).

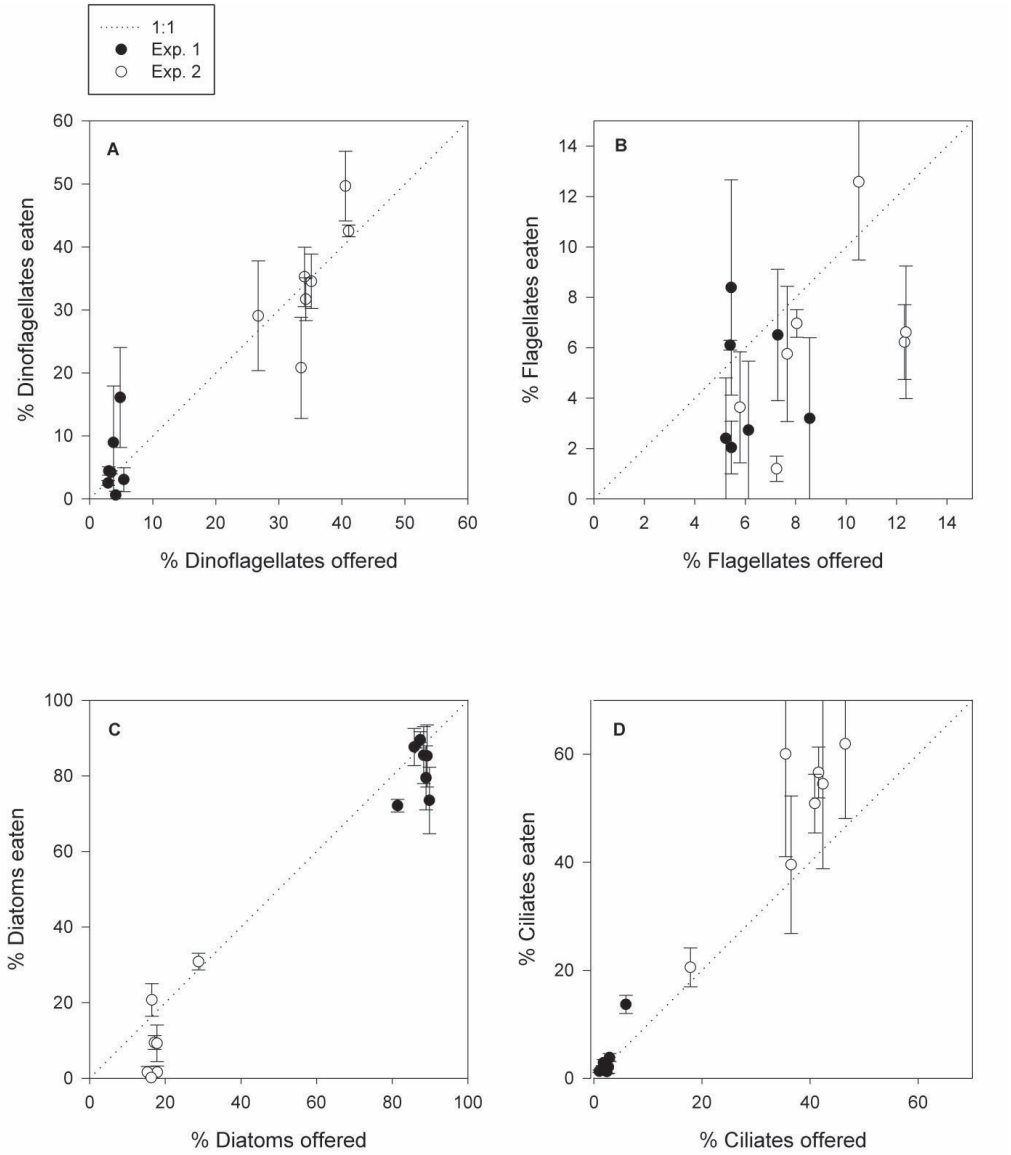


Figure 9. Percentage (mean ± SE) of (A) dinoflagellates (B) ciliates (C) diatoms and (D) flagellates in the diet of *C. finmarchicus* in relation to the 1:1 line. The data above and below the 1:1 line indicate positive and negative feeding selection, respectively. Figure taken from Paper IV.

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.

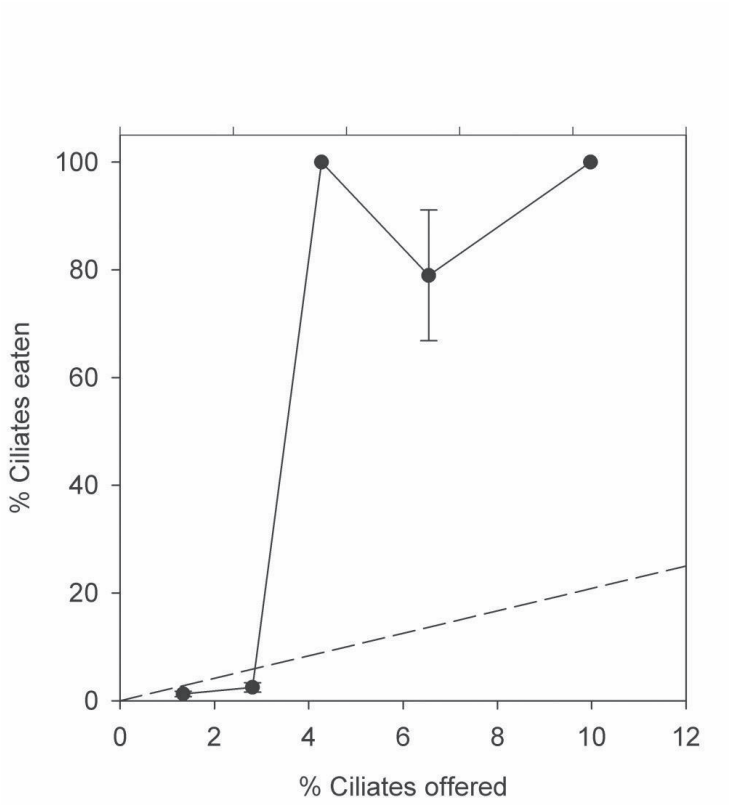


Figure 10. Percentage (mean ± SE, n = 5, from paper IV) offered ciliates eaten by *C. finmarchicus* in the experiment with surplus food and variable ciliate concentration in relation to the 1:1 line. The lack of error bars for 4.3 and 10 % ciliates offered was because the ciliates constituted 100% of 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 µm 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 chl*a* 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.

4. References

Ackman, R. G., Tocher, C. S. and Mclachlan, J. (1968) Marine Phytoplankter Fatty Acids. *J. Fish. Res. Board Can.,* **25,** 1603-1620.

Anderson, T. R. and Pond, D. W. (2000) Stoichiometric theory extended to micronutrients: Comparison of the roles of essential fatty acids, carbon, and nitrogen in the nutrition of marine copepods. *Limnol. Oceanogr.,* **45,** 1162-1167.

Aubert, A. B., Svensen, C., Hessen, D. O. and Tamelander, T. (2013) CNP stoichiometry of a lipid-synthesising zooplankton, *Calanus finmarchicus*, from winter to spring bloom in a sub-Arctic sound. *J. Mar. Syst.,* **111,** 19-28.

Bagoien, E., Kaartvedt, S., Aksnes, D. L. and Eiane, K. (2001) Vertical distribution and mortality of overwintering Calanus. *Limnol. Oceanogr.,* **46,** 1494-1510.

Ban, S. H., Burns, C., Castel, J., Chaudron, Y., Christou, E., Escribano, R., Umani, S. F., Gasparini, S., Ruiz, F. G., Hoffmeyer, M., Ianora, A., Kang, H. K., Laabir, M., Lacoste, A., Miralto, A., Ning, X. R., Poulet, S., Rodriguez, V., Runge, J., Shi, J. X., Starr, M., Uye, S. and Wang, Y. J. (1997) The paradox of diatom-copepod interactions. *Mar. Ecol.: Prog. Ser.,* **157,** 287-293.

Basedow, S. L., Edvardsen, A. and Tande, K. S. (2006) Spatial patterns of surface blooms and recruitment dynamics of *Calanus finmarchicus* in the NE Norwegian Sea. *J. Plankton Res.,* **28,** 1181-1190.

Basedow, S. L. and Tande, K. S. (2006) Cannibalism by female *Calanus finmarchicus* on naupliar stages. *Mar. Ecol.: Prog. Ser.,* **327,** 247-255.

Bell, M. V., Dick, J. R., Anderson, T. R. and Pond, D. W. (2007) Application of liposome and stable isotope tracer techniques to study polyunsaturated fatty acid biosynthesis in marine zooplankton. *J. Plankton Res.,* **29,** 417-422.

Bonnet, D., Titelman, J. and Harris, R. (2004) *Calanus* the cannibal. *J. Plankton Res.,* **26,** 937-948.

Braarud, T. and Nygaard, I. (1978) Phytoplankton observations in offshore norwegian coastal waters between 62°N and 69°N I. Variation in time of the spring diatom maximum 1968-1971. *Fiskeridirektoratets Skrifter Serie Havundersokelser,* **16,** 489-505.

Bradford-Grieve, J. M. (2002) Colonization of the pelagic realm by calanoid copepods. *Hydrobiologia,* **485,** 223-244.

Breteler, W. C. M. K., Schogt, N. and Rampen, S. (2005) Effect of diatom nutrient limitation on copepod development: role of essential lipids. *Mar. Ecol.: Prog. Ser.,* **291,** 125-133.

Broms, C., Melle, W. and Kaartvedt, S. (2009) Oceanic distribution and life cycle of *Calanus* species in the Norwegian Sea and adjacent waters. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.,* **56,** 1910-1921.

Burkill, P. H. and Kendall, T. F. (1982) Production of the Copepod *Eurytemora affinis* in the Bristol Channel. *Mar. Ecol.: Prog. Ser.,* **7,** 21-31.

Calbet, A. and Saiz, E. (2005) The ciliate-copepod link in marine ecosystems. *Aquat. Microb. Ecol.,* **38,** 157-167.

Campbell, R. G., Wagner, M. M., Teegarden, G. J., Boudreau, C. A. and Durbin, E. G. (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Mar. Ecol.: Prog. Ser.,* **221,** 161-183.

Carlotti, F. and Radach, G. (1996) Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled one-dimensional model. *Limnol. Oceanogr.,* **41,** 522-539.

Castellani, C., Irigoien, X., Mayor, D. J., Harris, R. P. and Wilson, D. (2008) Feeding of *Calanus finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea, North Atlantic. *J. Plankton Res.,* **30,** 1095-1116.

Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y. and Irigoien, X. (2014) Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES J. Mar. Sci.,* **71,** 241-253.

Conover, R. J. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high-latitudes of the northern hemisphere. *Hydrobiologia,* **167,** 127-142.

Corkett, C. J., Mclaren, I. A. and Sevigny, J.-M. (1986) The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Krøyer, with comment on the equiproportional rule. *Sylleogeus (Nat Mus Can),* **58,** 539-546.

Dilling, L., Wilson, J., Steinberg, D. and Alldredge, A. (1998) Feeding by the euphausiid *Euphausia pacifica* and the copepod *Calanus pacificus* on marine snow. *Mar. Ecol.: Prog. Ser.,* **170,** 189-201.

Evjemo, J. O., Reitan, K. I. and Olsen, Y. (2003) Copepods as live food organisms in the larval rearing of halibut larvae (*Hippoglossus hippoglossus* L.) with special emphasis on the nutritional value. *Aquaculture,* **227,** 191-210.

Evjemo, J. O., Tokle, N., Vadstein, O. and Olsen, Y. (2008) Effect of essential dietary fatty acids on egg production and hatching success of the marine copepod *Temora longicornis*. *J. Exp. Mar. Biol. Ecol.,* **365,** 31-37.

Fao (2014) The State of World Fisheries and Aquaculture. Opportunities and challenges. *Food and Agriculture Organization of the United Nations.*

Fiskeridir.No (2013) Forslag til prioriterte utviklingstiltak i 2014. www.fiskeridir.no.

Fleminger, A. and Hulsemann, K. (1977) Geographical range and taxonomic divergence in North Atlantic *Calanus* (*Calanus helgolandicus*, *Calanus finmarchicus* and *Calanus glacialis*). *Mar. Biol.,* **40,** 233-248.

Fosshagen, A. and Iliffe, T. M. (1988) A new genus of Platycopioida (Copepoda) from a marine cave on Bermuda. *Hydrobiologia,* **167,** 357-361.

Frost, B. W. (1972) Effects of size and concentration of food particles on feeding behavior of marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.,* **17,** 805-815.

Gatten, R. R., Sargent, J. R., Forsberg, T. E. V., O'hara, S. C. M. and Corner, E. D. S. (1980) On the nutrition and metabolism of zooplankton. XIV. Utilization of lipid by *Calanus helgolandicus* during maturation and reproduction. *J. Mar. Biol. Assoc. U.K.,* **60,** 391-399.

Gifford, D. J., Fessenden, L. M., Garrahan, P. R. and Martin, E. (1995) Grazing by microzooplankton and mesozooplankton in the high-latitude North-Atlantic ocean - spring versus summer dynamics. *J. Geophys. Res.-Oceans,* **100,** 6665-6675.

Gismervik, I., Andersen, T. and Vadstein, O. (1996) Pelagic food webs and eutrophication of coastal waters: Impact of grazers on algal communities. *Mar. Pollut. Bull.,* **33,** 22-35.

Graeve, M., Kattner, G. and Hagen, W. (1994) Diet-induced changes in the fatty acid composition of arctic herbivorous copepods: Experimental evidence of trophic markers. *J. Exp. Mar. Biol. Ecol.,* **182,** 97-110.

Greene, C. H. and Pershing, A. J. (2000) The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-scale forcing associated with the North Atlantic Oscillation. *ICES J. Mar. Sci.,* **57,** 1536-1544.

Gunnerus, J. E. (1770) Nogle smaa rare og meestendeelen nye Norske søedyr. *Skrifter som udi det Kiøbenhavnske Selskap af Laerdoms og Videnskabers Elskere ere fremlagte og oplaeste,* **10,** 166-176.

Hallegraeff, G. M., Nichols, P. D., Volkman, J. K., Blackburn, S. I. and Everitt, D. A. (1991) Pigments, fatty-acids, and sterols of the toxic dinoflagellate *Gymnodinium catenatum*. *J. Phycol.,* **27,** 591-599.

Hansen, B. H., Altin, D., Nordtug, T. and Olsen, A. J. (2007) Suppression subtractive hybridization library prepared from the copepod *Calanus finmarchicus* exposed to a sublethal mixture of environmental stressors. *Comparative Biochemistry and Physiology D-Genomics & Proteomics,* **2,** 250-256.

Hansen, B. W., Bjørnsen, P. K. and Hansen, P. J. (1994) The size ratio between planktonic predators and their prey. *Limnol. Oceanogr.,* **39,** 395-403.

Hansen, P. J., Bjørnsen, P. K. and Hansen, B. W. (1997) Zooplankton grazing and growth: Scaling within the 2-2,000 µm body size range. *Limnol. Oceanogr.,* **42,** 687-704.

Harris, R. P., Irigoien, X., Head, R. N., Rey, C., Hygum, B. H., Hansen, B. W., Niehoff, B., Meyer-Harms, B. and Carlotti, F. (2000) Feeding, growth, and reproduction in the genus *Calanus*. *ICES J. Mar. Sci.,* **57,** 1708-1726.

Haug, A., Myklestad, S. and Sakshaug, E. (1973) Studies on the phytoplankton ecology of the Trondheimsfjord. I. The chemical composition of phytoplankton populations. *J. Exp. Mar. Biol. Ecol.,* **11,** 15-26.

Head, E. J. H., Harris, L. R., Ringuette, M. and Campbell, R. W. (2013a) Characteristics of egg production of the planktonic copepod, *Calanus finmarchicus*, in the Labrador Sea: 1997-2010. *J. Plankton Res.,* **35,** 281-298.

Head, E. J. H., Melle, W., Pepin, P., Bagoien, E. and Broms, C. (2013b) On the ecology of *Calanus finmarchicus* in the Subarctic North Atlantic: A comparison of population dynamics and environmental conditions in areas of the Labrador Sea-Labrador/Newfoundland Shelf and Norwegian Sea Atlantic and Coastal Waters. *Prog. Oceanogr.,* **114,** 46-63.

Heath, M. R., Rasmussen, J., Ahmed, Y., Allen, J., Anderson, C. I. H., Brierley, A. S., Brown, L., Bunker, A., Cook, K., Davidson, R., Fielding, S., Gurney, W. S. C., Harris, R., Hay, S., Henson, S., Hirst, A. G., Holliday, N. P., Ingvarsdottir, A., Irigoien, X., Lindeque, P., Mayor, D. J., Montagnes, D., Moffat, C., Pollard, R., Richards, S., Saunders, R. A., Sidey, J., Smerdon, G., Speirs, D., Walsham, P., Waniek, J., Webster, L. and Wilson, D. (2008) Spatial demography of *Calanus finmarchicus* in the Irminger Sea. *Prog. Oceanogr.,* **76,** 39-88.

Helland-Hansen, B. and Nansen, F. (1909) The Norwegian Sea. *Report on Norwegian Fishery and Marine Investigations,* **II**.

Helland, S., Nejstgaard, J. C., Humlen, R., Fyhn, H. J. and Bamstedt, U. (2003) Effects of season and maternal food on *Calanus finmarchicus* reproduction, with emphasis on free amino acids. *Mar. Biol.,* **142,** 1141-1151.

Hessen, D. O. (1992) Nutrient Element Limitation of Zooplankton Production. *Am. Nat.,* **140,** 799-814.

Hirche, H. J. and Kattner, G. (1993) Egg-production and lipid-content of *Calanus glacialis* in spring - indication of a food-dependent and food-independent reproductive mode. *Mar. Biol.,* **117,** 615-622.

Hirche, H. J., Meyer, U. and Niehoff, B. (1997) Egg production of *Calanus finmarchicus*: Effect of temperature, food and season. *Mar. Biol.,* **127,** 609-620.

Hjøllo, S. S., Huse, G., Skogen, M. D. and Melle, W. (2012) Modelling secondary production in the Norwegian Sea with a fully coupled physical/primary production/individual-based *Calanus finmarchicus* model system. *Mar. Biol. Res.,* **8,** 508-526.

Hygum, B. H., Rey, C. and Hansen, B. W. (2000a) Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. *Mar. Biol.,* **136,** 1075-1085.

Hygum, B. H., Rey, C., Hansen, B. W. and Carlotti, F. (2000b) Rearing cohorts of *Calanus finmarchicus* (Gunnerus) in mesocosms. *ICES J. Mar. Sci.,* **57,** 1740-1751.
Hygum, B. H., Rey, C., Hansen, B. W. and Tande, K. (2000c) Importance of food quantity to structural growth rate and neutral lipid reserves accumulated in *Calanus finmarchicus*. *Mar. Biol.,* **136,** 1057-1073.
Irigoien, X. (2004) Some ideas about the role of lipids in the life cycle of *Calanus finmarchicus*. *J. Plankton Res.,* **26,** 259-263.
Irigoien, X., Head, R., Klenke, U., Meyer-Harris, B., Harbour, D., Niehoff, B., Hirche, H. J. and Harris, R. (1998) A high frequency time series at weathership M, Norwegian Sea, during the 1997 spring bloom: Feeding of adult female *Calanus finmarchicus*. *Mar. Ecol.: Prog. Ser.,* **172,** 127-137.
Irigoien, X., Titelman, J., Harris, R. P., Harbour, D. and Castellani, C. (2003) Feeding of *Calanus finmarchicus* nauplii in the Irminger Sea. *Mar. Ecol.: Prog. Ser.,* **262,** 193-200.
Jacobson, P. (1983) Physical oceanography of the Trondheimsfjord. *Geophys. Astrophys. Fluid Dyn.,* **26,** 3-26.
Jonasdottir, S. H. (1999) Lipid content of *Calanus finmarchicus* during overwintering in the Faroe-Shetland Channel. *Fish. Oceanogr.,* **8,** 61-72.
Jonasdottir, S. H., Dutz, J., Koski, M., Yebra, L., Jakobsen, H. H., Vidoudez, C., Pohnert, G. and Nejstgaard, J. C. (2011) Extensive cross-disciplinary analysis of biological and chemical control of *Calanus finmarchicus* reproduction during an aldehyde forming diatom bloom in mesocosms. *Mar. Biol.,* **158,** 1943-1963.
Jonasdottir, S. H., Gudfinnsson, H. G., Gislason, A. and Astthorsson, O. S. (2002) Diet composition and quality for *Calanus finmarchicus* egg production and hatching success off south-west Iceland. *Mar. Biol.,* **140,** 1195-1206.
Jonasdottir, S. H., Richardson, K., Heath, M. R., Ingvarsdottir, A. and Christoffersen, A. (2008) Spring production of *Calanus finmarchicus* at the Iceland-Scotland ridge. *Deep Sea Res., Part I,* **55,** 471-489.
Jonasdottir, S. H., Trung, N. H., Hansen, F. and Gartner, S. (2005) Egg production and hatching success in the calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* in the North Sea from March to September 2001. *J. Plankton Res.,* **27,** 1239-1259.
Jonasdottir, S. H., Visser, A. W. and Jespersen, C. (2009) Assessing the role of food quality in the production and hatching of *Temora longicornis* eggs. *Mar. Ecol.: Prog. Ser.,* **382,** 139-150.
Kattner, G., Hagen, W., Lee, R. F., Campbell, R., Deibel, D., Falk-Petersen, S., Graeve, M., Hansen, B. W., Hirche, H. J., Jonasdottir, S. H., Madsen, M. L., Mayzaud, P., Muller-Navarra, D., Nichols, P. D., Paffenhofer, G. A., Pond, D., Saito, H., Stubing, D. and Virtue, P. (2007) Perspectives on marine zooplankton lipids. *Can. J. Fish. Aquat. Sci.,* **64,** 1628-1639.
Kattner, G. and Krause, M. (1987) Changes in lipids during the development of *Calanus finmarchicus* s.l. from Copepodid I to adult. *Mar. Biol.,* **96,** 511-518.
Kiørboe, T. (2011) What makes pelagic copepods so successful? *J. Plankton Res.,* **33,** 677-685.
Kiørboe, T. and Johansen, K. (1986) Studies of a larval herring (*Clupea harengus* L.) patch in the Buchan area. IV. Zooplankton distribution and productivity in relation to hydrographic features. *Dana: A Journal of Fisheries and Marine Research,* **6,** 37-51.
Koski, M. (2007) High reproduction of *Calanus finmarchicus* during a diatom-dominated spring bloom. *Mar. Biol.,* **151,** 1785-1798.

Koski, M. and Riser, C. W. (2006) Post-bloom feeding of *Calanus finmarchicus* copepodites: Selection for autotrophic versus heterotrophic prey. *Mar. Biol. Res.,* **2,** 109-119.
Koski, M., Yebra, L., Dutz, J., Jonasdottir, S. H., Vidoudez, C., Jakobsen, H. H., Pohnert, G. and Nejstgaard, J. C. (2012) The effect of egg versus seston quality on hatching success, naupliar metabolism and survival of *Calanus finmarchicus* in mesocosms dominated by *Phaeocystis* and diatoms. *Mar. Biol.,* **159,** 643-660.
Lee, R. F., Nevenzel, J. C. and Paffenhöfer, G.-A. (1972) The Presence of Wax Esters in Marine Planktonic Copepods. *Naturwissenschaften,* **59,** 406-411.
Levinsen, H., Turner, J. T., Nielsen, T. G. and Hansen, B. W. (2000) On the trophic coupling between protists and copepods in arctic marine ecosystems. *Mar. Ecol.: Prog. Ser.,* **204,** 65-77.
Lie, U. (1968) Variations in the quantity of zooplankton and the propagation of *Calanus finmarchicus* at station "M" in the Norwegian sea 1959-1966. *Fiskeridirektoratets Skrifter Serie Havundersokelser,* **14,** 121-128.
Mansour, M. P., Volkman, J. K., Jackson, A. E. and Blackburn, S. I. (1999) The fatty acid and sterol composition of five marine dinoflagellates. *J. Phycol.,* **35,** 710-720.
Marshall, S. M. (1924) The food of *Calanus finmarchicus* during 1923. *J. Mar. Biol. Assoc. U.K.,* **13,** 473-479.
Marshall, S. M. and Orr, A. P. (1952) On the biology of *Calanus finmarchicus*. 7. Factors affecting egg production. *J. Mar. Biol. Assoc. U.K.,* **30,** 527-&.
Marshall, S. M. and Orr, A. P. (1955) *The biology of a marine copepod Calanus finmarchicus (Gunnerus).* Oliver & Boyd, Edinburgh: Tweeddale Court.
Mauchline, J. (1998) *The biology of Calanoid Copepods.* Academic Press Ltd-Elsevier Science Ltd, London.
Mayor, D. J., Anderson, T. R., Irigoien, X. and Harris, R. (2006) Feeding and reproduction of *Calanus finmarchicus* during non-bloom conditions in the Irminger Sea. *J. Plankton Res.,* **28,** 1167-1179.
Mayor, D. J., Anderson, T. R., Pond, D. W. and Irigoien, X. (2009a) Egg production and associated losses of carbon, nitrogen and fatty acids from maternal biomass in *Calanus finmarchicus* before the spring bloom. *J. Mar. Syst.,* **78,** 505-510.
Mayor, D. J., Anderson, T. R., Pond, D. W. and Irigoien, X. (2009b) Limitation of egg production in *Calanus finmarchicus* in the field: A stoichiometric analysis. *J. Mar. Syst.,* **78,** 511-517.
Mayor, D. J., Cook, K., Thornton, B., Walsham, P., Witte, U. F. M., Zuur, A. F. and Anderson, T. R. (2011) Absorption efficiencies and basal turnover of C, N and fatty acids in a marine Calanoid copepod. *Funct. Ecol.,* **25,** 509-518.
Melle, W., Runge, J., Head, E., Plourde, S., Castellani, C., Licandro, P., Pierson, J., Jonasdottir, S., Johnson, C., Broms, C., Debes, H., Falkenhaug, T., Gaard, E., Gislason, A., Heath, M., Niehoff, B., Nielsen, T. G., Pepin, P., Stenevik, E. K. and Chust, G. (2014) The North Atlantic Ocean as habitat for *Calanus finmarchicus*: Environmental factors and life history traits. *Prog. Oceanogr.,* **129,** 244-284.
Melle, W. and Skjoldal, H. R. (1998) Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. *Mar. Ecol.: Prog. Ser.,* **169,** 211-228.
Miller, C. B., Morgan, C. A., Prahl, F. G. and Sparrow, M. A. (1998) Storage lipids of the copepod Calanus jinmarchicus from Georges Bank and the Gulf of Maine. *Limnol. Oceanogr.,* **43,** 488-497.
Møller, E. F., Maar, M., Jónasdóttir, S. H., Nielsen, T. G. and Tönnesson, K. (2012) The effect of changes in temperature and food on the development of *Calanus*

finmarchicus and *Calanus helgolandicus* populations. *Limnol. Oceanogr.,* **57,** 211-220.
Moore, P. G. (2011) The background to the proposition that plankton be used as food in the United Kingdom during the Second World War. *Arch. Nat. Hist.,* **38,** 287-299.
Nejstgaard, J. C., Gismervik, I. and Solberg, P. T. (1997) Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliania huxleyi*. *Mar. Ecol.: Prog. Ser.,* **147,** 197-217.
Nejstgaard, J. C., Witte, H. J., Vanderwal, P. and Jacobsen, A. (1994) Copepod grazing during a mesocosm study of an *Emiliania huxleyi* (Prymnesiophyceae) bloom. *Sarsia,* **79,** 369-377.
Niehoff, B. (2004) The effect of food limitation on gonad development and egg production of the planktonic copepod *Calanus finmarchicus*. *J. Exp. Mar. Biol. Ecol.,* **307,** 237-259.
Nordgård, O. (1926) *Trondhjems Biologiske Stasjon 1900-1925.* Aktietrykkeriet i Trondhjem, Trondheim.
Ohman, M. D., Eiane, K., Durbin, E. G., Runge, J. A. and Hirche, H. J. (2004) A comparative study of *Calanus finmarchicus* mortality patterns at five localities in the North Atlantic. *ICES J. Mar. Sci.,* **61,** 687-697.
Ohman, M. D. and Hirche, H. J. (2001) Density-dependent mortality in an oceanic copepod population. *Nature,* **412,** 638-641.
Ohman, M. D. and Runge, J. A. (1994) Sustained fecundity when phytoplankton resources are in short supply: Omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. *Limnol. Oceanogr.,* **39,** 21-36.
Olsen, Y. (2011) Resources for fish feed in future mariculture. *Aquac. Environ. Interact.,* **1,** 187-200.
Olsen, Y. (2013) Ecological Principles and Options for Seafood Production. In: J. Grue and K. A. Almas (eds) *Food from the Ocean - Norway's Opportunities.* Novus forlag, Oslo, pp. 63-80.
Olsen, Y., Andersen, T., Gismervik, I. and Vadstein, O. (2011) Marine heterotrophic bacteria, protozoan and metazoan zooplankton may experience protein N or mineral P limitation in coastal waters. *Mar. Ecol.: Prog. Ser.,* **436,** 81-100.
Olsen, Y., Jensen, A., Reinertsen, H., Borsheim, K. Y., Heldal, M. and Langeland, A. (1986) Dependence of the rate of release of phosphorus by zooplankton on the P:C ratio in the food supply, as calculated by a recycling model. *Limnol. Oceanogr.,* **31,** 34-44.
Omori, M. (1978) Zooplankton fisheries of world: A review. *Mar. Biol.,* **48,** 199-205.
Owre, H. B. and Foyo, M. (1967) *Copepods of the Florida Current.*
Paffenhöfer, G.-A. (1971) Grazing and ingestion rates of nauplii, copepodids and adults of the marine planktonic copepod *Calanus helgolandicus*. *Mar. Biol.,* **11,** 286-298.
Paffenhöfer, G.-A. and Strickland, J. H. D. (1970) A note on feeding of *Calanus helgolandicus* on detritus. *Mar. Biol.,* **5,** 97-99.
Pasternak, A., Tande, K. S., Arashkevich, E. and Melle, W. (2004) Reproductive patterns of *Calanus finmarchicus* at the Norwegian midshelf in 1997. *J. Plankton Res.,* **26,** 839-849.
Planque, B. and Batten, S. D. (2000) *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. *ICES J. Mar. Sci.,* **57,** 1528-1535.
Pond, D., Harris, R., Head, R. and Harbour, D. (1996) Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. *Mar. Ecol.: Prog. Ser.,* **143,** 45-63.

Poulet, S. A., Ianora, A., Laabir, M. and Breteler, W. (1995) Towards the measurement of secondary production and recruitment in copepods. *ICES J. Mar. Sci.,* **52,** 359-368.
Reitan, K. I., Rainuzzo, J. R. and Olsen, Y. (1994) Effect of nutrient limitation on fatty-acid and lipid-content of marine microalgae. *J. Phycol.,* **30,** 972-979.
Richardson, K., Jónasdóttir, S. H., Hay, S. J. and Christoffersen, A. (1999) *Calanus finmarchicus* egg production and food availability in the Faroe–Shetland Channel and northern North Sea: October–March. *Fish. Oceanogr.,* **8,** 153-162.
Runge, J. A. (1985) Egg production of *Calanus finmarchicus* in the sea off Nova Scotia. *Archiv für Hydrobiologie Beih. Ergebn. Limnol.,* **21,** 8.
Runge, J. A., Mclaren, I. A., Corkett, C. J., Bohrer, R. N. and Koslow, J. A. (1985) Molting rates and cohort development of *Calanus finmarchicus* and *Calanus glacialis* in the sea off southwest Nova Scotia. *Mar. Biol.,* **86,** 241-246.
Ruyter, B., Rosjo, C., Masoval, K., Einen, O. and Thomassen, M. S. (2000) Influence of dietary n-3 fatty acids on the desaturation and elongation of [1-^{14}C] 18:2 n-6 and [1-^{14}C] 18:3 n-3 in Atlantic salmon hepatocytes. *Fish Physiol. Biochem.,* **23,** 151-158.
Ryther, J. H. (1969) Photosynthesis and fish production in sea. *Science,* **166,** 72-76.
Saage, A. (2006) *A comparison of phytoplankton and ciliate feeding by marine calanoid copepods.* Christian-Albrechts Universität zu Kiel.
Saage, A., Altin, D., Vadstein, O. and Sommer, U. (2008) Trophic position of *Calanus finmarchicus* (Copepoda, Calanoida) in the Trondheim Fjord. *J. Sea Res.,* **59,** 162-172.
Sætre, R. (2007) Introduction. In: R. Sætre (ed) *The Norwegian Coastal Current - Oceanography and Climate.* Tapir Academic Press, Trondheim, pp. 9-18.
Sakshaug, E. (1972) Phytoplankton Investigations in Trondheimsfjord, 1963–1966. *Skr. - K. Nor. Vidensk. Selsk.,* **1,** 1–56.
Sakshaug, E. and Myklestad, S. (1973) Studies on the phytoplankton ecology of the Trondheimsfjord. III. Dynamics of phytoplankton blooms in relation to environmental factors, bioassay experiments and parameters for the physiological state of the populations. *J. Exp. Mar. Biol. Ecol.,* **11,** 157-188.
Sakshaug, E. and Sneli, J. A. (2000) *Trondheimsfjorden.* Tapir forlag, Trondheim.
Sakshaug, E. and Tangen, K. (2000) The light, nutrients and the phytoplankton. In: E. Sakshaug and J. A. Sneli (eds) *Trondheimsfjorden.* Tapir Academic Press, Trondheim, pp. 83-95.
Samuelsen, A., Huse, G. and Hansen, C. (2009) Shelf recruitment of *Calanus finmarchicus* off the west coast of Norway: role of physical processes and timing of diapause termination. *Mar. Ecol.: Prog. Ser.,* **386,** 163-180.
Sargent, J. R. and Falk-Petersen, S. (1988) The lipid biochemistry of calanoid copepods. *Hydrobiologia,* **167,** 101-114.
Sargent, J. R. and Henderson, R. J. (1986) *The Biological chemistry of marine copepods.* Clarendon Press, Oxford.
Sargent, J. R. and Whittle, K. J. (1981) Lipids and hydrocarbons in the marine food web. In: A. R. Longhurst (ed) *Analysis of marine ecosystems.* Academic Press, London, pp. 491-533.
Skreslet, S., Olsen, K., Mohus, A. and Tande, K. S. (2000) Stage-specific habitats of *Calanus finmarchicus* and *Calanus helgolandicus* in a stratified northern Norwegian fjord. *ICES J. Mar. Sci.,* **57,** 1656-1663.
Slagstad, D. and Gjøsæter, H. (2009) Plankton and fish modelling. In: E. Sakshaug, G. Johnsen and K. Kovacs (eds) *Ecosystem Barents Sea.* Tapir Academic Press, Trondheim.

Slagstad, D. and Tande, K. S. (2007) Structure and resilience of overwintering habitats of *Calanus finmarchicus* in the Eastern Norwegian Sea. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.,* **54,** 2702-2715.

Slagstad, D., Tande, K. S. and Wassmann, P. (1999) Modelled carbon fluxes as validated by field data on the north Norwegian shelf during the productive period in 1994. *Sarsia,* **84,** 303-317.

Sømme, I. D. (1934) *Animal plankton of the Norwegian coast waters and the open sea, I, Production of Calanus finmarchicus (Gunnerus) and Calanus hyperboreus (Krøyer) in the Lofoten Area.* Direktoratet., Bergen.

St. John, M. A. and Lund, T. (1996) Lipid biomarkers: Linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. *Mar. Ecol.: Prog. Ser.,* **131,** 75-85.

Sterner, R. W. and Elser, J. J. (2002) *Ecological Stoichiometry. The biology of elements from molecules to the biosphere.* Princeton University Press, New Jersey.

Stibor, H., Vadstein, O., Diehl, S., Gelzleichter, A., Hansen, T., Hantzsche, F., Katechakis, A., Lippert, B., Loseth, K., Peters, C., Roederer, W., Sandow, M., Sundt-Hansen, L. and Olsen, Y. (2004) Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. *Ecol. Lett.,* **7,** 321-328.

Strømgren, T. (1971) *Zooplankton investigations in Skjomen: preliminary report, November 1969 - January 1971.* K. norske Vidensk. Selsk. Mus. Miscellanea Trondheim.

Strømgren, T. (1974) *Zooplankton and hydrography in Trondheimsfjorden on the west coast of Norway.* K. norske Vidensk. Selsk. Mus. Miscellanea 17, Trondheim.

Tande, K. S. (1982) Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: Generation cycles, and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). *J. Exp. Mar. Biol. Ecol.,* **62,** 129-142.

Tande, K. S. (1988) Aspects of developmental and mortality-rates in *Calanus finmarchicus* related to equiproportional development. *Mar. Ecol.: Prog. Ser.,* **44,** 51-58.

Teegarden, G. J., Campbell, R. G., Anson, D. T., Ouellett, A., Westman, B. A. and Durbin, E. G. (2008) Copepod feeding response to varying *Alexandrium* spp. cellular toxicity and cell concentration among natural plankton samples. *Harmful Algae,* **7,** 33-44.

Teegarden, G. J., Campbell, R. G. and Durbin, E. G. (2001) Zooplankton feeding behavior and particle selection in natural plankton assemblages containing toxic Alexandrium spp. *Mar. Ecol.-Prog. Ser.,* **218,** 213-226.

Tocher, D. R., Bell, J. G., Macglaughlin, P., Mcghee, F. and Dick, J. R. (2001) Hepatocyte fatty acid desaturation and polyunsaturated fatty acid composition of liver in salmonids: effects of dietary vegetable oil. *Comp. Biochem. Physiol. B-Biochem. Mol. Biol.,* **130,** 257-270.

Verity, P. G. and Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol.: Prog. Ser.,* **130,** 277-293.

Wassmann, P., Slagstad, D., Riser, C. W. and Reigstad, M. (2006) Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone II. Carbon flux and interannual variability. *J. Mar. Syst.,* **59,** 1-24.

Wiborg, K. F. (1954) *Investigations on zooplankton in coastal and offshore waters of Western and Northwestern Norway: with a special reference to the copepods.* Direktoratet., Bergen.

Wiborg, K. F. (1976) Fishery and commercial exploitation of *Calanus finmarchicus* in Norway. *Journal Du Conseil,* **36,** 251-258.

Winberg, G. G. (1971) *Methods for the estimation of production of aquatic animals.* Academic Press, London.

Paper I

Reproduction in *Calanus finmarchicus* in a central Norwegian fjord, effects from potential food and maternal essential fatty acid content

Øystein Leiknes[1]*, Maria Bergvik[1], Olav Vadstein[2], Yngvar Olsen[1]

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

[2]NTNU 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*

36 **ABSTRACT**

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

51

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 chl*a* 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 chl*a* measurements (Irigoien 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 chl*a* 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* (Irigoien 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 (Irigoien 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; Kiørboe, 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 chl*a* 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*a*, 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 µm 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_2SO_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 µm) 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°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 µm 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*a* 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*a* 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 chl*a* concentrations during the winter (0.1 to 0.8 µg chl*a* L^{-1}) and a spring bloom from late March to early April (Table I). The observed chl*a* 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 PUFAs 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 PUFAs 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 28th 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 18th 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 27th 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

303 = 0.55, p = 0.014) on EPR, but we could not detect any difference between years. The effects
304 of temperature and Julian day were, however difficult to separate, as these variables were
305 heavily correlated (Rs = 0.92, p < 0.0001). Furthermore, the temperature was positively
306 correlated with many of the food concentration variables. EPR was positively correlated with
307 many of the food concentration variables but the variable that best explained the variation in
308 EPR was the biomass of diatoms (Rs = 0.76, p = 0.0004). The EPR was also significantly
309 correlated with the microplankton, especially when we considered the particles within the
310 optimum size spectrum of *C. finmarchicus* (Gifford et al., 1995; Hansen et al., 1994; Hansen
311 et al., 1997) and removed particles <10 µm (Rs = 0.74, p = 0.001, Fig. 4 A). The relationship
312 could be described by a two-parameter rectangular hyperbola (EPR_{max} = 19.1 ± 1.8 eggs
313 $female^{-1}$ d^{-1}, half saturation constant (K) = 0.44 ± 0.26 µg C L^{-1}, r^2 = 0.39, p = 0.008). We
314 found a slight effect of food concentration on EPR when chl*a* (Rs = 0.45, p = 0.049) was used
315 as a proxy for food concentration

316 EPR was also positively correlated to the concentration of particular organic carbon (POC)
317 (Table II, Rs = 0.66, p = 0.004). Because the ratio C:N and P:C was relatively stable, we
318 found a similar significant pattern for EPR and the concentration of PON (Rs = 0.65, p =
319 0.005) and POP (Rs = 0.60, p = 0.015). For the latter correlations, we removed the POC, PON
320 and POP data from the 18th of May 2010. At this date, hydrological measurements from
321 nearby rivers showed discharge rates corresponding to a five-year flood the week before this
322 sampling date, and the POC and PON concentrations were higher than previously recorded
323 during a 10-year monitoring program at the same sampling station. The relationship between
324 EPR and POC could be described by a linear regression (r^2 = 0.51, slope 0.04 ± 0.01, p =
325 0.001, Figure 4B).

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

332 Both the spawning frequency and the EPR were significantly correlated with the content of
333 EPA, DHA and the sum of EPA and DHA in the females of *C. finmarchicus* (Table II).
334 Regression analysis showed no saturation, the EPR was linearly related to the content EPA

335 and DHA in female *C. finmarchicus* (EPA: $r^2 = 0.55$, slope 2.58 ± 0.08, $p = 0.009$, Fig. 6A,
336 DHA: $r^2 = 0.38$, slope 2.62 ± 0.04, $p = 0.044$, Fig. 6B).

337

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

community. 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 suggests 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

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

519 The above calculations assume that the *C. finmarchicus* females are consuming the seston
520 material in the proportions offered. One way for *C. finmarchicus* to mitigate potential DHA
521 deficiency will be to graze selectively on food particles that are high in DHA. Dinoflagellates
522 and smaller flagellates are generally rich in DHA and low or moderate in EPA, whereas
523 diatoms are rich in EPA and low in DHA (Reitan et al., 1994). We found higher DHA
524 contents in the seston in May–June, when the microplankton community was dominated by
525 dinoflagellates, small flagellates, and ciliates (Table I). Previous studies on the trophic
526 position of *C. finmarchicus* have revealed that it is omnivorous (Saage et al., 2008). Food
527 selectivity experiments have confirmed these findings, and ciliates are generally consumed in
528 higher proportions than offered (Leiknes et al., 2014; Nejstgaard et al., 1994). These findings
529 contradict some previous experiments showing that *C. finmarchicus* females selectively graze
530 on diatoms (Koski, 2007; Koski and Riser, 2006). Previous results from the study of the
531 dynamics of the lipid content of copepodite stage V *C. finmarchicus* have also shown that the
532 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

This work was supported by the Norwegian Research Council through the Harvest project (project number 178447). We would like to thank the captain and the crew of R/V Gunnerus for smooth cruise operations. We also would like to thank Anja Striberny for counting microplankton, Siv Anina Etter and Kjersti Andresen for help with the nutrient analyses and Kjersti Rennan Dahl for analyzing fatty acids in seston and female *Calanus finmarchicus*.

559 **References**

560 Ackman, R.G., Tocher, C.S., McLachlan, J., 1968. Marine Phytoplankter Fatty Acids. J. Fish.
561 Res. Board Can. 25, 1603-1620.
562 Anderson, T.R., Pond, D.W., 2000. Stoichiometric theory extended to micronutrients:
563 Comparison of the roles of essential fatty acids, carbon, and nitrogen in the nutrition of
564 marine copepods. Limnol. Oceanogr. 45, 1162-1167.
565 Antia, N.J., Desai, I.D., Romilly, M.J., 1970. The tocopherol, vitamin K, and related
566 isoprenoid quinone composition of a unicellular red alga (*Porphyridium cruentum*). J. Phycol.
567 6, 305-312.
568 Aubert, A.B., Svensen, C., Hessen, D.O., Tamelander, T., 2013. CNP stoichiometry of a lipid-
569 synthesising zooplankton, *Calanus finmarchicus*, from winter to spring bloom in a sub-Arctic
570 sound. J. Mar. Syst. 111, 19-28.
571 Ban, S.H., Burns, C., Castel, J., Chaudron, Y., Christou, E., Escribano, R., Umani, S.F.,
572 Gasparini, S., Ruiz, F.G., Hoffmeyer, M., Ianora, A., Kang, H.K., Laabir, M., Lacoste, A.,
573 Miralto, A., Ning, X.R., Poulet, S., Rodriguez, V., Runge, J., Shi, J.X., Starr, M., Uye, S.,
574 Wang, Y.J., 1997. The paradox of diatom-copepod interactions. Mar. Ecol.: Prog. Ser. 157,
575 287-293.
576 Basedow, S.L., Tande, K.S., 2006. Cannibalism by female *Calanus finmarchicus* on naupliar
577 stages. Mar. Ecol.: Prog. Ser. 327, 247-255.
578 Bell, M.V., Dick, J.R., Anderson, T.R., Pond, D.W., 2007. Application of liposome and stable
579 isotope tracer techniques to study polyunsaturated fatty acid biosynthesis in marine
580 zooplankton. J. Plankton Res. 29, 417-422.
581 Bergvik, M., Leiknes, Ø., Altin, D., Dahl, K.R., Olsen, Y., 2012. Dynamics of the Lipid
582 Content and Biomass of *Calanus finmarchicus* (copepodite V) in a Norwegian Fjord. Lipids
583 47, 881-895.
584 Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification.
585 Canadian Journal of Biochemistry and Physiology 37, 911-917.
586 Bonnet, D., Titelman, J., Harris, R., 2004. *Calanus* the cannibal. J. Plankton Res. 26, 937-948.
587 Campbell, R.G., Runge, J.A., Durbin, E.G., 2001. Evidence for food limitation of *Calanus*
588 *finmarchicus* production rates on the southern flank of Georges Bank during April 1997.
589 Deep-Sea Res. Part II-Top. Stud. Oceanogr. 48, 531-549.

590 Carlotti, F., Radach, G., 1996. Seasonal dynamics of phytoplankton and *Calanus*
591 *finmarchicus* in the North Sea as revealed by a coupled one-dimensional model. Limnol.
592 Oceanogr. 41, 522-539.
593 Checkley, D.M., 1980. Food limitation of egg production by a marine, planktonic copepod in
594 the sea off southern California. Limnol. Oceanogr. 25, 991-998.
595 Diel, S., Tande, K., 1992. Does the spawning of *Calanus finmarchicus* in high latitudes
596 follow a reproducible pattern? Mar. Biol. 113, 21-31.
597 Dilling, L., Wilson, J., Steinberg, D., Alldredge, A., 1998. Feeding by the euphausiid
598 *Euphausia pacifica* and the copepod *Calanus pacificus* on marine snow. Mar. Ecol.: Prog.
599 Ser. 170, 189-201.
600 Durbin, E.G., Campbell, R.G., Casas, M.C., Ohman, M.D., Niehoff, B., Runge, J., Wagner,
601 M., 2003. Interannual variation in phytoplankton blooms and zooplankton productivity and
602 abundance in the Gulf of Maine during winter. Mar. Ecol.: Prog. Ser. 254, 81-100.
603 Evjemo, J.O., Tokle, N., Vadstein, O., Olsen, Y., 2008. Effect of essential dietary fatty acids
604 on egg production and hatching success of the marine copepod *Temora longicornis*. J. Exp.
605 Mar. Biol. Ecol. 365, 31-37.
606 Fleminger, A., Hulsemann, K., 1977. Geographical range and taxonomic divergence in North
607 Atlantic *Calanus* (*Calanus helgolandicus*, *Calanus finmarchicus* and *Calanus glacialis*). Mar.
608 Biol. 40, 233-248.
609 Frost, B.W., 1972. Effects of size and concentration of food particles on feeding behavior of
610 marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17, 805-815.
611 Gifford, D.J., Fessenden, L.M., Garrahan, P.R., Martin, E., 1995. Grazing by
612 microzooplankton and mesozooplankton in the high-latitude North-Atlantic ocean - spring
613 versus summer dynamics. J. Geophys. Res.-Oceans 100, 6665-6675.
614 Goericke, R., Montoya, J.P., 1998. Estimating the contribution of microalgal taxa to
615 chlorophyll *a* in the field - variations of pigment ratios under nutrient- and light-limited
616 growth. Mar. Ecol.: Prog. Ser. 169, 97-112.
617 Goodwin, T.W., 1973. Comparative biochemistry of sterols in eukaryotic microorganisms, in:
618 Erwin, J.A. (Ed.), Lipids and Biomembranes of Eukaryotic Microorganisms. Academic Press,
619 New York, pp. 1-40.
620 Grasshoff, K., Erhardt, M., Kremling, K., 1983. Methods of Seawater Analysis. Verlag
621 Chemie, Basel.

622 Guehler, P.F., Peterson, L., Tsuchiya, H.M., Dodson, R.M., 1964. Microbiological
623 transformations. XIII. Composition of wax formed by *Euglena gracilis*. Archives of
624 Biochemistry and Biophysics 106, 294-298.
625 Guisande, C., Riveiro, I., Maneiro, I., 2000. Comparisons among the amino acid composition
626 of females, eggs and food to determine the relative importance of food quantity and food
627 quality to copepod reproduction. Mar. Ecol.: Prog. Ser. 202, 135-142.
628 Hallegraeff, G.M., Nichols, P.D., Volkman, J.K., Blackburn, S.I., Everitt, D.A., 1991.
629 Pigments, fatty-acids, and sterols of the toxic dinoflagellate *Gymnodinium catenatum*. J.
630 Phycol. 27, 591-599.
631 Hansen, B.W., Bjørnsen, P.K., Hansen, P.J., 1994. The size ratio between planktonic
632 predators and their prey. Limnol. Oceanogr. 39, 395-403.
633 Hansen, P.J., Bjørnsen, P.K., Hansen, B.W., 1997. Zooplankton grazing and growth: Scaling
634 within the 2-2,000 μm body size range. Limnol. Oceanogr. 42, 687-704.
635 Head, E.J.H., Harris, L.R., Ringuette, M., Campbell, R.W., 2013a. Characteristics of egg
636 production of the planktonic copepod, *Calanus finmarchicus*, in the Labrador Sea: 1997-2010.
637 J. Plankton Res. 35, 281-298.
638 Head, E.J.H., Melle, W., Pepin, P., Bagoien, E., Broms, C., 2013b. On the ecology of *Calanus*
639 *finmarchicus* in the Subarctic North Atlantic: A comparison of population dynamics and
640 environmental conditions in areas of the Labrador Sea-Labrador/Newfoundland Shelf and
641 Norwegian Sea Atlantic and Coastal Waters. Prog. Oceanogr. 114, 46-63.
642 Helland, S., Nejstgaard, J.C., Humlen, R., Fyhn, H.J., Bamstedt, U., 2003. Effects of season
643 and maternal food on *Calanus finmarchicus* reproduction, with emphasis on free amino acids.
644 Mar. Biol. 142, 1141-1151.
645 Hillebrand, H., Durselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume
646 calculation for pelagic and benthic microalgae. J. Phycol. 35, 403-424.
647 Hirche, H.J., 1990. Egg-production of *Calanus finmarchicus* at low temperature. Mar. Biol.
648 106, 53-58.
649 Hirche, H.J., Bohrer, R.N., 1987. Reproduction of the arctic copepod *Calanus glacialis* in
650 Fram Strait. Mar. Biol. 94, 11-17.
651 Hirche, H.J., Meyer, U., Niehoff, B., 1997. Egg production of *Calanus finmarchicus*: Effect
652 of temperature, food and season. Mar. Biol. 127, 609-620.
653 Hygum, B.H., Rey, C., Hansen, B.W., Tande, K., 2000. Importance of food quantity to
654 structural growth rate and neutral lipid reserves accumulated in *Calanus finmarchicus*. Mar.
655 Biol. 136, 1057-1073.

Irigoien, X., 2004. Some ideas about the role of lipids in the life cycle of *Calanus finmarchicus*. J. Plankton Res. 26, 259-263.

Irigoien, X., Head, R., Klenke, U., Meyer-Harris, B., Harbour, D., Niehoff, B., Hirche, H.J., Harris, R., 1998. A high frequency time series at weathership M, Norwegian Sea, during the 1997 spring bloom: Feeding of adult female *Calanus finmarchicus*. Mar. Ecol.: Prog. Ser. 172, 127-137.

Jacobson, P., 1983. Physical oceanography of the Trondheimsfjord. Geophys. Astrophys. Fluid Dyn. 26, 3-26.

Jakobsen, A.N., Aasen, I.M., Josefsen, K.D., Strom, A.R., 2008. Accumulation of docosahexaenoic acid-rich lipid in thraustochytrid *Aurantiochytrium* sp. strain T66: effects of N and P starvation and O_2 limitation. Appl. Microbiol. Biotechnol. 80, 297-306.

Jonasdottir, S.H., 1994. Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica* - laboratory observations. Mar. Biol. 121, 67-81.

Jonasdottir, S.H., Dutz, J., Koski, M., Yebra, L., Jakobsen, H.H., Vidoudez, C., Pohnert, G., Nejstgaard, J.C., 2011. Extensive cross-disciplinary analysis of biological and chemical control of *Calanus finmarchicus* reproduction during an aldehyde forming diatom bloom in mesocosms. Mar. Biol. 158, 1943-1963.

Jonasdottir, S.H., Fields, D., Pantoja, S., 1995. Copepod egg-production in Long Island Sound, USA, as a function of the chemical composition of seston. Mar. Ecol.: Prog. Ser. 119, 87-98.

Jonasdottir, S.H., Gudfinnsson, H.G., Gislason, A., Astthorsson, O.S., 2002. Diet composition and quality for *Calanus finmarchicus* egg production and hatching success off south-west Iceland. Mar. Biol. 140, 1195-1206.

Jonasdottir, S.H., Richardson, K., Heath, M.R., Ingvarsdottir, A., Christoffersen, A., 2008. Spring production of *Calanus finmarchicus* at the Iceland-Scotland ridge. Deep Sea Res., Part I 55, 471-489.

Jonasdottir, S.H., Trung, N.H., Hansen, F., Gartner, S., 2005. Egg production and hatching success in the calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* in the North Sea from March to September 2001. J. Plankton Res. 27, 1239-1259.

Kiørboe, T., 1989. Phytoplankton growth-rate and nitrogen-content - implications for feeding and fecundity in a herbivorous copepod. Mar. Ecol.: Prog. Ser. 55, 229-234.

Kleppel, G.S., Burkart, C.A., Houchin, L., 1998. Nutrition and the regulation of egg production in the calanoid copepod *Acartia tonsa*. Limnol. Oceanogr. 43, 1000-1007.

689 Koski, M., 2007. High reproduction of *Calanus finmarchicus* during a diatom-dominated
690 spring bloom. Mar. Biol. 151, 1785-1798.
691 Koski, M., Riser, C.W., 2006. Post-bloom feeding of *Calanus finmarchicus* copepodites:
692 Selection for autotrophic versus heterotrophic prey. Mar. Biol. Res. 2, 109-119.
693 Koski, M., Yebra, L., Dutz, J., Jonasdottir, S.H., Vidoudez, C., Jakobsen, H.H., Pohnert, G.,
694 Nejstgaard, J.C., 2012. The effect of egg versus seston quality on hatching success, naupliar
695 metabolism and survival of *Calanus finmarchicus* in mesocosms dominated by *Phaeocystis*
696 and diatoms. Mar. Biol. 159, 643-660.
697 Kragberg, A., Bauman, M., Dürselen, C.-D., 2010. Coastal Phytoplankton. Photo Guide for
698 Northern European Seas. Verlag Dr. Friedrich Pfeil, München.
699 Laabir, M., Poulet, S.A., Ianora, A., 1995. Measuring production and viability of eggs in
700 *Calanus helgolandicus*. J. Plankton Res. 17, 1125-1142.
701 Leiknes, Ø., Striberny, A., Tokle, N.E., Olsen, Y., Vadstein, O., Sommer, U., 2014. Feeding
702 selectivity of *Calanus finmarchicus* in the Trondheimsfjord. J. Sea Res. 85, 292-299.
703 Levinsen, H., Turner, J.T., Nielsen, T.G., Hansen, B.W., 2000. On the trophic coupling
704 between protists and copepods in arctic marine ecosystems. Mar. Ecol.: Prog. Ser. 204, 65-77.
705 Mansour, M.P., Volkman, J.K., Jackson, A.E., Blackburn, S.I., 1999. The fatty acid and sterol
706 composition of five marine dinoflagellates. J. Phycol. 35, 710-720.
707 Marshall, S.M., Orr, A.P., 1955. The biology of a marine copepod *Calanus finmarchicus*
708 (Gunnerus). Oliver & Boyd, Edinburgh: Tweeddale Court.
709 Mayor, D.J., Anderson, T.R., Irigoien, X., Harris, R., 2006. Feeding and reproduction of
710 *Calanus finmarchicus* during non-bloom conditions in the Irminger Sea. J. Plankton Res. 28,
711 1167-1179.
712 Mayor, D.J., Anderson, T.R., Pond, D.W., Irigoien, X., 2009a. Egg production and associated
713 losses of carbon, nitrogen and fatty acids from maternal biomass in *Calanus finmarchicus*
714 before the spring bloom. J. Mar. Syst. 78, 505-510.
715 Mayor, D.J., Anderson, T.R., Pond, D.W., Irigoien, X., 2009b. Limitation of egg production
716 in *Calanus finmarchicus* in the field: A stoichiometric analysis. J. Mar. Syst. 78, 511-517.
717 Meireles, L.A., Guedes, A.C., Malcata, F.X., 2003. Lipid class composition of the microalga
718 *Pavlova lutheri*: Eicosapentaenoic and docosahexaenoic acids. J. Agric. Food Chem. 51,
719 2237-2241.
720 Melle, W., Skjoldal, H.R., 1998. Reproduction and development of *Calanus finmarchicus*, *C.*
721 *glacialis* and *C. hyperboreus* in the Barents Sea. Mar. Ecol.: Prog. Ser. 169, 211-228.

722 Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates,
723 diatoms, and other protist plankton. Limnol. Oceanogr. 45, 569-579.
724 Metcalfe, L.D., Schmitz, A.A., Pelka, J.R., 1966. Rapid preparation of fatty acid esters from
725 lipids for gas chromatographic analysis. Analytical Chemistry 38, 514-&.
726 Møller, E.F., Maar, M., Jónasdóttir, S.H., Nielsen, T.G., Tönnesson, K., 2012. The effect of
727 changes in temperature and food on the development of *Calanus finmarchicus* and *Calanus*
728 *helgolandicus* populations. Limnol. Oceanogr. 57, 211-220.
729 Nejstgaard, J.C., Gismervik, I., Solberg, P.T., 1997. Feeding and reproduction by *Calanus*
730 *finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the
731 coccolithophore *Emiliania huxleyi*. Mar. Ecol.: Prog. Ser. 147, 197-217.
732 Nejstgaard, J.C., Witte, H.J., Vanderwal, P., Jacobsen, A., 1994. Copepod grazing during a
733 mesocosm study of an *Emiliania huxleyi* (Prymnesiophyceae) bloom. Sarsia 79, 369-377.
734 Niehoff, B., 2004. The effect of food limitation on gonad development and egg production of
735 the planktonic copepod *Calanus finmarchicus*. J. Exp. Mar. Biol. Ecol. 307, 237-259.
736 Niehoff, B., Hirche, H.J., 2000. The reproduction of *Calanus finmarchicus* in the Norwegian
737 Sea in spring. Sarsia 85, 15-22.
738 Niehoff, B., Klenke, U., Hirche, H.J., Irigoien, X., Head, R., Harris, R., 1999. A high
739 frequency time series at Weathership M, Norwegian Sea, during the 1997 spring bloom: The
740 reproductive biology of *Calanus finmarchicus*. Mar. Ecol.: Prog. Ser. 176, 81-92.
741 Ohman, M.D., Eiane, K., Durbin, E.G., Runge, J.A., Hirche, H.J., 2004. A comparative study
742 of *Calanus finmarchicus* mortality patterns at five localities in the North Atlantic. ICES J.
743 Mar. Sci. 61, 687-697.
744 Ohman, M.D., Hirche, H.J., 2001. Density-dependent mortality in an oceanic copepod
745 population. Nature 412, 638-641.
746 Ohman, M.D., Runge, J.A., 1994. Sustained fecundity when phytoplankton resources are in
747 short supply: Omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. Limnol.
748 Oceanogr. 39, 21-36.
749 Olenina, I., Hajdu, S., Edler, L., Andersson, A., Wasmund, N., Busch, S., Göbel, J., Gromisz,
750 S., Huseby, S., Huttunen, M., Jaanus, A., Kokkonen, P., Ledaine, I., Niemkiewicz, E., 2006.
751 Biovolumes and size-classes of phytoplankton in the Baltic Sea. HELCOM Balt. Sea Environ.
752 Proc. 106.
753 Olsen, Y., Andersen, T., Gismervik, I., Vadstein, O., 2011. Marine heterotrophic bacteria,
754 protozoan and metazoan zooplankton may experience protein N or mineral P limitation in
755 coastal waters. Mar. Ecol.: Prog. Ser. 436, 81-100.

Paffenhöfer, G.-A., 1971. Grazing and ingestion rates of nauplii, copepodids and adults of the marine planktonic copepod *Calanus helgolandicus*. Mar. Biol. 11, 286-298.

Paffenhofer, G.-A., Ianora, A., Miralto, A., Turner, J.T., Kleppel, G.S., d'Alcala, M.R., Casotti, R., Caldwell, G.S., Pohnert, G., Fontana, A., Muller-Navarra, D., Jonasdottir, S., Armbrust, V., Bamstedt, U., Ban, S., Bentley, M.G., Boersma, M., Bundy, M., Buttino, I., Calbet, A., Carlotti, F., Carotenuto, Y., d'Ippolito, G., Frost, B., Guisande, C., Lampert, W., Lee, R.F., Mazza, S., Mazzocchi, M.G., Nejstgaard, J.C., Poulet, S.A., Romano, G., Smetacek, V., Uye, S., Wakeham, S., Watson, S., Wichard, T., 2005. Colloquium on diatom-copepod interactions. Mar. Ecol.: Prog. Ser. 286, 293-305.

Paffenhöfer, G.-A., Strickland, J.H.D., 1970. A note on feeding of *Calanus helgolandicus* on detritus. Mar. Biol. 5, 97-99.

Patterson, G.W., 1971. The distribution of sterols in algae. Lipids 6, 120-127.

Peterson, W.T., 1988. Rates of egg production by the copepod *Calanus marshallae* in the laboratory and in the sea off Oregon, USA. Mar. Ecol.: Prog. Ser. 47, 229-237.

Plourde, S., Runge, J.A., 1993. Reproduction of the planktonic copepod *Calanus finmarchicus* in the lower St. Lawrence estuary - relation to the cycle of phytoplankton production and evidence for a *Calanus* pump. Mar. Ecol.: Prog. Ser. 102, 217-227.

Pond, D., Harris, R., Head, R., Harbour, D., 1996. Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. Mar. Ecol.: Prog. Ser. 143, 45-63.

Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon - volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. Limnol. Oceanogr. 34, 1097-1103.

Reitan, K.I., Rainuzzo, J.R., Olsen, Y., 1994. Effect of nutrient limitation on fatty-acid and lipid-content of marine microalgae. J. Phycol. 30, 972-979.

Rey, C., Carlotti, F., Tande, K., Hygum, B.H., 1999. Egg and faecal pellet production of *Calanus finmarchicus* females from controlled mesocosms and in situ populations: influence of age and feeding history. Mar. Ecol.: Prog. Ser. 188, 133-148.

Richardson, K., Jónasdóttir, S.H., Hay, S.J., Christoffersen, A., 1999. *Calanus finmarchicus* egg production and food availability in the Faroe–Shetland Channel and northern North Sea: October–March. Fish. Oceanogr. 8, 153-162.

Rosenberg, A., 1967. *Euglena gracilis*: a novel lipid energy reserve and arachidonic acid enrichment during fasting. Science 157, 1189-1191.

789 Runge, J.A., 1984. Egg production of the marine, planktonic copepod, *Calanus pacificus*
790 Brodsky: laboratory observations. J. Exp. Mar. Biol. Ecol. 74, 53-66.
791 Runge, J.A., Plourde, S., Joly, P., Niehoff, B., Durbin, E., 2006. Characteristics of egg
792 production of the planktonic copepod, *Calanus finmarchicus*, on Georges Bank: 1994-1999.
793 Deep Sea Res., Part II 53, 2618-2631.
794 Runge, J.A., Roff, J.C., 2000. 9 - The measurement of growth and reproductive rates, in:
795 Harris, R., Wiebe, P., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), ICES Zooplankton
796 Methodology Manual. Academic Press, London, pp. 401-454.
797 Saage, A., 2006. A comparison of phytoplankton and ciliate feeding by marine calanoid
798 copepods, Mathematisch-Naturwissenschaftlichen Fakultät. Christian-Albrechts Universität
799 zu Kiel, Kiel, p. 73.
800 Saage, A., Altin, D., Vadstein, O., Sommer, U., 2008. Trophic position of *Calanus*
801 *finmarchicus* (Copepoda, Calanoida) in the Trondheim Fjord. J. Sea Res. 59, 162-172.
802 Sakshaug, E., 1972. Phytoplankton Investigations in Trondheimsfjord, 1963–1966. Skr. - K.
803 Nor. Vidensk. Selsk. 1, 1–56.
804 Sargent, J.R., Falk-Petersen, S., 1988. The lipid biochemistry of calanoid copepods.
805 Hydrobiologia 167, 101-114.
806 Sargent, J.R., Whittle, K.J., 1981. Lipids and hydrocarbons in the marine food web, in:
807 Longhurst, A.R. (Ed.), Analysis of marine ecosystems. Academic Press, London, pp. 491-533.
808 St. John, M.A., Lund, T., 1996. Lipid biomarkers: Linking the utilization of frontal plankton
809 biomass to enhanced condition of juvenile North Sea cod. Mar. Ecol.: Prog. Ser. 131, 75-85.
810 Sterner, R.W., Elser, J.J., 2002. Ecological Stoichiometry. The biology of elements from
811 molecules to the biosphere. Princeton University Press, New Jersey.
812 Straile, D., 1997. Gross growth efficiencies of protozoan and metazoan zooplankton and their
813 dependence on food concentration, predator-prey weight ratio, and taxonomic group. Limnol.
814 Oceanogr. 42, 1375-1385.
815 Strickland, J.H.D., Parsons, T.R., 1972. A Practical Handbook of Seawater Analysis, 2 ed.
816 Fisheries Research Board of Canada, Ottawa.
817 Strømgren, T., 1974. Zooplankton and hydrography in Trondheimsfjorden on the west coast
818 of Norway. K. norske Vidensk. Selsk. Mus. Miscellanea 17, Trondheim.
819 Tande, K.S., 1982. Ecological investigations on the zooplankton community of Balsfjorden,
820 northern Norway - generation cycles, and variations in body-weight and body content of
821 Carbon and Nitrogen related to overwintering and reproduction in the copepod *Calanus*
822 *finmarchicus* (Gunnerus). J. Exp. Mar. Biol. Ecol. 62, 129-142.

823 Utermöhl, H., 1958. Zur Vervollkommung der qualitativen Phytoplankton-Methodik. Mitt Int
824 Theor Angew Limnol 9, 1-38.
825 Verity, P.G., Langdon, C., 1984. Relationships between lorica volume, carbon, nitrogen, and
826 ATP content of tintinnids in Narragansett Bay. J. Plankton Res. 6, 859-868.
827 Zhu, C.J., Lee, Y.K., Chao, T.M., 1997. Effects of temperature and growth phase on lipid and
828 biochemical composition of *Isochrysis galbana* TK1. J. Appl. Phycol. 9, 451-457.

829

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.

Sampling date	Temperature	Salinity	Chlorophyll *a*	POC	PON	POP	Ciliates	Phytoplankton	Diatoms	Dinoflagellates	Flagellates	Ciliates
	°C	PSU	µg chl*a* L^{-1}	µg C L^{-1}	µg N L^{-1}	µg P L^{-1}	µg C L^{-1}	µg C L^{-1}	%	%	%	%
23/02/2009	5.4	32.9	0.1	137	29	1.3	0.04	1.3	15	5	77	3
30/03/2009	5.4	32.6	5.0	430	71	4.6	4.2	208.7	18	1	79	2
27/04/2009	7.5	24.0	2.0	313	58	4.9	0.4	76.9	0	1	99	0
18/05/2009	8.6	28.9	1.1	285	51	4.1	2.7	21.4	32	16	41	11
26/01/2010	4.3	33.3	0.8	nd	nd	nd	nd	nd	nd	nd	nd	nd
18/02/2010	4.2	32.7	0.1	147	23	1.3	0.06	3.5	7	3	88	2
15/03/2010	4.3	33.0	0.6	124	24	1.8	3.8	28.0	6	6	76	12
06/04/2010	5.4	33.6	2.3	436	67	8.1	6.9	254.3	84	1	13	2
18/05/2010	8.8	28.5	1.1	726	121	nd	13.0	103.9	34	39	16	11
25/01/2011	4.3	32.9	0.1	110	25	1.4	0.04	1.0	0	12	85	3
14/02/2011	3.4	32.5	0.6	75	12	1.2	0.19	1.5	19	20	50	11
07/03/2011	4.2	32.8	0.3	88	17	1.5	0.38	0.7	9	40	15	36
22/03/2011	4.5	32.8	2.2	215	43	4.5	7.1	45.6	10	65	11	14
26/04/2011	6.9	26.0	4.6	374	66	6.5	1.7	58.8	1	5	91	3
09/05/2011	7.4	26.2	4.7	216	39	4.1	2.7	75.2	0	15	82	3
30/05/2011	9.2	26.0	0.5	357	58	4.9	5.7	104.8	64	21	10	5
20/06/2011	13.0	24.9	0.8	317	52	5.4	17.5	35.5	3	40	24	33
16/08/2011	12.8	27.0	0.6	307	49	3.8	6.9	118.8	2	72	21	5

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.

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

Table III: Summary of variables which significantly influenced egg production rates (EPR).

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

	Two-parameter hyperbola				
Variable	N	EPR_{max}	K	R^2	p
Protist C >10 µm	16	19.1 ± 1.83	0.44 ± 0.26	0.385	0.008

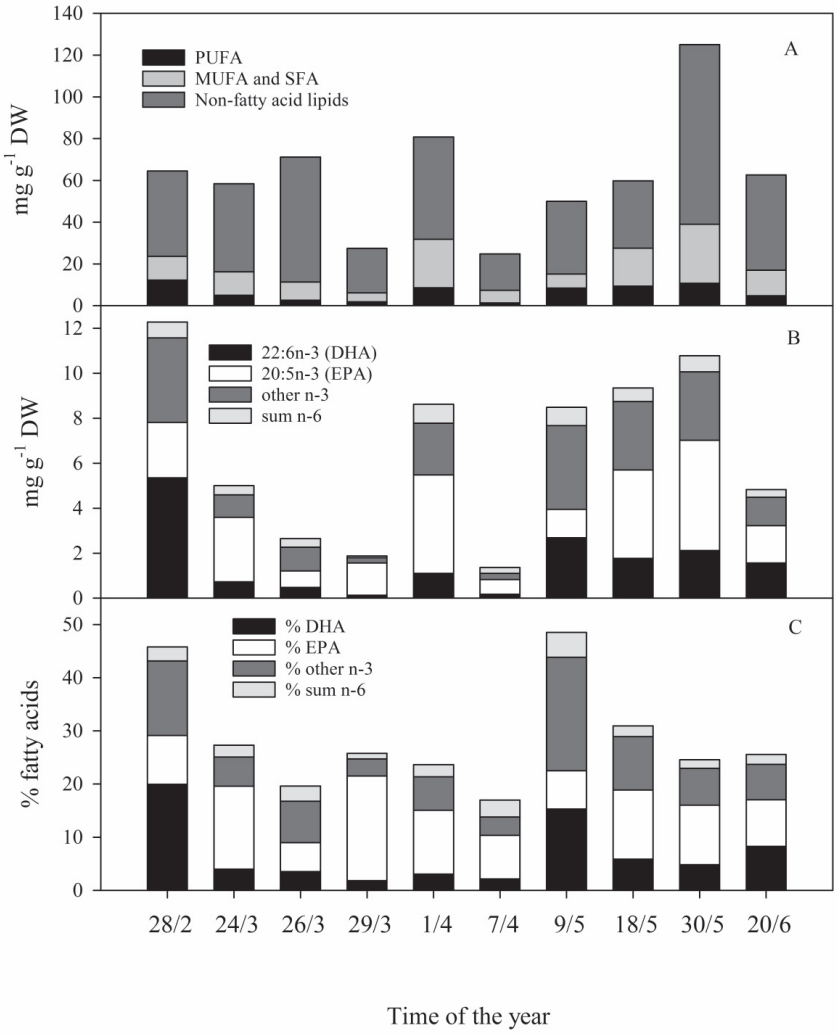


Fig. 1. Fatty acid profiles of the seston. A: Total content of polyunsaturated (PUFA), monounsaturated (MUFA) and saturated (SFA) fatty acids and the fraction of non-fatty acid lipids (mg g^{-1} DW). The total height of the bars represents the total lipid content of the samples. B: Quantitative content (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.

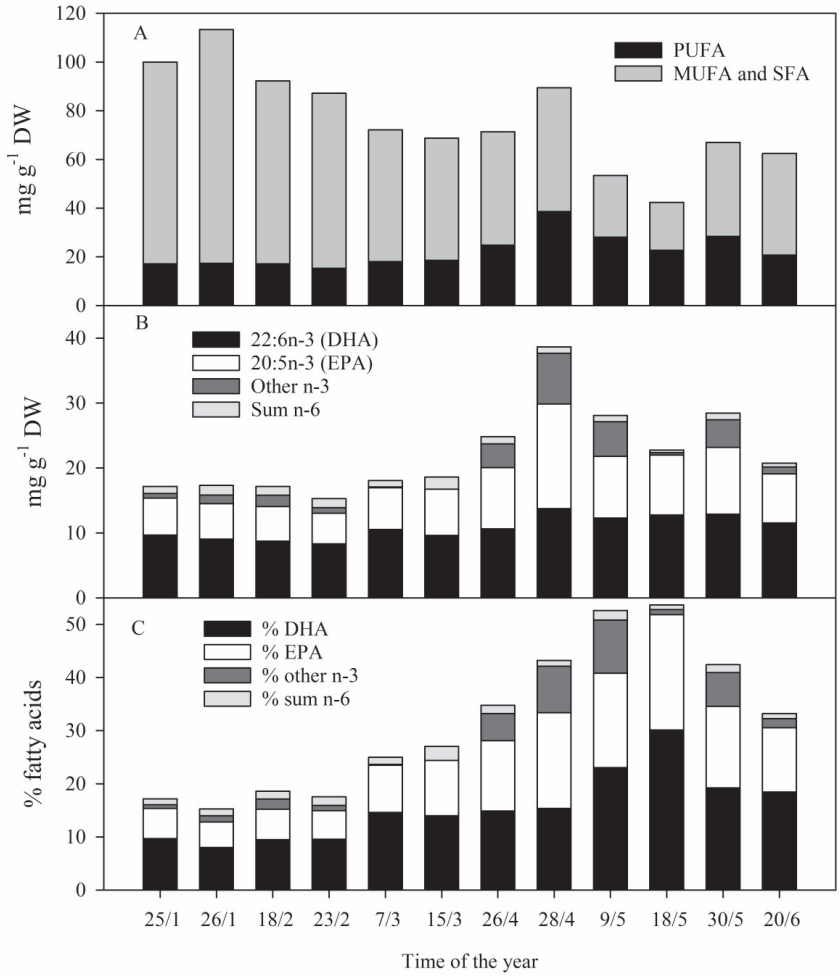


Fig. 2. Fatty acid profiles of female *C. finmarchicus.* A: Fatty acid content of females (mg g^{-1} DW). PUFA: polyunsaturated fatty acids, MUFA: monounsaturated fatty acids, SFA: saturated fatty acids. The total height of the bar represents the total lipid content of the samples. B: Quantitative content (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.

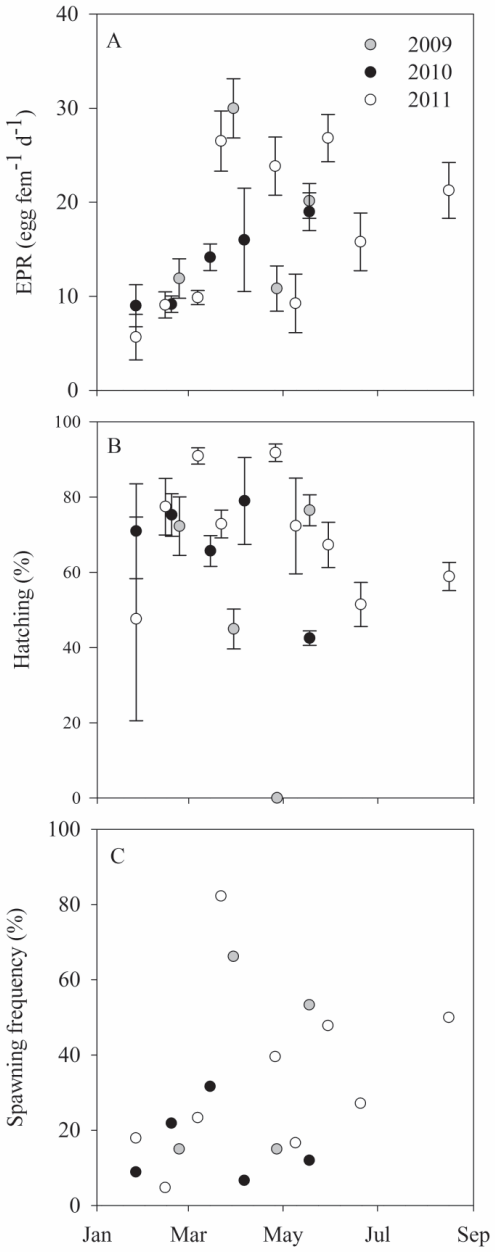


Fig. 3. Reproductive rates of *Calanus finmarchicus* sampled in 2009-2011. A: Egg production rate (EPR, number of eggs produced female^{-1} day^{-1}, mean ± SE). B: Hatching success (percent hatching per sampling day, mean ± SE). C: Spawning frequency (% of females spawning).

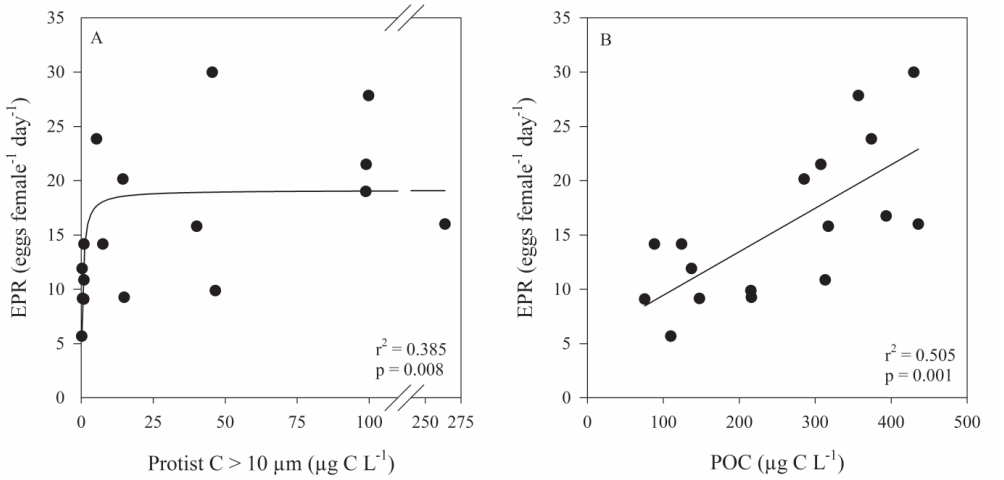


Fig. 4. A: EPR of *Calanus finmarchicus* females as a function of food concentration measured as A: Protist C >10 µm and B: Concentrations of POC < 200 µm.

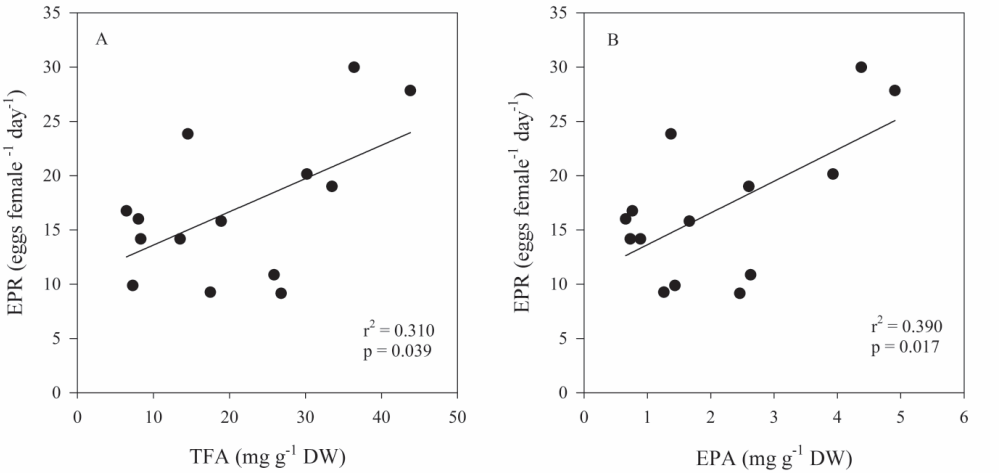


Fig. 5. EPR of *C. finmarchicus* females as a function of food quality measured as A: Total fatty acid content in the seston and B: EPA concentration in the seston.

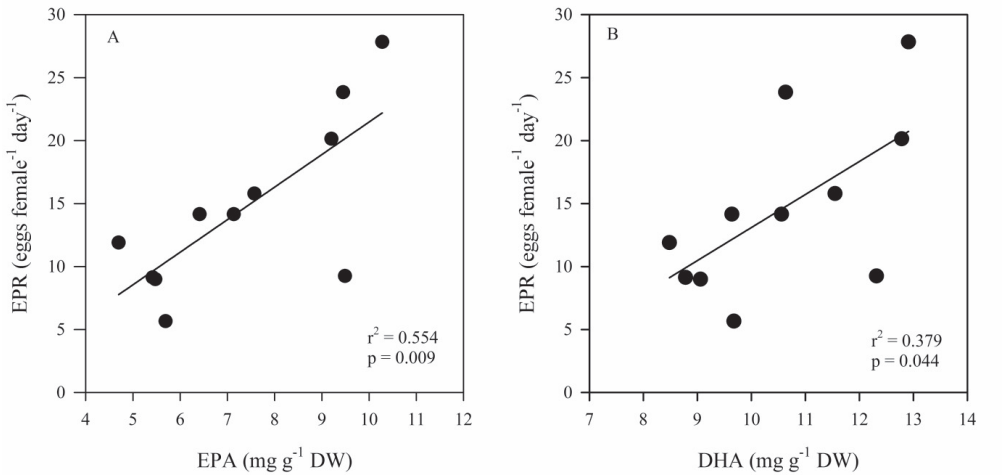


Fig. 6. EPR of *C. finmarchicus* females as a function of female fatty acid content. A: Concentration of EPA (mg EPA g^{-1} DW). B: Concentration of DHA (mg g^{-1} DW).

Paper II

The effect of essential fatty acids for the somatic growth in nauplii of *Calanus finmarchicus*

Øystein Leiknes [1]*, Siv Anina Etter[1], Nils Egil Tokle[2], Maria Bergvik[1], Olav Vadstein[3], Yngvar Olsen[1]

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

molts, but starts to gain weight from nauplii stage III and onwards. The main storage lipid increments takes 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 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 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 mesh net (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 N_2 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.

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 Trondhjem 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 Chl*a*, particulate organic carbon (POC) and nitrogen (PON). Chl*a* 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:

$$\text{Biovolume } (V_t, \mu m^3) = \frac{\pi * L * W^2}{12}$$

Instantaneous specific growth rates of the nauplii (IGR_{nau}, d^{-1}) were calculated from the average biovolume at the beginning ($\bar{V}_0$) and the end ($\bar{V}_t$) of the growth periods.

$$IGR_{nau}\ (d^{-1}) = \frac{\ln \frac{\bar{V}_t}{\bar{V}_0}}{t}$$

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):

$$IGR_{fem}\,(d^{-1}) = \frac{\ln\left(\frac{W_{Eggs} + W_{Female}}{W_{Female}}\right)}{t}$$

W_{Female} and W_{Eggs} 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 µg Chl*a* L^{-1}, respectively (Table 2). During the remaining growth periods the Chl *a* concentration fluctuated between 1.1 and 2.3 µg 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 µm 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

nauplia fed cultured microalgae than for nauplia 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 ($r^2 = 0.670$, 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 Chl*a* (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: $r^2 = 0.350$, half-saturation constant (K) = 1.42 ± 1.28, $p = 0.043$, Figure 8 (A), DHA: $r^2 = 0.472$, 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 (IGR_{nau}, d^{-1}). The IGR_{nau} 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 Chl*a*-concentrations (C:Chla conversion factor of 64 µg C:µg Chla, Vadstein et al., 2004), the Chl*a*-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 (Paffenhöfer and Strickland, 1970;Carlotti and Radach, 1996;Dilling et al., 1998). We therefore suggest that the nauplii grazing selectively on phytoplankton and ciliates

(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_{nau} 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_{nau} of the nauplii fed cultured algae were throughout higher than those of the nauplii fed natural seston; the IGR_{nau} of nauplii fed cultured algae was typically 12–493 % higher than the IGR_{nau} 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 ± 0.20 (mean ± 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 ± 0.83 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 µg C L^{-1}, Campbell et al., 2001b). As the temperature did not vary widely between the sampling dates, we expected that IGR_{nau} was similar for the experiments with nauplii fed surplus cultured food. However, the IGR_{nau} was not equal for the different growth periods (Figure 5), and we observed that there was a significant relationship between the IGR_{nau} 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).

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_{nau} 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 *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_{nau} was found to decrease significantly with increasing IGR_{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_{nau} 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.

7 References

Ackman, R.G., Tocher, C.S., and McLachlan, J. (1968). Marine Phytoplankter Fatty Acids. *Journal of the Fisheries Research Board of Canada* 25**,** 1603-1620.

Båmstedt, U. (1986). "Chemical composition and energy content.," in *The Biological chemistry of marine copepods,* eds. E.D.S. Corner & S.C.M. O'Hara. (Oxford: Clarendon Press), 1-58.

Basedow, S.L., and Tande, K.S. (2006). Cannibalism by female *Calanus finmarchicus* on naupliar stages. *Marine Ecology Progress Series* 327**,** 247-255.

Bell, M.V., Dick, J.R., Anderson, T.R., and Pond, D.W. (2007). Application of liposome and stable isotope tracer techniques to study polyunsaturated fatty acid biosynthesis in marine zooplankton. *Journal of Plankton Research* 29**,** 417-422. doi: 10.1093/plankt/fbm025.

Bergvik, M., Leiknes, Ø., Altin, D., Dahl, K.R., and Olsen, Y. (2012a). Dynamics of the Lipid Content and Biomass of *Calanus finmarchicus* (copepodite V) in a Norwegian Fjord. *Lipids* 47**,** 881-895. doi: 10.1007/s11745-012-3700-3.

Bergvik, M., Overrein, I., Bantle, M., Evjemo, J.O., and Rustad, T. (2012b). Properties of *Calanus finmarchicus* biomass during frozen storage after heat inactivation of autolytic enzymes. *Food Chemistry* 132**,** 209-215. doi: 10.1016/j.foodchem.2011.10.058.

Blachowiak-Samolyk, K., Kwasniewski, S., Dmoch, K., Hop, H., and Falk-Petersen, S. (2007). Trophic structure of zooplankton in the Fram Strait in spring and autumn 2003. *Deep-Sea Research Part Ii-Topical Studies in Oceanography* 54**,** 2716-2728. doi: 10.1016/j.dsr2.2007.08.004.

Bonnet, D., Titelman, J., and Harris, R. (2004). *Calanus* the cannibal. *Journal of plankton research* 26**,** 937-948. doi: 10.1093/plankt/fbh087.

Breteler, W.C.M.K., Schogt, N., and Rampen, S. (2005). Effect of diatom nutrient limitation on copepod development: role of essential lipids. *Marine Ecology Progress Series* 291**,** 125-133.

Calbet, A., Trepat, I., and Arin, L. (2000). Naupliar growth versus egg production in the calanoid copepod *Centropages typicus*. *Journal of Plankton Research* 22**,** 1393-1402. doi: 10.1093/plankt/22.7.1393.

Campbell, R.G., Runge, J.A., and Durbin, E.G. (2001a). Evidence for food limitation of *Calanus finmarchicus* production rates on the southern flank of Georges Bank during April 1997. *Deep-Sea Research Part Ii-Topical Studies in Oceanography* 48**,** 531-549.

Campbell, R.G., Wagner, M.M., Teegarden, G.J., Boudreau, C.A., and Durbin, E.G. (2001b). Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Marine Ecology Progress Series* 221**,** 161-183. doi: 10.3354/meps221161.

Carlotti, F., and Radach, G. (1996). Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled one-dimensional model. *Limnology and Oceanography* 41**,** 522-539.

Castellani, C., Irigoien, X., Mayor, D.J., Harris, R.P., and Wilson, D. (2008). Feeding of *Calanus finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea, North Atlantic. *Journal of plankton research* 30**,** 1095-1116. doi: 10.1093/plankt/fbn074.

Conover, R.J. (1988). Comparative life histories in the genera *Calanus* and *Neocalanus* in high-latitudes of the northern hemisphere. *Hydrobiologia* 167**,** 127-142. doi: 10.1007/bf00026299.

480 Corkett, C.J., McLaren, I.A., and Sevigny, J.-M. (1986). The rearing of the marine calanoid
481 copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus*
482 Krøyer, with comment on the equiproportional rule. *Sylleogeus (Nat Mus Can)* 58**,** 539-
483 546.

484 Custódio, L., Soares, F., Pereira, H., Barreira, L., Vizetto-Duarte, C., Rodrigues, M., Rauter, A.,
485 Alberício, F., and Varela, J. (2014). Fatty acid composition and biological activities of
486 *Isochrysis galbana* T-ISO, *Tetraselmis* sp. and *Scenedesmus* sp.: possible application in
487 the pharmaceutical and functional food industries. *Journal of Applied Phycology* 26**,** 151-
488 161. doi: 10.1007/s10811-013-0098-0.

489 Dalpadado, P., Yamaguchi, A., Ellertsen, B., and Johannessen, S. (2008). Trophic interactions of
490 macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea.
491 *Deep-Sea Research Part Ii-Topical Studies in Oceanography* 55**,** 2266-2274. doi:
492 10.1016/j.dsr2.2008.05.016.

493 Dilling, L., Wilson, J., Steinberg, D., and Alldredge, A. (1998). Feeding by the euphausiid
494 *Euphausia pacifica* and the copepod *Calanus pacificus* on marine snow. *Marine Ecology*
495 *Progress Series* 170**,** 189-201. doi: 10.3354/meps170189.

496 Dodds, L.A., Black, K.D., Orr, H., and Roberts, J.M. (2009). Lipid biomarkers reveal
497 geographical differences in food supply to the cold-water coral *Lophelia pertusa*
498 (Scleractinia). *Marine Ecology Progress Series* 397**,** 113-124. doi: Doi
499 10.3354/Meps08143.

500 Dommasnes, A., Melle, W., Dalpadado, P., and Ellertsen, B. (2004). Herring as a major consumer
501 in the Norwegian Sea. *Ices Journal of Marine Science* 61**,** 739-751. doi:
502 10.1016/j.icesjms.2004.04.001.

503 Eiane, K., Aksnes, D.L., Ohman, M.D., Simon, W., and Martinussen, M.B. (2002). Stage-specific
504 mortality of *Calanus* spp. under different predation regimes. *Limnology and*
505 *Oceanography* 47**,** 636-645.

506 Evjemo, J.O., Reitan, K.I., and Olsen, Y. (2003). Copepods as live food organisms in the larval
507 rearing of halibut larvae (*Hippoglossus hippoglossus* L.) with special emphasis on the
508 nutritional value. *Aquaculture* 227**,** 191-210. doi: 10.1016/s0044-8486(03)00503-9.

509 Evjemo, J.O., Tokle, N., Vadstein, O., and Olsen, Y. (2008). Effect of essential dietary fatty acids
510 on egg production and hatching success of the marine copepod *Temora longicornis*.
511 *Journal of Experimental Marine Biology and Ecology* 365**,** 31-37.

512 Gatten, R.R., Sargent, J.R., Forsberg, T.E.V., O'Hara, S.C.M., and Corner, E.D.S. (1980). On the
513 nutrition and metabolism of zooplankton. XIV. Utilization of lipid by *Calanus*
514 *helgolandicus* during maturation and reproduction. *Journal of the Marine Biological*
515 *Association of the United Kingdom* 60**,** 391-399.

516 Gismervik, I., Andersen, T., and Vadstein, O. (1996). Pelagic food webs and eutrophication of
517 coastal waters: Impact of grazers on algal communities. *Marine Pollution Bulletin* 33**,** 22-
518 35. doi: 10.1016/s0025-326x(96)00134-8.

519 Guillard, R.R.L. (ed.). (1975). *Culture of phytoplankton for feeding marine invertebrates.* New
520 York: Plenum Press.

521 Hallegraeff, G.M., Nichols, P.D., Volkman, J.K., Blackburn, S.I., and Everitt, D.A. (1991).
522 Pigments, fatty-acids, and sterols of the toxic dinoflagellate *Gymnodinium catenatum*.
523 *Journal of Phycology* 27**,** 591-599. doi: 10.1111/j.0022-3646.1991.00591.x.

524 Hansen, B.H., Altin, D., Nordtug, T., and Olsen, A.J. (2007). Suppression subtractive
525 hybridization library prepared from the copepod *Calanus finmarchicus* exposed to a

sublethal mixture of environmental stressors. *Comparative Biochemistry and Physiology D-Genomics & Proteomics* 2**,** 250-256. doi: 10.1016/j.cbd.2007.04.006.

Hansen, B.W., Bjørnsen, P.K., and Hansen, P.J. (1994). The size ratio between planktonic predators and their prey. *Limnology and Oceanography* 39**,** 395-403.

Harris, R.P., Irigoien, X., Head, R.N., Rey, C., Hygum, B.H., Hansen, B.W., Niehoff, B., Meyer-Harms, B., and Carlotti, F. (2000). Feeding, growth, and reproduction in the genus *Calanus*. *Ices Journal of Marine Science* 57**,** 1708-1726.

Hirche, H.J. (1990). Egg-production of *Calanus finmarchicus* at low temperature. *Marine Biology* 106**,** 53-58. doi: 10.1007/bf02114674.

Hopcroft, R.R., and Roff, J.C. (1998). Zooplankton growth rates: the influence of female size and resources on egg production of tropical marine copepods. *Marine Biology* 132**,** 79-86. doi: 10.1007/s002270050373.

Hygum, B.H., Rey, C., and Hansen, B.W. (2000a). Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. *Marine Biology* 136**,** 1075-1085. doi: 10.1007/s002270000313.

Hygum, B.H., Rey, C., Hansen, B.W., and Carlotti, F. (2000b). Rearing cohorts of *Calanus finmarchicus* (Gunnerus) in mesocosms. *Ices Journal of Marine Science* 57**,** 1740-1751. doi: 10.1006/jmsc.2000.0956.

Ianora, A., Poulet, S.A., and Miralto, A. (2003). The effects of diatoms on copepod reproduction: a review. *Phycologia* 42**,** 351-363. doi: 10.2216/i0031-8884-42-4-351.1.

Irigoien, X., Titelman, J., Harris, R.P., Harbour, D., and Castellani, C. (2003). Feeding of *Calanus finmarchicus* nauplii in the Irminger Sea. *Marine Ecology Progress Series* 262**,** 193-200. doi: 10.3354/meps262193.

Jonasdottir, S.H. (1999). Lipid content of *Calanus finmarchicus* during overwintering in the Faroe-Shetland Channel. *Fisheries Oceanography* 8**,** 61-72. doi: 10.1046/j.1365-2419.1999.00003.x.

Jonasdottir, S.H., Gudfinnsson, H.G., Gislason, A., and Astthorsson, O.S. (2002). Diet composition and quality for *Calanus finmarchicus* egg production and hatching success off south-west Iceland. *Marine Biology* 140**,** 1195-1206. doi: 10.1007/s00227-002-0782-0.

Jonasdottir, S.H., Richardson, K., Heath, M.R., Ingvarsdottir, A., and Christoffersen, A. (2008). Spring production of *Calanus finmarchicus* at the Iceland-Scotland ridge. *Deep Sea Research, Part I: Oceanographic Research Papers* 55**,** 471-489. doi: 10.1016/j.dsr.2007.12.009.

Jonasdottir, S.H., Trung, N.H., Hansen, F., and Gartner, S. (2005). Egg production and hatching success in the calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* in the North Sea from March to September 2001. *Journal of plankton research* 27**,** 1239-1259. doi: 10.1093/plankt/fbi091.

Jonasdottir, S.H., Visser, A.W., and Jespersen, C. (2009). Assessing the role of food quality in the production and hatching of *Temora longicornis* eggs. *Marine Ecology Progress Series* 382**,** 139-150. doi: 10.3354/meps07985.

Kane, J. (1984). The feeding-habits of co-occurring cod and haddock larvae from Georges Bank. *Marine Ecology Progress Series* 16**,** 9-20. doi: 10.3354/meps016009.

Kattner, G., Hagen, W., Lee, R.F., Campbell, R., Deibel, D., Falk-Petersen, S., Graeve, M., Hansen, B.W., Hirche, H.J., Jonasdottir, S.H., Madsen, M.L., Mayzaud, P., Muller-Navarra, D., Nichols, P.D., Paffenhofer, G.A., Pond, D., Saito, H., Stubing, D., and

571 Virtue, P. (2007). Perspectives on marine zooplankton lipids. *Canadian Journal of*
572 *Fisheries and Aquatic Sciences* 64**,** 1628-1639. doi: 10.1139/f07-122.

573 Kiørboe, T., and Johansen, K. (1986). Studies of a larval herring (*Clupea harengus* L.) patch in
574 the Buchan area. IV. Zooplankton distribution and productivity in relation to hydrographic
575 features. *Dana: A Journal of Fisheries and Marine Research* 6**,** 37-51.

576 Koski, M., Dutz, J., Breteler, W.K., Rampen, S., and Noordeloos, A. (2010). Seasonal changes in
577 food quantity and quality of the common North Sea copepods *Temora longicornis* and
578 *Pseudocalanus elongatus*: a bioassay approach. *Marine Ecology Progress Series* 399**,**
579 141-155. doi: 10.3354/meps08357.

580 Koski, M., Yebra, L., Dutz, J., Jonasdottir, S.H., Vidoudez, C., Jakobsen, H.H., Pohnert, G., and
581 Nejstgaard, J.C. (2012). The effect of egg versus seston quality on hatching success,
582 naupliar metabolism and survival of *Calanus finmarchicus* in mesocosms dominated by
583 *Phaeocystis* and diatoms. *Marine Biology* 159**,** 643-660. doi: 10.1007/s00227-011-1843-z.

584 Lee, R.F., Hagen, W., and Kattner, G. (2006). Lipid storage in marine zooplankton. *Marine*
585 *Ecology Progress Series* 307**,** 273-306. doi: 10.3354/meps307273.

586 Lee, R.F., Nevenzel, J.C., and Paffenhöfer, G.-A. (1972). The Presence of Wax Esters in Marine
587 Planktonic Copepods. *Naturwissenschaften* 59**,** 406-411.

588 Lee, R.F., and Walker, A. (1995). Lipovitellin and lipid droplet accumulation in oocytes during
589 ovarian maturation in the blue crab, *Callinectes sapidus*. *Journal of Experimental Zoology*
590 271**,** 401-412. doi: 10.1002/jez.1402710510.

591 Lee, S.-Y., Kim, S.-H., Hyun, S.-H., Suh, H.W., Hong, S.-J., Cho, B.-K., Lee, C.-G., Lee, H., and
592 Choi, H.-K. (2014). Fatty acids and global metabolites profiling of *Dunaliella tertiolecta*
593 by shifting culture conditions to nitrate deficiency and high light at different growth
594 phases. *Process Biochemistry* 49**,** 996-1004. doi:
595 http://dx.doi.org/10.1016/j.procbio.2014.02.022.

596 Mansour, M.P., Volkman, J.K., Jackson, A.E., and Blackburn, S.I. (1999). The fatty acid and
597 sterol composition of five marine dinoflagellates. *Journal of Phycology* 35**,** 710-720. doi:
598 10.1046/j.1529-8817.1999.3540710.x.

599 Melle, W., Runge, J., Head, E., Plourde, S., Castellani, C., Licandro, P., Pierson, J., Jonasdottir,
600 S., Johnson, C., Broms, C., Debes, H., Falkenhaug, T., Gaard, E., Gislason, A., Heath, M.,
601 Niehoff, B., Nielsen, T.G., Pepin, P., Stenevik, E.K., and Chust, G. (2014). The North
602 Atlantic Ocean as habitat for *Calanus finmarchicus*: Environmental factors and life history
603 traits. *Progress in Oceanography* 129**,** 244-284. doi: 10.1016/j.pocean.2014.04.026.

604 Møller, E.F., Maar, M., Jónasdóttir, S.H., Nielsen, T.G., and Tönnesson, K. (2012). The effect of
605 changes in temperature and food on the development of *Calanus finmarchicus* and
606 *Calanus helgolandicus* populations. *Limnology and Oceanography* 57**,** 211-220. doi:
607 10.4319/lo.2012.57.1.0211.

608 Ohman, M.D., Durbin, E.G., Runge, J.A., Sullivan, B.K., and Field, D.B. (2008). Relationship of
609 predation potential to mortality of *Calanus finmarchicus* on Georges Bank, Northwest
610 Atlantic. *Limnology and Oceanography* 53**,** 1643-1655.

611 Ohman, M.D., Eiane, K., Durbin, E.G., Runge, J.A., and Hirche, H.J. (2004). A comparative
612 study of *Calanus finmarchicus* mortality patterns at five localities in the North Atlantic.
613 *Ices Journal of Marine Science* 61**,** 687-697. doi: 10.1016/j.icesjms.2004.03.016.

614 Ohman, M.D., and Runge, J.A. (1994). Sustained fecundity when phytoplankton resources are in
615 short supply: Omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. *Limnology*
616 *and Oceanography* 39**,** 21-36.

617 Olsen, Y., Evjemo, J.O., Kjorsvik, E., Larssen, H., Li, K.S., Overrein, I., and Rainuzzo, J. (2014).
618 DHA content in dietary phospholipids affects DHA content in phospholipids of cod larvae
619 and larval performance. *Aquaculture* 428**,** 203-214. doi:
620 10.1016/j.aquaculture.2014.03.002.

621 Paffenhöfer, G.-A., and Strickland, J.H.D. (1970). A note on feeding of *Calanus helgolandicus* on
622 detritus. *Marine Biology* 5**,** 97-99. doi: 10.1007/bf00352591.

623 Payne, P.M., Wiley, D.N., Young, S.B., Pittman, S., Clapham, P.J., and Jossi, J.W. (1990).
624 Recent fluctuations in the abundance of baleen whales in the southern Gulf of Maine in
625 relation to changes in selected prey. *Fishery Bulletin* 88**,** 687-696.

626 Planque, B., and Batten, S.D. (2000). *Calanus finmarchicus* in the North Atlantic: the year of
627 *Calanus* in the context of interdecadal change. *Ices Journal of Marine Science* 57**,** 1528-
628 1535. doi: 10.1006/jmsc.2000.0970.

629 Pond, D., Harris, R., Head, R., and Harbour, D. (1996). Environmental and nutritional factors
630 determining seasonal variability in the fecundity and egg viability of *Calanus*
631 *helgolandicus* in coastal waters off Plymouth, UK. *Marine Ecology Progress Series* 143**,**
632 45-63. doi: 10.3354/meps143045.

633 Poulet, S.A., Ianora, A., Laabir, M., and Breteler, W. (1995). Towards the measurement of
634 secondary production and recruitment in copepods. *Ices Journal of Marine Science* 52**,**
635 359-368. doi: 10.1016/1054-3139(95)80051-4.

636 Reitan, K.I., Rainuzzo, J.R., and Olsen, Y. (1994). Effect of nutrient limitation on fatty-acid and
637 lipid-content of marine microalgae. *Journal of Phycology* 30**,** 972-979.

638 Rey, C., Harris, R., Irigoien, X., Head, R., and Carlotti, F. (2001). Influence of algal diet on
639 growth and ingestion of *Calanus helgolandicus* nauplii. *Marine Ecology Progress Series*
640 216**,** 151-165. doi: 10.3354/meps216151.

641 Richardson, K., Jónasdóttir, S.H., Hay, S.J., and Christoffersen, A. (1999). *Calanus finmarchicus*
642 egg production and food availability in the Faroe–Shetland Channel and northern North
643 Sea: October–March. *Fisheries Oceanography* 8**,** 153-162. doi: 10.1046/j.1365-
644 2419.1999.00007.x.

645 Runge, J.A. (1988). Should we expect a relationship between primary production and fisheries?
646 The role of copepod dynamics as a filter of trophic variability. *Hydrobiologia* 167**,** 61-71.
647 doi: 10.1007/bf00026294.

648 Ruyter, B., Rosjo, C., Masoval, K., Einen, O., and Thomassen, M.S. (2000). Influence of dietary
649 n-3 fatty acids on the desaturation and elongation of [1-^{14}C] 18:2 n-6 and [1-^{14}C] 18:3 n-3
650 in Atlantic salmon hepatocytes. *Fish Physiology and Biochemistry* 23**,** 151-158. doi:
651 10.1023/a:1007893317923.

652 Sargent, J.R., and Falk-Petersen, S. (1988). The lipid biochemistry of calanoid copepods.
653 *Hydrobiologia* 167**,** 101-114.

654 Sargent, J.R., and Whittle, K.J. (1981). "Lipids and hydrocarbons in the marine food web," in
655 *Analysis of marine ecosystems,* ed. A.R. Longhurst. (London: Academic Press), 491-533.

656 St. John, M.A., and Lund, T. (1996). Lipid biomarkers: Linking the utilization of frontal plankton
657 biomass to enhanced condition of juvenile North Sea cod. *Marine Ecology Progress*
658 *Series* 131**,** 75-85. doi: 10.3354/meps131075.

659 Strickland, J.H.D., and Parsons, T.R. (1972). *A Practical Handbook of Seawater Analysis.*
660 Ottawa: Fisheries Research Board of Canada.

661 Suroy, M., Moriceau, B., Boutorh, J., and Goutx, M. (2014). Fatty acids associated with the
662 frustules of diatoms and their fate during degradation—A case study in *Thalassiosira*
663 *weissflogii*. *Deep Sea Research Part I: Oceanographic Research Papers* 86**,** 21-31. doi:
664 http://dx.doi.org/10.1016/j.dsr.2014.01.001.

665 Tande, K.S. (1988). Aspects of developmental and mortality-rates in *Calanus finmarchicus*
666 related to equiproportional development. *Marine Ecology Progress Series* 44**,** 51-58. doi:
667 10.3354/meps044051.

668 Tocher, D.R., Bell, J.G., MacGlaughlin, P., McGhee, F., and Dick, J.R. (2001). Hepatocyte fatty
669 acid desaturation and polyunsaturated fatty acid composition of liver in salmonids: effects
670 of dietary vegetable oil. *Comparative Biochemistry and Physiology B-Biochemistry &*
671 *Molecular Biology* 130**,** 257-270. doi: 10.1016/s1096-4959(01)00429-8.

672 Tönnesson, K., Nielsen, T.G., and Tiselius, P. (2006). Feeding and production of the carnivorous
673 copepod *Pareuchaeta norvegica* in the Skagerrak. *Marine Ecology Progress Series* 314**,**
674 213-225.

675 Turner, J.T., Levinsen, H., Nielsen, T.G., and Hansen, B.W. (2001). Zooplankton feeding
676 ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle
677 nauplii in Disko Bay, West Greenland. *Marine Ecology Progress Series* 221**,** 209-219.
678 doi: 10.3354/meps221209.

679 Vadstein, O., Stibor, H., Lippert, B., Loseth, K., Roederer, W., Sundt-Hansen, L., and Olsen, Y.
680 (2004). Moderate increase in the biomass of omnivorous copepods may ease grazing
681 control of planktonic algae. *Marine Ecology-Progress Series* 270**,** 199-207.

682 Watling, L. (2007). Predation on copepods by an Alaskan cladorhizid sponge. *Journal of the*
683 *Marine Biological Association of the United Kingdom* 87**,** 1721-1726. doi:
684 10.1017/s0025315407058560.

685 Winberg, G.G. (1971). *Methods for the estimation of production of aquatic animals.* London:
686 Academic Press.

687

688 **8 Tables and Figures**

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

692

Category	Size fraction (µm)	Distribution (% biovolume)					
		Egg	Nauplii	Cop.	*Cosc.*	*Proto.*	*Ceratium*
Protoperidinium sp.	70–80		0.1		6.4	93.4	
Coscinodiscus sp.	190–200		5.0		95.0		
Eggs (17.02.2010)	80–150	84.5	1.4	9.6	2.0		2.5
Eggs (28.02.2010)	80–150	86.7	1.2	1.3	10.7		0.1
Eggs (10.03.2007)	140–150	47.7	9.9		42.4		
NII-NIII	106–110	2.7	46.9	15.9	34.5		
NIII-NIV	200–300	0.2	51.3		48.5		
CII-CIII	400–600			100			
CIII-CIV	600-1300			100			

693

694 **Table 2.** Experimental dates, incubation temperatures (°C) and concentration of Chl*a* (µg L^{-1}),
695 and particulate organic carbon (POC, µg C L^{-1}) for the growth periods.
696

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

697

698
699 ## 8.1 Figure legends
700
701 **Figure 1.** Fatty acid profiles of the seston, <55 µm. (A): Total content of fatty acids and lipids.
702 (B): Quantitative content (mg g^{-1} DW) of different groups of fatty acids. Important essential fatty
703 acids (EFAs; DHA and EPA) are separated. (C): Relative content of the different groups of fatty
704 acids (% of total fatty acids).
705
706 **Figure 2.** Total lipid and total fatty acids content (mg g^{-1} DW) in eggs, nauplii and copepodites of
707 *C. finmarchicus* and of the microalgae *Coscinodiscus* sp. and *Protoperidinium* sp.
708
709 **Figure 3.** Fatty acid profiles of eggs, nauplii and copepodites of *C. finmarchicus* and of the
710 microalgae *Coscinodiscus* sp. and *Protoperidinium* sp. (A): quantitative fatty acid content (mg g^{-1}
711 DW). (B): relative content (% of total fatty acids). The samples from 17/2 and from 25/2
712 contained a fraction of unknown fatty acids not included in the figure.
713
714 **Figure 4.** Content of the different lipid classes; phosphatidylethanolamine (PE),
715 phosphatidylcholine (PC), wax ester (WE), triacylglycerol (TAG), and free fatty acids (FFA) in
716 *C. finmarchicus* eggs. (A): Quantitative content (mg g^{-1} DW). (B): Relative content (% of total
717 lipids). Error bars equals standard error (n = 2).
718
719 **Figure 5.** Scatterplot of biovolume-specific growth rates (day^{-1}) through three seasons (Mean ±
720 SE). Filled symbols indicate nauplii fed natural seston (< 55 µm), open symbols indicate nauplii
721 fed cultured algae. Asterisk indicates growth periods where there is a difference between growth
722 of nauplii fed natural seston and cultured microalgae (Student T-test, $p < 0.05$).

723
724 **Figure 6.** Growth in nauplii fed natural seston (d^{-1}) versus nauplii fed cultured microalgae (d^{-1}).
725 Dots indicate average, error bars standard error. Lines indicate linear regression line with 95%
726 confidence interval.
727
728 **Figure 7.** Biovolume-specific growth rate (day^{-1}) of nauplii of *C. finmarchicus* versus Chl *a* < 55
729 µm (Pearson correlation coefficient 0.497, p = 0.103).
730
731 **Figure 8.** Scatterplot of growth rates (day^{-1}, mean ± SE) of nauplii versus (A): the content of EPA
732 and (B): the content of DHA in the seston (mg g DW^{-1}). Lines indicate regressions (2-parameter
733 hyperbola) with 95% confidence intervals.

Figure 1

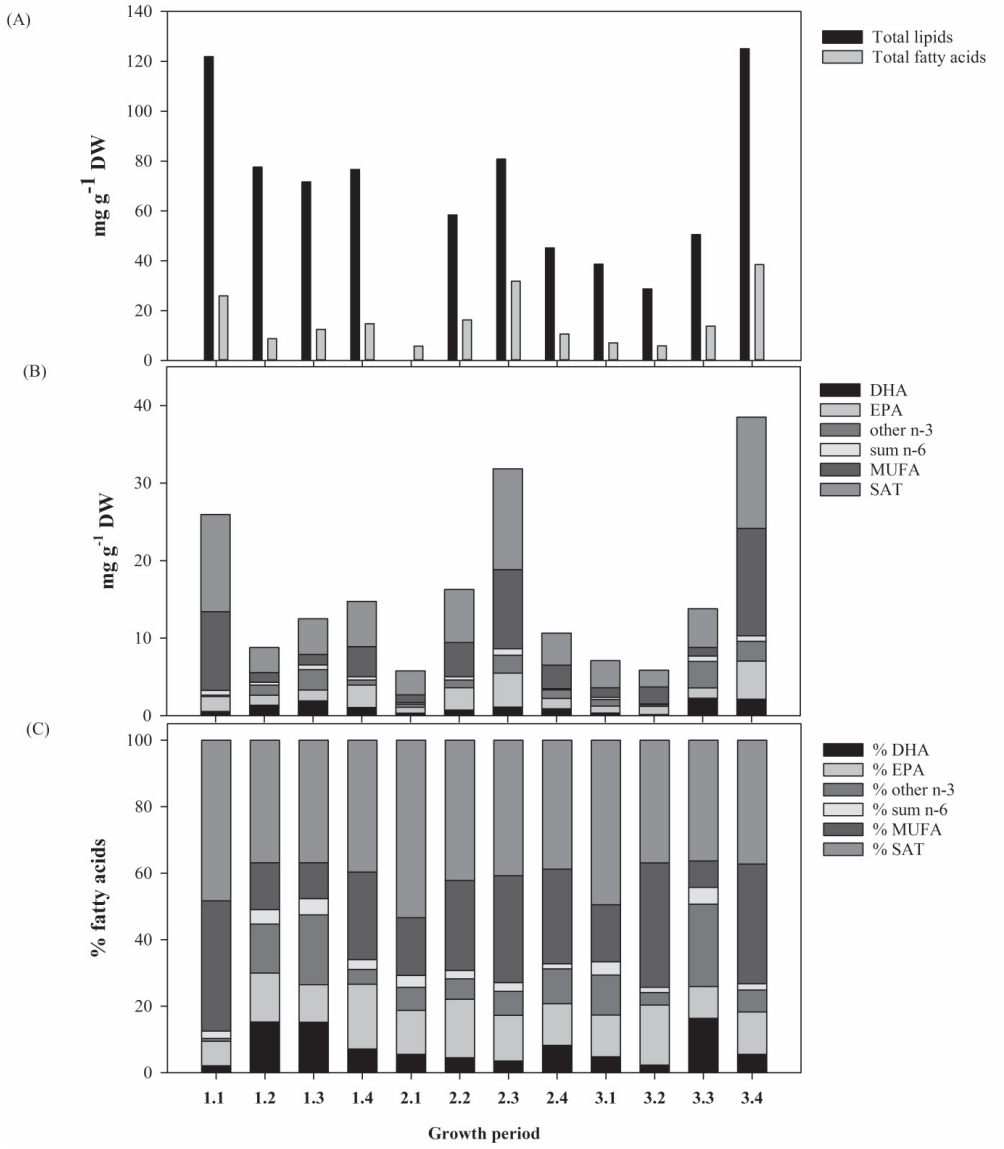

(A)
mg g-1 DW
Total lipids
Total fatty acids
(B)
mg g-1 DW
DHA
EPA
other n-3
sum n-6
MUFA
SAT
(C)
% fatty acids
% DHA
% EPA
% other n-3
% sum n-6
% MUFA
% SAT
1.1
1.2
1.3
1.4
2.1
2.2
2.3
2.4
3.1
3.2
3.3
3.4
Growth period

Figure 2

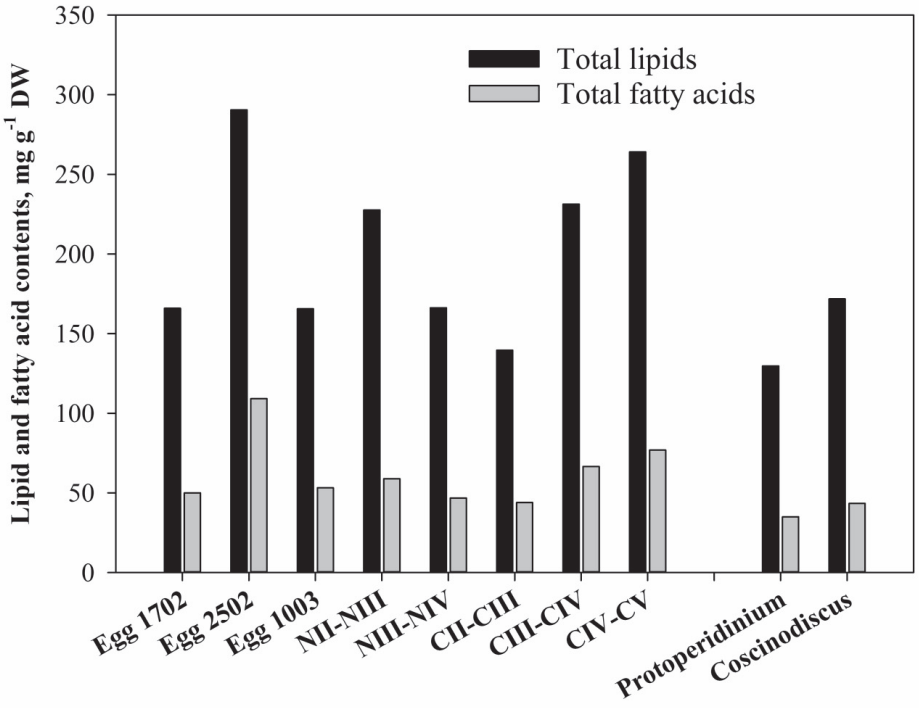

Lipid and fatty acid contents, mg g-1 DW
350
300
250
200
150
100
50
0
Total lipids
Total fatty acids
Egg 1702
Egg 2502
Egg 1003
NII-NIII
NIII-NIV
CII-CIII
CIII-CIV
CIV-CV
Protoperidinium
Coscinodiscus

Figure 3

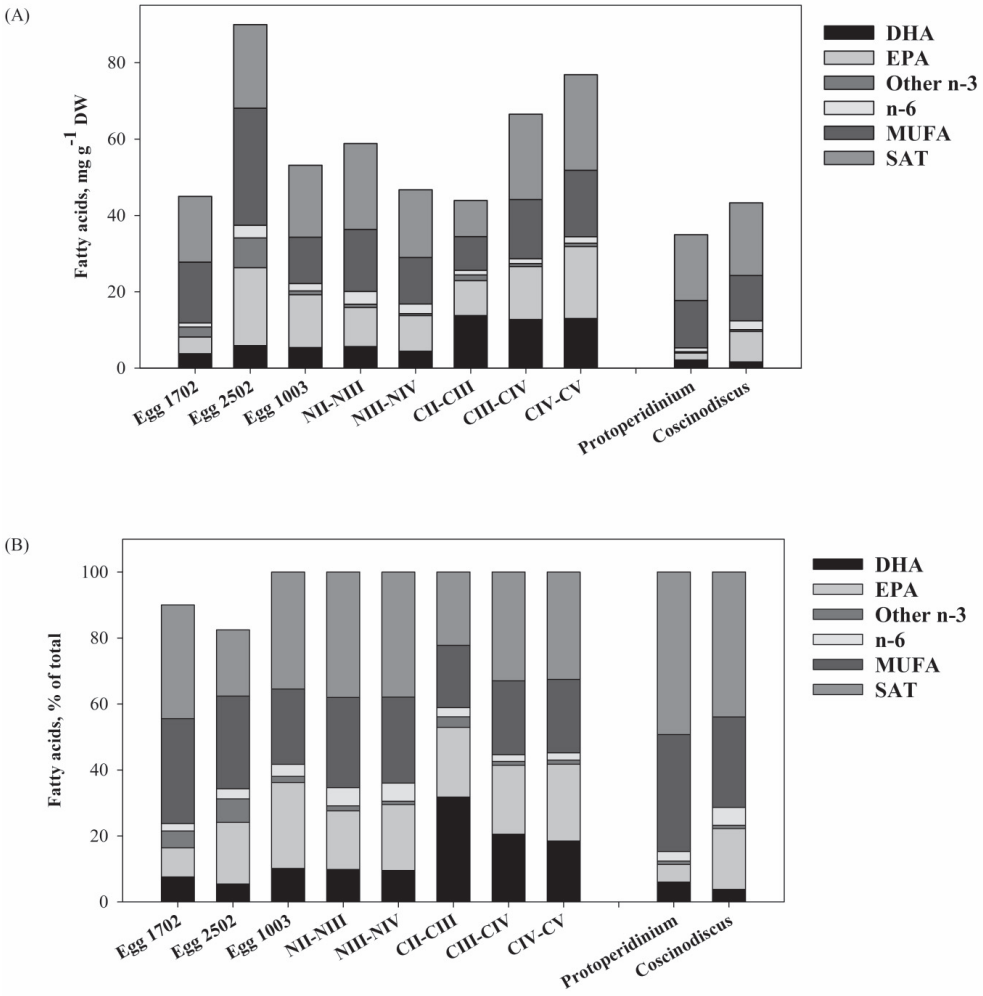

(A)
Fatty acids, mg g-1 DW
0
20
40
60
80
DHA
EPA
Other n-3
n-6
MUFA
SAT
Egg 1702
Egg 2502
Egg 1003
NII-NIII
NIII-NIV
CII-CIII
CIII-CIV
CIV-CV
Protoperidinium
Coscinodiscus
(B)
Fatty acids, % of total
0
20
40
60
80
100
DHA
EPA
Other n-3
n-6
MUFA
SAT
Egg 1702
Egg 2502
Egg 1003
NII-NIII
NIII-NIV
CII-CIII
CIII-CIV
CIV-CV
Protoperidinium
Coscinodiscus

Figure 4

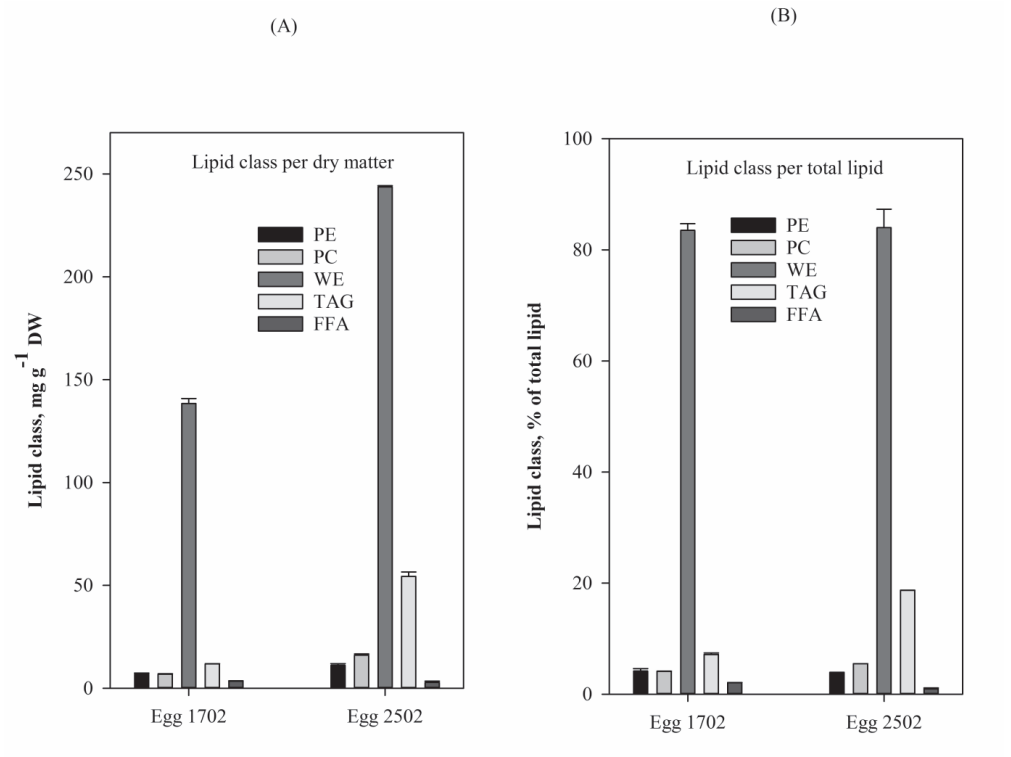

(A)
(B)
Lipid class per dry matter
Lipid class per total lipid
PE
PC
WE
TAG
FFA
Lipid class, mg g-1 DW
Lipid class, % of total lipid
0
50
100
150
200
250
0
20
40
60
80
100
Egg 1702
Egg 2502

Figure 5

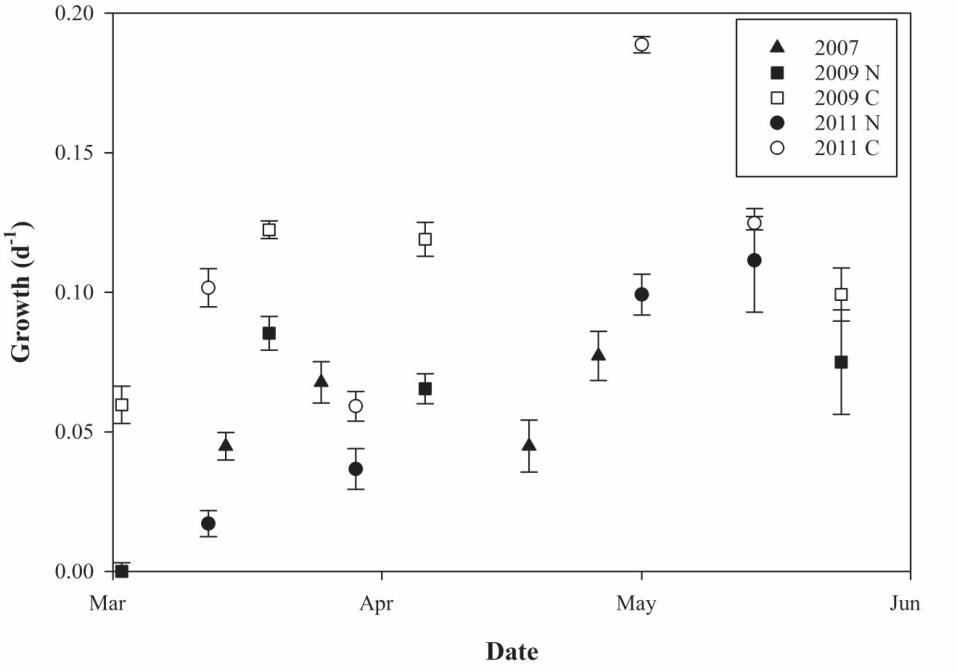

0.20
0.15
0.10
0.05
0.00
Growth (d-1)
Mar
Apr
May
Jun
Date
2007
2009 N
2009 C
2011 N
2011 C

Figure 6

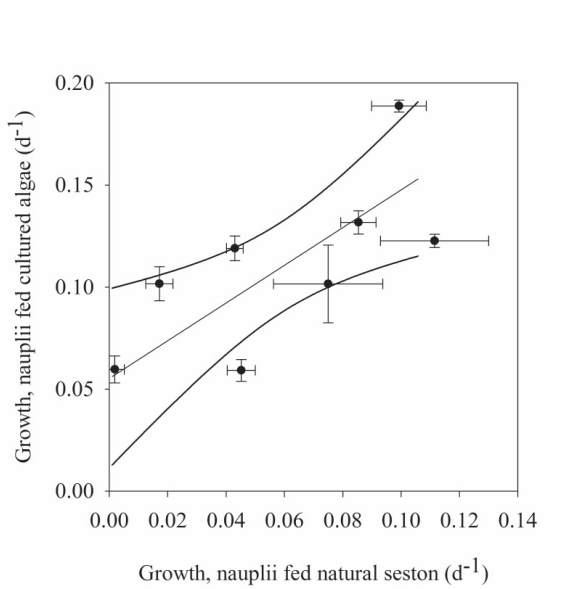

0.20
0.15
0.10
0.05
0.00
0.00 0.02 0.04 0.06 0.08 0.10 0.12 0.14
Growth, nauplii fed cultured algae (d-1)
Growth, nauplii fed natural seston (d-1)

Figure 7

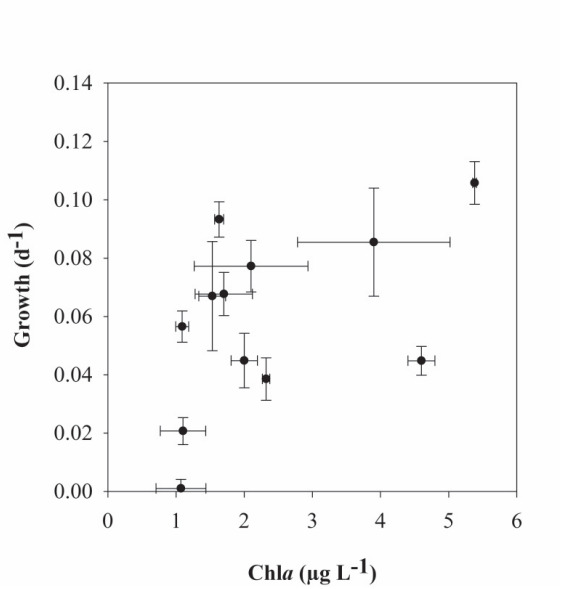


Figure 8

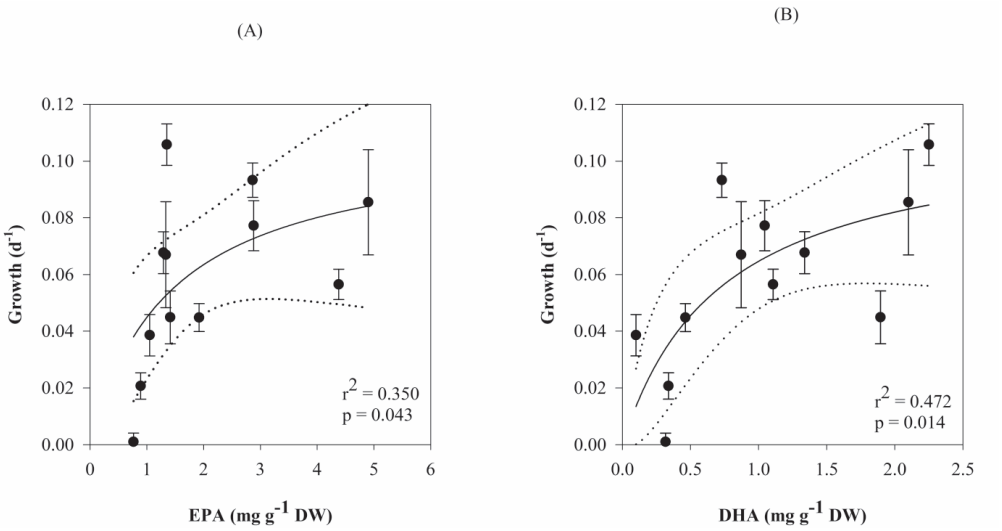
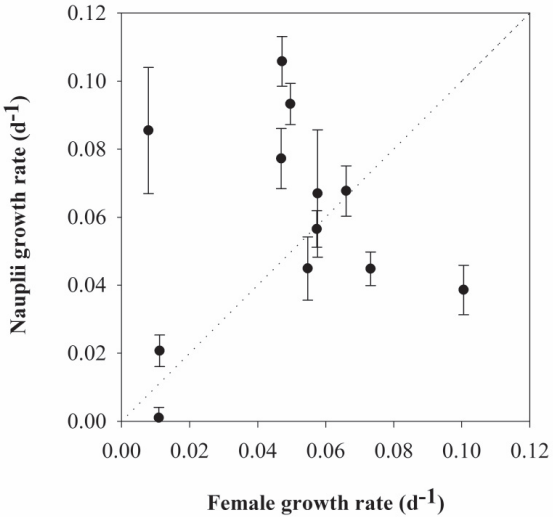

(A)
(B)
Growth (d-1)
EPA (mg g-1 DW)
DHA (mg g-1 DW)
r2 = 0.350
p = 0.043
r2 = 0.472
p = 0.014

Figure 9


0.12
0.10
0.08
0.06
0.04
0.02
0.00
0.00
0.02
0.04
0.06
0.08
0.10
0.12
Nauplii growth rate (d-1)
Female growth rate (d-1)

Paper III

Is not included due to copyright

Paper IV

Journal of Sea Research 85 (2014) 292–299

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Feeding selectivity of *Calanus finmarchicus* in the Trondheimsfjord

Øystein Leiknes [a,*,1], Anja Striberny [b], Nils Egil Tokle [c], Yngvar Olsen [a], Olav Vadstein [d], Ulrich Sommer [e]

[a] Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway
[b] Institute of Arctic and Marine Biology, University of Tromsø, N-9037 Tromsø, Norway
[c] Planktonic AS, N-8850 Herøy, Norway
[d] Department of Biotechnology, Norwegian University of Science Technology, N-7491 Trondheim, Norway
[e] GEOMAR | Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, D-24105 Kiel, Germany

ARTICLE INFO

Article history:
Received 9 January 2012
Received in revised form 23 May 2013
Accepted 26 May 2013
Available online 19 June 2013

Keywords:
Calanus finmarchicus
Trondheimsfjord
Selective feeding
Ciliates
Phytoplankton

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*.

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 (Planque and Batten, 2000) and plays a crucial role in the energy transfer from primary producers to higher trophic levels in this important fisheries region. 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 Radach, 1996; Slagstad et al., 1999). These models rely on proper parameterization of important biological mechanisms. One of the key questions with limited knowledge is whether *C. finmarchicus* is mainly herbivorous or if the species has the ability to actively select heterotrophic food particles. We also need increased knowledge on how the differences in microplankton composition affects the feeding selectivity.

The trophic state of *C. finmarchicus* has been described as herbivorous (Graeve et al., 1994; Koski and Riser, 2006; Teegarden et al., 2001), whereas other studies have indicated that *C. finmarchicus* is omnivorous. In some experiments, *C. finmarchicus* has shown selectivity for ciliates over other food particles available (Irigoien et al., 1998; Nejstgaard et al., 1994, 1997), while some investigations have shown non-selective consumption of ciliates (e.g. Levinsen et al., 2000). Ohman and Runge (1994) explained a sustained high egg production of *C. finmarchicus* in the Gulf of St. Lawrence at low phytoplankton densities by consumption of microzooplankton, and a stable isotope analysis in the Trondheimsfjord (Central Norway) indicated *C. finmarchicus* to be omnivorous with an average trophic level of 2.4 (Saage et al., 2008). Besides this, the role of diatoms as the dominant food for copepods was challenged in the late 1990s when negative effects of certain diatom species on egg production and hatching success were found (Ban et al., 1997; Miralto et al., 1999; Turner et al., 2001). More recent findings contradict, however, these studies (Dutz et al., 2008; Jonasdottir et al., 2011).

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 (Bergvik et al., 2012; Jonasdottir et al., 2008; Marshall and Orr,

* Corresponding author at: Dept. of Biology, Trondhjem Biological Station, Norwegian University of Science and Technology, N-7491 Trondheim, Norway. Tel.: +47 73591573, +47 93227617 (mobile); fax: +47 73591597.
E-mail addresses: oystein.leiknes@ntnu.no (Ø. Leiknes), anja.striberny@uit.no (A. Striberny), nils.tokle@gmail.com (N.E. Tokle), yngvar.olsen@ntnu.no (Y. Olsen), olav.vadstein@ntnu.no (O. Vadstein), usommer@ifm-geomar.de (U. Sommer).
[1] Visiting address: Trondhjem Biological Station, Bynesveien 46, 7491 Trondheim, Norway.

1385-1101/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.seares.2013.05.012

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 composition has previously been studied in incubation 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 ratios 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 *Pelagostrobilidium spirale* (formerly known as *Strobilidium spiralis*). 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 Trondhjem Biological Station. Zooplankton was sampled in the Trondheimsfjord at the station "Trollet" (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 Trondhjem 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). Silicone tubes were placed at the bottom of the container, and heavy air bubbling was provided with a compressor system designed to provide airlift 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 discarded.

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 (T_0) 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 (Hopavågen) outside the Trondheimsfjord 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 Guillards 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 cryptophyceae *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 μg C L^{-1}), whereas the ciliates were offered in a gradient from 5 to 50 μg 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 (Image J). Six random images were obtained (resolution 1024 × 768 pixels) from each sedimented phytoplankton sample using a fire-wire 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 Putt and Stoecker (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 T_0 and T_1. Grazing coefficients, clearance rate (CR), 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 (CR_{phyto}) and ciliates (CR_{cil}) as:

$$CR_{phyto} = \left\{ \left[\ln\left(C_{p1}/C_{p2}\right)/t \right] - \left(CR_{cildino} \times C_{cil}\right) \right\} \times V/n$$
$$CR_{cil} = \{\mu_{cil} - [\ln(C_{c2}/C_{c1})]/t\} \times V/n.$$

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 t is incubation time. The growth of the ciliates during the incubation was corrected by applying a growth factor, μ_{cil} of 0.7 day^{-1} (Gismervik, 2005). $CR_{cildino}$ is a correction factor for the clearance rate by the ciliate community on phytoplankton, and was estimated from grazing experiments with *P. spirale* and six concentrations of *K. veneficum* (Gismervik, unpublished results). A constant $CR_{cildino}$ 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. finmarchicus*. C_{cil} is the weighted average ciliate concentration during the incubation.

The ingestion rate (I) was calculated as the product of B and CR, and expressed in terms of μg C $Ind.^{-1}$ day^{-1}. Feeding preferences of *C. finmarchicus* 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} (19.0–48.1% 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-nitzschia delicatissima* complex, *Thalassionema* spp., and *Navicula* spp. Thecate dinoflagellates such as *Ceratium* spp., *Dinophysis* sp., and individuals of the order Peridinales 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 dinoflagellates ranged from 6.7 to 9 μg C L^{-1}. Small flagellates such as *Teleaulax* sp. and *Plagioselmis* sp. were found in biomass of around 10 μg C L^{-1}. The ciliate biomass was 12.2 μg C L^{-1} in the untreated water in Exp. 1. Aloricate ciliates were dominated by *Strombidium* spp. of different size classes. Larger ciliates were represented by *Laboea* sp., *Strobilidium* sp., and *S. conicum*. Smaller ciliates consisted of *Strombidium* spp., *Lohmaniella oviformis* (aggregated in the group 'conic ciliates <35 μm'), and *Strobilidium* sp. The numerically most abundant group of ciliates in untreated seawater was 'conic ciliates <35 μm'.

In Exp. 2 the phytoplankton community consisted mainly of small single cells of *Thalassiosira* sp. and *Thalassionema* spp. which constituted 5 μg C L^{-1}. Chain forming diatoms were only scarcely observed and thus not counted. Both thecate and athecate dinoflagellates were present. The biomass of dinoflagellates was in the same range (~9 μg C L^{-1}) as in Exp. 1. Most dinoflagellates belonged to the order Peridinales (length 20–30 μm). The ciliate community was similar in both experiments with the exception that *M. rubrum* appeared in two different size classes in Exp. 2. The large form of *M. rubrum* occurred at high biomass and the group 'conic ciliates <35 μm' was less abundant during Exp. 2.

3.2. Feeding selectivity of C. finmarchicus

Diatoms of the order Centrales, in particular *Thalassiosira* spp. and *Chaetoceros* spp., constituted more than 80% of the total microplankton biomass in Exp. 1 and the diatoms were consumed in proportions according to the availability in the diet (Fig. 1). The relative contribution of dinoflagellates to the total microplankton biomass fluctuated

Table 1
Biomass [μg C L^{-1}] of the microplankton groups in the different treatments. The biomass was calculated as the geometric mean based on data from the start and the termination of the experiments (T_0 and T_1 values of the control bottle). Values in parentheses are the % contribution to the total biomass.

Treat.	Ciliates		Diatoms		Dinoflagellates		Flagellates		Tot. biomass	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
1	1.4 (1.0)	3.0 (19.0)	123 (88.9)	4.5 (28.3)	6.7 (4.8)	6.4 (40.4)	7.3 (5.2)	1.9 (12.1)	139	15.8
2	2.8 (1.6)	11.9 (44.1)	159 (89.2)	4.3 (16.0)	6.7 (3.8)	8.8 (32.5)	9.7 (5.4)	2.0 (7.4)	178	26.9
3	3.9 (1.8)	7.9 (36.6)	200 (89.8)	3.8 (17.3)	6.7 (3.0)	7.2 (33.7)	12.0 (5.4)	2.6 (12.1)	222	21.5
4	4.5 (2.7)	12.0 (37.5)	143 (85.8)	5.4 (16.9)	9.0 (5.4)	12.7 (39.9)	10.2 (6.1)	1.8 (5.7)	167	31.9
5	7.1 (2.9)	11.6 (43.1)	218 (88.3)	4.0 (14.9)	8.3 (3.4)	9.3 (34.3)	13.4 (5.4)	2.1 (7.8)	247	27.0
6	6.4 (2.4)	10.7 (42.0)	232 (87.4)	4.4 (17.5)	7.8 (2.9)	8.5 (33.4)	19.4 (7.3)	1.8 (7.1)	266	25.5
7	12.2 (5.6)	10.7 (48.1)	169 (82.5)	3.5 (15.8)	8.6 (3.9)	5.8 (25.6)	17.7 (8.1)	2.3 (10.1)	207	22.2

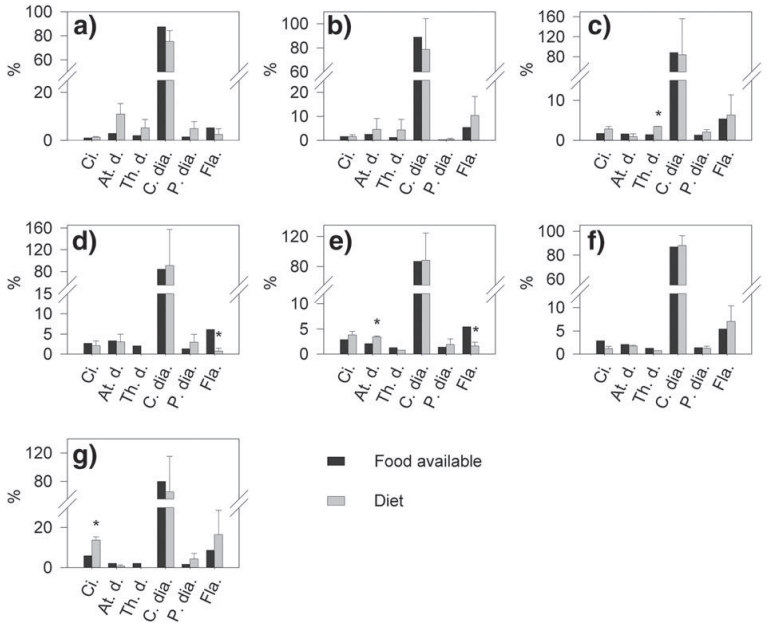


Fig. 1. Percent contribution of the different microplankton groups to the composition of the food offered and in the diet consumed by *C. finmarchicus* during feeding experiment 1. a–g: treatments 1–7. Ci.: ciliates. At. d.: athecate dinoflagellates. Th. d.: thecate dinoflagellates. C. dia.: centric diatoms. P. dia.: pennate diatoms. Fla.: flagellates <10 μm. The star indicates food species that has a significantly different share of the diet compared to the food available (one-sample *t*-test, $P < 0.05$).

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 <10 μm 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 generally a 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

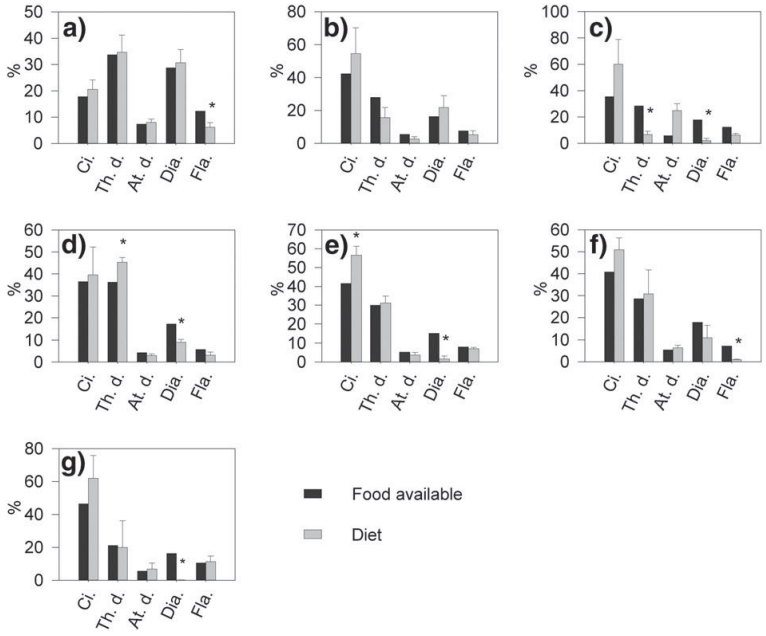


Fig. 2. Percent contribution of the different microplankton groups to the composition of the food offered and the diet consumed by *C. finmarchicus* during feeding experiment 2. a–g: treatments 1–7. Ci.: ciliates. At. d.: athecate dinoflagellates. Th. d.: thecate dinoflagellates. Dia: diatoms. Fla.: flagellates <10 μm. The star indicates food species that has a significantly different share of the diet compared to the food available (one-sample *t*-test, $P < 0.05$).

index for *Thalassiosira* changed from an average of 0.6 in treatments 1–4, with 1.0–2.7% ciliates, towards zero and slightly negative values with ciliate concentration > 2.4%.

The selectivity indices for ciliates 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. finmarchicus* 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 ($D = -0.97$ in treatment 7, with high ciliate biomass and a high fraction of 'conic ciliates > 35 μm') of diatoms by *C. finmarchicus*. Ciliates were positively selected by *C. finmarchicus*, although not significantly for all treatments. Large conic ciliates were ingested preferably by *C. finmarchicus*, as showed 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. finmarchicus* 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. finmarchicus* 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. finmarchicus* 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

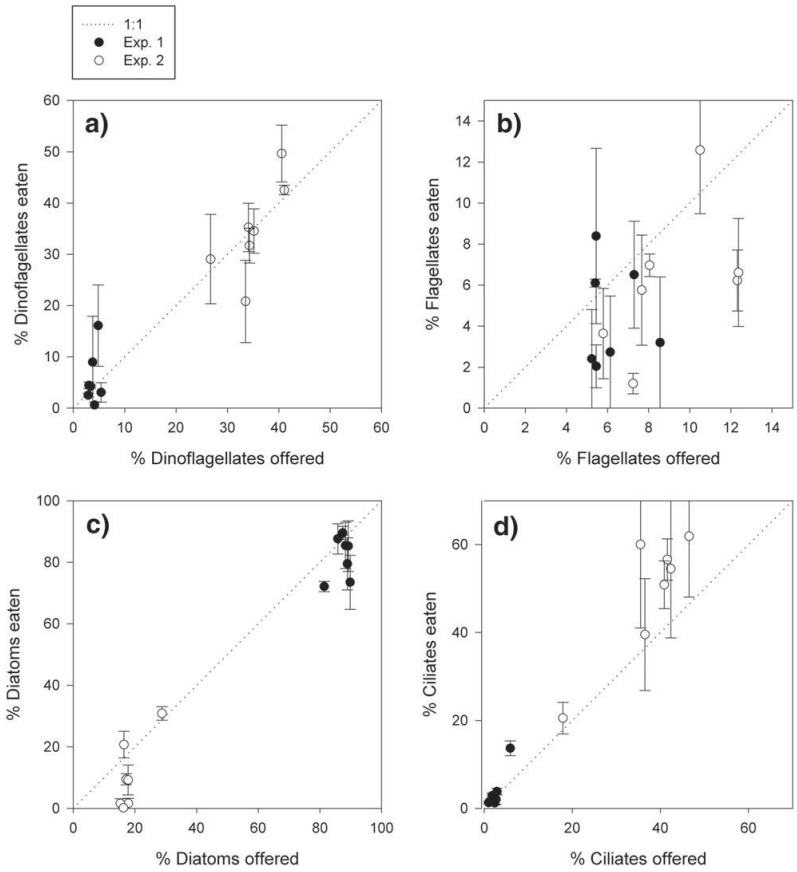


Fig. 3. Percentage (mean ± SE) of (a) dinoflagellates, (b) ciliates, (c) diatoms and (d) flagellates in the diet of *C. finmarchicus* in relation to the 1:1 line. The data above and below the 1:1 line indicate positive and negative feeding selectivity, respectively.

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.

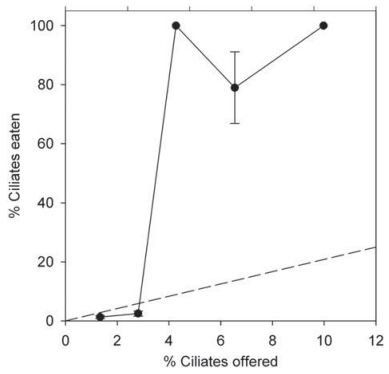


Fig. 4. Percentage (mean ± SE, n = 5) of offered ciliates eaten by *C. finmarchicus* in the experiment with surplus food and variable ciliate concentration in relation to the 1:1 line. The lack of error bars for 4.3 and 10% ciliates offered was due to the ciliates constituting 100% of the consumed food particles in all replicates.

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 a negative selective feeding behavior. 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).

Treat.	Diatoms		Ciliates		*Thalassiosira* spp.	Conic ciliates > 35 μm	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 1	Exp. 2
	D ± SE	D ± SE	D ± SE	D ± SE	D ± SE	D ± SE	D ± SE
1	−0.25 ± 0.35	0.06 ± 0.08	0.13 ± 0.08	**0.15 ± 0.04**	**0.65 ± 0.06**	−0.54 ± 0.46	**0.23 ± 0.07**
2	0.00 ± 0.35	**−0.25 ± 0.02**	−0.08 ± 0.13	0.29 ± 0.12	0.61 ± 0.28	−0.61 ± 0.39	**0.68 ± 0.03**
3	−0.45 ± 0.23	**−0.83 ± 0.17**	0.47 ± 0.28	**0.45 ± 0.12**	**0.57 ± 0.18**	−0.74 ± 0.26	**0.81 ± 0.08**
4	0.20 ± 0.29	**−0.44 ± 0.12**	0.06 ± 0.52	0.06 ± 0.29	0.55 ± 0.27	0.19 ± 0.60	**0.49 ± 0.07**
5	0.04 ± 0.31	**−0.89 ± 0.11**	0.17 ± 0.30	**0.44 ± 0.14**	−0.12 ± 0.39	0.13 ± 0.28	**0.60 ± 0.00**
6	0.13 ± 0.16	−0.47 ± 0.27	−0.40 ± 0.22	0.31 ± 0.16	**−0.34 ± 0.07**	−0.30 ± 0.32	**0.67 ± 0.06**
7	−0.56 ± 0.22	**−0.97 ± 0.03**	0.61 ± 0.26	0.46 ± 0.17	0.26 ± 0.30	**0.72 ± 0.18**	**0.78 ± 0.11**

predation mortality by using jumping as a predator-escape mechanism when they are caught in the feeding current of a copepod (Jakobsen, 2001). In Exp. 3, we used *P. spirale*, which is known to increase its jumping frequency and length of jumps when approached by a copepod (Broglio et al., 2001).

C. finmarchicus showed non-selective feeding, when ciliate concentrations were low. When ciliates contributed to more than 3% of offered food or if ciliate biomass was more than 5 μg C L^{-1}, *C. finmarchicus* switched to a predatory strategy and utilized ciliates as nearly the sole food source even though phytoplankton was in excess concentration. From these results, we infer that *C. finmarchicus* has the ability to exploit larger, moving prey, like ciliates and dinoflagellates, both during periods of high and low algal food availability and that this is dependent on the proportion of alternate food sources available.

One possible explanation of the selection for ciliates might be that large size is an advantage during predatory feeding because of higher energy intake per attack. Typical length ratios between prey and predator are between 1:10 and 1:100 (Fenchel, 1988). The energy-gain-to-energy-loss ratio due to hunting the prey increases with increasing size of the prey. However, the total ingestion goes down after switching in Exp. 3. This suggests that other factors such as nutrition may be of significance. The large fraction of ciliates consumed, their positive selection indices and the low ingestion rates of diatoms suggest an overall predatory feeding of *C. finmarchicus* during post-bloom conditions.

C. finmarchicus in the Trondheimsfjord ascend to the surface from February to early April. There is a peak of copepod stages I–III during April, indicating that the new generation develops during the spring bloom (Bergvik et al., 2012; Strømgren, 1974). In the Trondheimsfjord, we also find females spawning in surface layers during August (unpublished data), and it has been suggested that a part of the population develops directly into females instead of descending to deep waters, thus giving a second generation of *C. finmarchicus* (Bergvik et al., 2012). Big year to year variations on the onset of the spring bloom and the subsequent variations in concentrations of alternate food particles would imply a need for flexibility regarding the food selectivity of *C. finmarchicus*.

Overall, the diet composition and the selectivity indices support previous results that have classified *C. finmarchicus* as an omnivorous species (Nejstgaard et al., 2001; Ohman and Runge, 1994, Saage et al., 2008). We conclude that 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 behavior on a short term scale depending on the absolute and relative concentrations of prey. 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.

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.

References

Atienza, D., Saiz, E., Calbet, A., 2006. Feeding ecology of the marine cladoceran *Penilia avirostris*: natural diet, prey selectivity and daily ration. Marine Ecology Progress Series 315, 211–220.

Ban, S.H., Burns, C., Castel, J., Chaudron, Y., Christou, E., Escribano, R., Umani, S.F., Gasparini, S., Ruiz, F.G., Hoffmeyer, M., Ianora, A., Kang, H.K., Laabir, M., Lacoste, A., Miralto, A., Ning, X.R., Poulet, S., Rodriguez, V., Runge, J., Shi, J.X., Starr, M., Uye, S., Wang, Y.J., 1997. The paradox of diatom–copepod interactions. Marine Ecology Progress Series 157, 287–293.

Basedow, S.L., Tande, K.S., 2006. Cannibalism by female *Calanus finmarchicus* on naupliar stages. Marine Ecology Progress Series 327, 247–255.

Bergvik, M., Leiknes, O., Altin, D., Dahl, K.R., Olsen, Y., 2012. Dynamics of the lipid content and biomass of *Calanus finmarchicus* (copepodite V) in a Norwegian fjord. Lipids 47, 881–895.

Bonnet, D., Titelman, J., Harris, R., 2004. *Calanus* the cannibal. Journal of Plankton Research 26, 937–948.

Broglio, E., Johansson, M., Jonsson, P.R., 2001. Trophic interaction between copepods and ciliates: effects of prey swimming behavior on predation risk. Marine Ecology Progress Series 220, 179–186.

Campbell, R.G., Wagner, M.M., Teegarden, G.J., Boudreau, C.A., Durbin, E.G., 2001. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Marine Ecology Progress Series 221, 161–183.

Carlotti, F., Radach, G., 1996. Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled one-dimensional model. Limnology and Oceanography 41, 522–539.

Dutz, J., Koski, M., Jonasdottir, S.H., 2008. Copepod reproduction is unaffected by diatom aldehydes or lipid composition. Limnology and Oceanography 53, 225–235.

Eppley, R.W., Rogers, J.N., McCarthy, J.J., 1969. Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. Limnology and Oceanography 14, 912.

Fenchel, T., 1988. Marine plankton food-chains. Annual Review of Ecology and Systematics 19, 19–38.

Fileman, E., Petropavlovsky, A., Harris, R., 2010. Grazing by the copepods *Calanus helgolandicus* and *Acartia clausi* on the protozooplankton community at station L4 in the Western English Channel. Journal of Plankton Research 32, 709–724.

Frost, B.W., 1972. Effects of size and concentration of food particles on feeding behavior of marine planktonic copepod *Calanus pacificus*. Limnology and Oceanography 17, 805–815.

Gifford, D.J., 1985. Laboratory culture of marine planktonic oligotrichs (Ciliophora, Oligotrichida). Marine Ecology Progress Series 23, 257–267.

Gifford, D., 1993. Consumption of protozoa by copepods feeding on natural microplankton assemblages. In: Kemp, P.F., Sherr, B.F., Sherr, E.B., Cole, J.J. (Eds.), Handbook of Current Methods in Aquatic Microbiology. Lewis Publications, pp. 723–729.

Gismervik, I., 2005. Numerical and functional responses of choreo- and oligotrich planktonic ciliates. Aquatic Microbial Ecology 40, 163–173.

Graeve, M., Kattner, G., Hagen, W., 1994. Diet-induced changes in the fatty-acid composition of arctic herbivorous copepods — experimental-evidence of trophic markers. Journal of Experimental Marine Biology and Ecology 182, 97–110.

Guillard, R.R., Ryther, J.H., 1962. Studies of marine planktonic diatoms.1. *Cyclotella nana* Hustedt, and *Detonula confervacea* (Cleve) Gran. Canadian Journal of Microbiology 8, 229.

Hillebrand, H., Durselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. Journal of Phycology 35, 403–424.

Irigoien, X., Head, R., Klenke, U., Meyer-Harris, B., Harbour, D., Niehoff, B., Hirche, H.J., Harris, R., 1998. A high frequency time series at weathership M, Norwegian Sea, during the 1997 spring bloom: feeding of adult female *Calanus finmarchicus*. Marine Ecology Progress Series 172, 127–137.

Jacobs, J., 1974. Quantitative measurement of food selection — modification of forage ratio and Ivlev's electivity index. Oecologia 14, 413–417.
Jakobsen, H.H., 2001. Escape response of planktonic protists to fluid mechanical signals. Marine Ecology Progress Series 214, 67–78.
Jonasdottir, S.H., Richardson, K., Heath, M.R., Ingvarsdottir, A., Christoffersen, A., 2008. Spring production of *Calanus finmarchicus* at the Iceland–Scotland ridge. Deep Sea Research Part I: Oceanographic Research Papers 55, 471–489.
Jonasdottir, S.H., Dutz, J., Koski, M., Yebra, L., Jakobsen, H.H., Vidoudez, C., Pohnert, G., Nejstgaard, J.C., 2011. Extensive cross-disciplinary analysis of biological and chemical control of *Calanus finmarchicus* reproduction during an aldehyde forming diatom bloom in mesocosms. Marine Biology 158, 1943–1963.
Koski, M., 2007. High reproduction of *Calanus finmarchicus* during a diatom-dominated spring bloom. Marine Biology 151, 1785–1798.
Koski, M., Riser, C.W., 2006. Post-bloom feeding of *Calanus finmarchicus* copepodites: selection for autotrophic versus heterotrophic prey. Marine Biology Research 2, 109–119.
Kragberg, A., Bauman, M., Dürselen, C.-D., 2010. Coastal Phytoplankton. Photo Guide for Northern European Seas. Verlag Dr. Friedrich Pfeil, Müchen.
Levinsen, H., Turner, J.T., Nielsen, T.G., Hansen, B.W., 2000. On the trophic coupling between protists and copepods in arctic marine ecosystems. Marine Ecology Progress Series 204, 65–77.
Lucas, J.S., 1982. Quantitative studies of feeding and nutrition during larval development of the coral-reef asteroid *Acanthaster planci* (L.). Journal of Experimental Marine Biology and Ecology 65, 173–193.
Marshall, S.M., Orr, A.P., 1955. The Biology of a Marine Copepod, *Calanus finmarchicus* (Gunnerus). Oliver & Boyd, Edinburgh.
Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45, 569–579.
Meyer-Harms, B., Irigoien, X., Head, R., Harris, R., 1999. Selective feeding on natural phytoplankton by *Calanus finmarchicus* before, during, and after the 1997 spring bloom in the Norwegian Sea. Limnology and Oceanography 44, 154–165.
Miralto, A., Barone, G., Romano, G., Poulet, S.A., Ianora, A., Russo, G.L., Buttino, I., Mazzarella, G., Laabir, M., Cabrini, M., Giacobbe, M.G., 1999. The insidious effect of diatoms on copepod reproduction. Nature 402, 173–176.
Nejstgaard, J.C., Witte, H.J., Vanderwal, P., Jacobsen, A., 1994. Copepod grazing during a mesocosm study of an *Emiliania-huxleyi* (Prymnesiophyceae) bloom. Sarsia 79, 369–377.
Nejstgaard, J.C., Gismervik, I., Solberg, P.T., 1997. Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliania huxleyi*. Marine Ecology Progress Series 147, 197–217.
Nejstgaard, J.C., Naustvoll, L.J., Sazhin, A., 2001. Correcting for underestimation of microzooplankton grazing in bottle incubation experiments with mesozooplankton. Marine Ecology Progress Series 221, 59–75.
Ohman, M.D., Runge, J.A., 1994. Sustained fecundity when phytoplankton resources are in short supply — omnivory by *Calanus finmarchicus* in the Gulf of St-Lawrence. Limnology and Oceanography 39, 21–36.
Olenina, I., Hajdu, S., Edler, L., Andersson, A., Wasmund, N., Busch, S., Göbel, J., Gromisz, S., Huseby, S., Huttunen, M., Jaanus, A., Kokkonen, P., Ledaine, I., Niemkiewicz, E., 2006. Biovolumes and size-classes of phytoplankton in the Baltic Sea. HELCOM Balt. Sea Environ. Proc, 106.
Planque, B., Batten, S.D., 2000. *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. ICES Journal of Marine Science 57, 1528–1535.
Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon:volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. Limnology and Oceanography 34, 1097–1103.
Rasband, W.S., 1997–2009. ImageJ. 1.41. U.S. National Institutes of Health. Bethesda, MD, USA. http://rsb.info.nih.gov/ij/.
Saage, A., 2006. A comparison of phytoplankton and ciliate feeding by marine calanoid copepods. Dissertation zur Erlangung des Doktorades der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel., Mathematisch-Naturwissenschaftlichen Fakultät. Christian-Albrechts-Universität, Kiel. 73.
Saage, A., Altin, D., Vadstein, O., Sommer, U., 2008. Trophic position of *Calanus finmarchicus* (Copepoda, Calanoida) in the Trondheim Fjord. Journal of Sea Research 59, 162–172.
Saage, A., Vadstein, O., Sommer, U., 2009. Feeding behaviour of adult *Centropages hamatus* (Copepoda, Calanoida): functional response and selective feeding experiments. Journal of Sea Research 62, 16–21.
Saiz, E., Calbet, A., 2011. Copepod feeding in the ocean: scaling patterns, composition of their diet and the bias of estimates due to microzooplankton grazing during incubations. Hydrobiologia 666, 181–196.
Slagstad, D., Tande, K.S., Wassmann, P., 1999. Modelled carbon fluxes as validated by field data on the north Norwegian shelf during the productive period in 1994. Sarsia 84, 303–317.
Stoecker, D.K., Egloff, D.A., 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. Journal of Experimental Marine Biology and Ecology 110, 53–68.
Strømgren, T., 1974. Zooplankton and Hydrography in Trondheimsfjorden on the West Coast of Norway. Museet, Trondheim.
Teegarden, G.J., Campbell, R.G., Durbin, E.G., 2001. Zooplankton feeding behavior and particle selection in natural plankton assemblages containing toxic *Alexandrium* spp. Marine Ecology Progress Series 218, 213–226.
Tiselius, P., Jonsson, P.R., 1990. Foraging behavior of six calanoid copepods — observations and hydrodynamic analysis. Marine Ecology Progress Series 66, 23–33.
Turner, J.T., Ianora, A., Miralto, A., Laabir, M., Esposito, F., 2001. Decoupling of copepod grazing rates, fecundity and egg-hatching success on mixed and alternating diatom and dinoflagellate diets. Marine Ecology Progress Series 220, 187–199.
Utermöhl, H., 1958. Zur Vervollkommung der qualitativen Phytoplankton-Methodik. Mitteilung Internationale Vereinigung fuer Theoretische unde Amgewandte Limnologie 9, 1–38.
Verity, P.G., Langdon, C., 1984. Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. Journal of Plankton Research 6, 859–868.

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*

1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism

1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply

1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry

1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic

1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses

2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)

2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	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 pollutans (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 Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity

2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania

2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania

2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	ph.d Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*

2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	ph.d Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	ph.d Biology	Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural ecology
2012	Aleksander Handå	ph.d Biology	Cultivation of mussels (*Mytilus edulis):*Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	ph.d Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river
2012	Jisca Huisman	ph.d Biology	Gene flow and natural selection in Atlantic salmon
	Maria Bergvik	ph.d Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	ph.d Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	ph.d Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	ph.d Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	ph.d Biology	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
2012	Christer Moe Rolandsen	ph.d Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	ph.d Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	ph.d Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	ph.d Biology	Demographic, environmental and evolutionary aspects of sexual selection
	Bin Liu	ph.d Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	ph.d Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	ph.d Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	ph.d Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	ph.d Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	ph.d Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	ph.d Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	ph.d Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	ph.d Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night

2013	Sebastian Wacker	ph.d Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	ph.d Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	ph.d Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	ph.d Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	ph.d Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	ph.d Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	ph.d Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	ph.d Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	ph.d Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	ph.d Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	ph.d Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	ph.d Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	ph.d Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	ph.d Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	ph.d Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	ph.d Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	ph.d Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: Calanus, little auks (alle alle) and black-legged kittiwakes (Rissa tridactyla)
2014	Kristin Møller Gabrielsen	ph.d Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	ph.d Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	ph.d Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	ph.d Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	ph.d Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	ph.d Biology	Genetic variation and structure in peatmosses (*Sphagnum*)

2015	Keshuai Li	ph.d Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	ph.d Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	ph.d Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	ph.d Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*