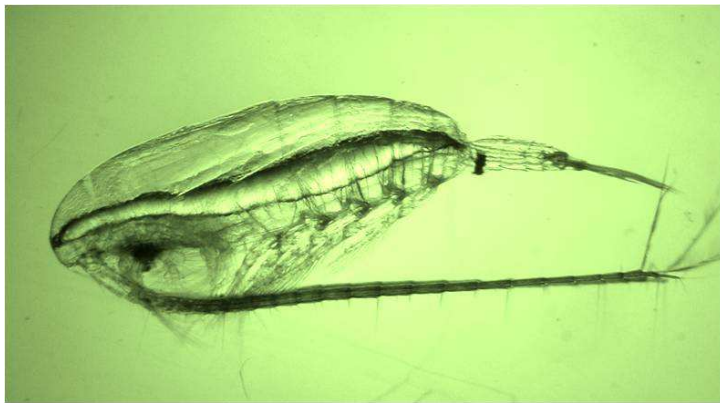


Stoichiometry of lipid synthesizing calanoid copepods in Arctic and sub-Arctic marine regions

Insights into limitation and elemental cycling from characterization of C:N:P ratios



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Preface

Living entities, from cells to entire organisms, do not exist in isolation, but interact with each other within a physical-biological system. Ecology is the part of science that looks at these interactions. The number of interactions and the levels of organization within a system make ecology a broad and complex discipline. In general, scientific theories are developed to facilitate the study of complex questions.

This thesis applies the theory of ecological stoichiometry to questions related to calanoid copepod development and ecology in the high-latitude marine regions. The goal of the thesis is to encourage the reader to apply this theory, which is increasingly being recognized as a powerful tool to study interactions of everything from genes to ecosystems (notably thanks to the work of Elser and Sterner). The thesis aims further to bring to light additional information on the biology of high-latitude copepods. It increases the number of applications of ecological stoichiometry by investigating interactions in an ecosystem where it has been rarely applied. Life in the sub-Arctic and Arctic is not more valuable or interesting than in other areas, but it represents a particular case due to adaptations required by the harsh environment and extensive seasonal variation. The adaptations lead to specific life traits of calanoid copepods, key species in the Arctic and sub-Arctic Ocean ecosystems.

From a personal point of view, this thesis is motivated by a fascination for life in the sea, from small to large creatures, and among them zooplankton, which live in this tremendous “Big Blue”, as I like to call the ocean. Hence, this work also aims to contribute to the general knowledge and understanding of life in the sea, as small as it may be.

I hope that the reader will become more interested in both ecological stoichiometry in general, and the world of zooplankton in particular.

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Abstract

Calanoid copepods, *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*, are key species in Arctic and sub-Arctic marine ecosystems. They represent important prey for a number of species such as juvenile herring and cod because of their high but seasonally variable calorific value: they synthesize and store lipids as part of their survival strategy. Limitations in food quantity and quality can have strong impact on the copepods' lipid synthesis and development, with implications for their predators and thus for the lipid-driven Arctic marine food web. Ecological stoichiometry, i.e. the study of the relative abundance of elements (most commonly carbon, nitrogen, and phosphorus) in biological entities, is a powerful tool to study potential limitation of aquatic organisms, particularly in primary producers and in omnivorous and herbivorous zooplankton grazers. However, studies that apply a stoichiometric approach to the high-latitude marine regions are extremely rare. The main aim of this thesis is to reveal the elemental requirements and potential limitation of high-latitude calanoid copepods by investigating their C:N:P composition in combination with information on other biochemical compounds. The impact of copepods on nutrient recycling and C:N:P export through fecal pellets is also investigated. The study was conducted in a sub-Arctic north-Norwegian fjord, and in the western part of the European Arctic Ocean, focusing on the period of intense primary production during spring. Somatic stoichiometric ratios in copepods were calculated by subtracting C in the lipid sac from the total body C. Due to the strong influence of lipid storage on total body stoichiometry, high-latitude calanoid copepods, and by implication lipid-synthesizing zooplankton in general, should be treated through a two-compartment stoichiometric approach, with lipid storage and somatic tissues separated. Both season and development stage influence the somatic elemental ratios. The somatic C:P ratios of high-latitude calanoid copepods are somewhat lower than those reported in marine copepods from other areas, suggesting that they have higher growth rates than temperate and tropical copepods. Seston C:N:P stoichiometry is used as a proxy for food quality in the calculation of copepod elemental limitation. The seston C:P and N:P ratios are among the first to be reported for the Arctic Ocean and indicate a higher relative proportion of nutrients (N and P) compared to published seston values from other marine regions. Seston C:N:P ratios varied according to bloom stage, which therefore also impacts the potential C, N or P limitation of copepods. Unless they have high assimilation efficiency for C, calanoid copepods are shown to be most likely subject to C limitation. However, variable requirements during ontogeny make specific stages, such as copepodite IV, and females more sensitive to nutrient limitation (N or P). This study is the first to present data on stoichiometric ratios including P for copepod fecal pellets in the Arctic, and shows their high potential not only to vertically export P at depth but also to provide a source of P in the upper layers during the productive season if degraded. The Arctic marine regions are experiencing the greatest climate change, and the potential future stoichiometric changes in the Arctic and how climate change affects copepod-seston interaction are discussed.

Key-words: *Calanus* spp., Lipid storage, Seston, Stoichiometry, Spring bloom, Carbon, Nitrogen, Phosphorus, Arctic Ocean

Résumé

Les copépodes calanoides *Calanus finmarchicus*, *C. glacialis* et *C. hyperboreus* sont des espèces clés dans les écosystèmes marins Arctiques et subarctiques. Ils constituent une proie de choix pour nombre d'espèces, dont notamment les juvéniles de hareng et de morue, en raison de leur forte valeur calorifique qui varie de façon saisonnière. En effet, ces copépodes synthétisent et stockent des lipides comme stratégie de survie. Les limitations liées à la quantité et à la qualité de leur nourriture peuvent avoir de fortes répercussions sur leur capacité à synthétiser des lipides et sur leur développement, et ainsi sur leurs prédateurs et sur la chaîne alimentaire Arctique, basée sur les lipides. La stœchiométrie écologique, l'étude de l'abondance relative des éléments (les plus communément utilisés étant le carbone, l'azote et le phosphore) dans les entités biologiques, est un outil puissant pour étudier les potentielles limitations des organismes aquatiques, particulièrement pour les producteurs primaires, et le zooplancton omnivore et herbivore. Les études prenant en considération la stœchiométrie dans les régions marines des hautes latitudes sont cependant quasi inexistantes. Le but principal de cette thèse est de révéler les besoins élémentaires et les potentielles limitations de ces copépodes, dans les régions Arctiques et subarctiques, en étudiant leur composition C:N:P tout en considérant les différents composants biochimiques associés. L'impact de ces copépodes sur le recyclage des nutriments et sur l'exportation C:N:P via leurs pelotes fécales est aussi étudié. L'étude a été réalisée dans un fjord subarctique du nord de la Norvège (Grøtsund), et dans la partie ouest de l'Océan Arctique européen, au printemps pendant la période d'intense production primaire. Les ratios stœchiométriques des copépodes sont calculés en soustrayant le carbone contenu dans les sacs lipidiques au carbone total présent dans l'organisme. En raison de l'influence du stock de lipides sur leur stœchiométrie, les copépodes calanoides des hautes latitudes, et par déduction toutes les espèces de zooplancton synthétisant des lipides, devraient être considérés via une approche stœchiométrique à deux compartiments, avec le stock de lipides d'une part et les tissus somatiques d'autre part. La saison et le stade de développement ont une influence sur les ratios élémentaires somatiques. Les ratios somatiques C:P des copépodes calanoides des hautes latitudes sont plus bas que ceux rapportés pour les copépodes marins d'autres régions, et suggèrent un plus fort taux de croissance que pour les copépodes des régions tempérées et tropicales. La stœchiométrie C:N:P dans le seston est utilisée comme un proxy de la qualité de la nourriture dans les calculs de limitation élémentaire des copépodes. Les ratios C:P and N:P dans le seston sont parmi les premiers mesurés pour l'Océan Arctique et indiquent une teneur relative en nutriments (N et P) plus élevée en comparaison avec les valeurs de seston publiées pour d'autres régions marines. Les ratios C:N:P dans le seston varient en fonction du stade de l'efflorescence phytoplanctonique, qui en conséquence a aussi une influence sur la limitation potentielle en C, N ou P des copépodes. À moins d'avoir un fort taux d'assimilation pour le carbone, les copépodes calanoides sont le plus souvent sujets à une limitation en carbone. Cependant, les besoins élémentaires diffèrent en fonction de l'ontogénie et certains stades comme les copépodites IV ou les femelles sont plus sensibles à des limitations en N ou P. Cette étude est la première à présenter des ratios stœchiométriques incluant P pour les pelotes fécales en Arctique et montre le fort potentiel de ces pelotes à exporter en profondeur du P mais aussi à en recycler, dans le cas où elles sont dégradées, dans les couches supérieures de l'Océan durant la période de production. Les régions marines Arctique sont les régions où les changements climatiques sont les plus intenses et leur influence sur le seston et les copépodes qui peut moduler leurs stoichiométries, et donc leur interaction, est discuté.

Mots clés: *Calanus* spp., Lipides, Seston, Stœchiométrie, Efflorescence phytoplanctonique, Carbone, Azote, Phosphore, Océan Arctique.

List of acronyms and abbreviations

ADP: Adenosine DiPhosphate

AE: Assimilation Efficiency

ATP: Adenosine TriPhosphate

C: Carbon

C:N: Elemental Carbon on Nitrogen ratio

C:N_s: Elemental Carbon on Nitrogen ratio in the somatic tissues

CO₂: Carbon diOxide

C:P: Elemental Carbon on Phosphorus ratio

C:P_s: Elemental Carbon on Phosphorus ratio in the somatic tissues

CIV: Copepodite IV

CV: Copepodite V

DIN:TP : Elemental ratio of Dissolved Inorganic Nitrogen on Total Phosphorus

DNA: DeoxyriboNucleic Acid

DW: Dry Weight

EGC: East Greenland Current

ESC: East Spitsbergen Current

GRH: Growth Rate Hypothesis

N: Nitrogen

NH₄⁺: Ammonium

N:P: Elemental Nitrogen on Phosphorus ratio

P: Phosphorus

PAR: Photosynthetically Active Radiation

POC: Particulate Organic Carbon

POM: Particulate Organic Matter

PON: Particulate Organic Nitrogen

RNA: RiboNucleic Acid

TER: Threshold Elemental Ratio

TPP: Total Particulate Phosphorus

WE: Wax Esters

WEAO: Western European Arctic Ocean

WSC: West Spitsbergen Current

List of Papers

This synthesis is based on the following papers which are referred by their Roman numerals **I-III**.

Paper I. Aubert, A.B., Svensen, C., Hessen, D., Tamelander, T., 2012. CNP stoichiometry of a lipid-synthesising calanoid copepod, *Calanus finmarchicus*, from winter to spring bloom in a sub-Arctic sound. *Journal of Marine Systems*. doi 10.1016/j.jmarsys.2012.09.004

Paper II. Aubert, A.B., Tamelander, T., (manuscript). Stoichiometric approach to elemental limitation of pelagic producers and grazers during the Arctic summer. *Submitted to Marine Ecology Progress Series*.

Paper III. Tamelander, T., Aubert, A. B., Wexels Riser, C., 2012. Export stoichiometry and contribution of copepod faecal pellets to vertical flux of particulate carbon, nitrogen and phosphorus. *Marine Ecology Progress Series*, 459, 17-28.

1. Introduction

1.1. Ecological stoichiometry

1.1.1. Definition

The word “stoichiometry” did not appear in the scientific vocabulary until the late 18th century, but its roots go back to the ancient Greek words στοιχείον (stoicheion) and μέτρον (metron), meaning element and measure (Surhone et al. 2010). The definition of stoichiometry has evolved considerably since its creation, as it was first used to describe line counts in the New Testament. Now stoichiometry is recognized primarily as a branch of chemistry (Szabadváry 1993). The first principles were set down in 1792 by the German scientist, Jeremias Benjamin Richter (1762-1807), who defined stoichiometry as “the science of measuring the quantitative proportions or mass ratios in which chemical elements stand to one another” (Hugh 1911; Partington 1948).

The stoichiometric theory had to wait nearly one-and-a-half a centuries before it was applied to the field of ecology. This was carried out by Alfred Clarence Redfield (Box. 1).

Box 1. Redfield, pioneer of ecological stoichiometry



Alfred Clarence Redfield

Photo by Johnathan Wood, Woods Hole Oceanographic Institution

Alfred Clarence Redfield (1890-1983) grew up in a renowned scientific family and became an acknowledged biologist, ecologist and oceanographer. In addition to holding many important positions, such as professor at Harvard faculty and associate director of the Wood Hole Oceanographic Institution, Redfield introduced several major advancements in the field of science. The discovery for which he is most famous is the Redfield ratio, which also bears his name. In the early 1930s, he was among the first to emphasize that the atomic proportion of elements in marine particulate matter was relatively constant over the world's oceans, particularly for carbon, nitrogen and phosphorus. He determined the atomic ratio of C:N:P to be 106:16:1 (Revelle 1995). Since its presentation, the Redfield ratio has been used, over-used and considered “The Rule”. However, major deviations from this ratio in marine particulate matter have been underlined by several studies and by Redfield himself (Redfield 1958; Hecky et al. 1993; Geider and La Roche 2002; Ptacnik et al. 2010).

Later, others contributed significantly to the development of so-called ecological stoichiometry, among them Reiners (1896) and notably Sterner and Elser (2002) who provided the following definition: “Ecological stoichiometry is the balance of multiple chemical substances in ecological interactions and processes, or the study of this balance. Also sometimes refers to the balance of energy and materials”. Ecological stoichiometry has mainly developed toward a focus on elements, and more generally on three macro-elements: carbon (C), considered as the energy source, and nitrogen (N) and phosphorus (P), the essential nutrients. Trace elements such as Fe and Si have been also studied, albeit somewhat less (Sterner and Elser 2002; Ho et al. 2003; Van Nieuwerburgh et al. 2004). The term “balance”, as used in the definition cited above, refers to the relative proportion of elements in an entity. The common unit in ecological stoichiometry is the elemental ratio, and the C:N and C:P ratios are the ones most frequently used. The scope and power of ecological stoichiometry is wide since interactions can be studied at different levels of organization: the cell, the individual, the population, the community or the entire ecosystem (Elser et al. 2000b; Makino et al. 2003; Elser and Hamilton 2007).

1.1.2. A versatile tool to study consumer-producer interactions

The basis of ecological stoichiometry lies in physical, chemical and biological principles such as the law of conservation of matter and energy. The approach consists in considering organisms as the result of chemical reactions whose variations have implications for the structure of the ecosystems (Sterner and Elser 2002; Kuyper et al. 2004; Hessen et al. 2008). The elemental composition of organisms and how it is regulated is thus one of the major concerns of ecological stoichiometry. The autotrophic organisms at the base of the food chain are particularly flexible in their elemental composition, exhibiting a large range of body C:N:P elemental ratios in nature. This is due to their differential uptake of C versus nutrients, C being obtained by CO₂ fixation while nutrients are obtained from inorganic compounds in the environment (Harvey 1926; Geider and La Roche 2002; Hessen et al. 2008). As a result, autotrophs, e.g. phytoplankton in aquatic systems, have a body elemental composition that partly reflects the availability of the resources in their environment (Nielsen et al. 1996; Sterner and Elser 2002). In contrast, heterotrophs tend to regulate their body composition to constant proportions, a process called homeostasis (Sterner and Elser 2002; Logan et al. 2004; Anderson et al. 2005). Herbivores, and to a lesser extent omnivores, thus consume food with

an elemental composition that can diverge strongly from their own body composition, leading to what is called stoichiometric imbalance (Elser and Hassett 1994; Hassett et al. 1997; Hessen et al. 2004). Stoichiometric imbalance in a producer-consumer interaction indicates that the food does not match the consumer requirements. Given that elements are immutable and organisms are unable to synthesize them *de novo*, the element in shortest relative supply in regard to demand is defined as the limiting factor (Urabe 1993; Sterner and Elser 2002). Several heterotrophs, such as zooplankton, are able to cope to a certain extent with food limitation by mechanisms such as food selection, and modulation of assimilation and excretion rates to maintain homeostasis (Gulati and DeMott 1997; Touratier et al. 1999; Persson et al. 2010). These adaptations have, however, a cost that is detrimental to growth and/or reproduction. Elemental limitation affects the physiological mechanisms of the consumer in different ways, because elements are related to biochemical compounds, as described in Box 2.

Box 2. Links between body stoichiometry and biochemical compounds in consumers

Understanding where and how elements are used in organisms, is of fundamental importance for determining how an organism's physiology will be affected in the case of elemental limitation, and vice versa, to predict which element is potentially limiting depending on the consumer's physiological needs. One of the few studies that have focused on trying to link biochemical compounds (i.e. the chemical components present in an organism) to elemental composition is that of Ventura (2006). It underlined the low variation in general biochemical composition among various limnic and marine zooplankton species. Zooplankton were shown to be mainly composed of lipids and proteins, with a smaller amount of free amino acids, chitin and carbohydrates, and a much smaller amount of genetic material, nucleic acids (RNA, DNA), and nucleotides (ATP, ADP). Carbon (C) is the major element in the body and represents from 33 to 72% of the body dry weight (DW). Most C is contained in the lipids and proteins. Nitrogen (N), the second most abundant element, is mainly present in proteins and in free amino acids. Phosphorus (P) is much less abundant, representing on average 0.6 to 2.5 % of the DW, and is mostly present in nucleic acids, nucleotides and phospholipids (Sterner and Elser 2002; Ventura 2006). The role of P in living organisms has been particularly underlined since studies have shown its close relation to RNA, more particularly to the ribosomal RNA. The latter is involved in the protein synthesis required for growth (Hessen and Lyche 1991; Sterner 1995; Elser et al. 1996). From these studies and a number of others a new approach in ecological stoichiometry emerged: the growth rate hypothesis (GRH). The GRH states that fast-growing organisms have higher protein synthesis and thus greater demand for RNA. This results in higher relative body P content which modulates their elemental C:N:P body ratios. Organisms with a fast growth rate tend thus to have lower C:P and N:P body ratios than organisms with lower growth rates (Main et al. 1997; Elser et al. 2000a; Carrillo et al. 2001). Such differential growth rates are important to consider since their impact on body stoichiometry also has consequences for nutrient recycling and population interaction.

In addition, consumers release part of their diet in the form of dissolved and particulate organic matter. The elemental composition of these products fluctuates in relation to the food consumed, but also in relation to the elemental composition of the consumer itself. They can have a crucial role in nutrient recycling and for vertical export of particulate organic matter (Andersen 1997; Sterner and Elser 2002).

Consumer-producer stoichiometric interaction studies have flourished in the context of anthropogenic eutrophication, i.e., nutrient enrichment of ecosystems. Most of these studies are from freshwater systems and focus particularly on *Daphnia*, a key organism in these environments. They have underlined the power of ecological stoichiometry in helping to understand everything from small-scale consumer-producer interactions to larger-scale processes such as efficiency of the biological pump in nutrient cycling or ecosystem stability (Andersen 1997; DeMott et al. 1998; Elser et al. 2000c; Urabe et al. 2002). Far less work has been devoted to marine systems, and even less to high-latitude marine ecosystems exposed to rapid climate change (Carmack and McLaughlin 2011; Wassmann et al. 2011).

1.2. The Arctic marine ecosystem

1.2.1. A special environment: Seasonality and primary production

Arctic seas, and to a lesser extent the sub-Arctic marine regions, present a number of distinct characteristics, the most important of which are presented in Fig. 1, that make them different compared to lower latitude marine systems. They are characterized by a strong seasonal variability in incident solar radiation, with a dark winter and midnight sun during summer. The sea ice and snow cover regime also leads to strong variability on short and long time scales (Proshutinsky et al. 1999; Falk-Petersen et al. 2000). When sea ice is present, the penetration of photosynthetically active radiation (PAR) is poor, which strongly limits primary production. Conversely, when ice and snow melt, and PAR is no longer blocked, this is accompanied by ice algae and phytoplankton blooms. Freshwater release creates strong stratification and restricts replenishment of nutrients to the upper mixed layer. This favors an intensive, but transient plankton algae bloom, as does the increase of the photoperiod in spring (Hansen et al. 2003).

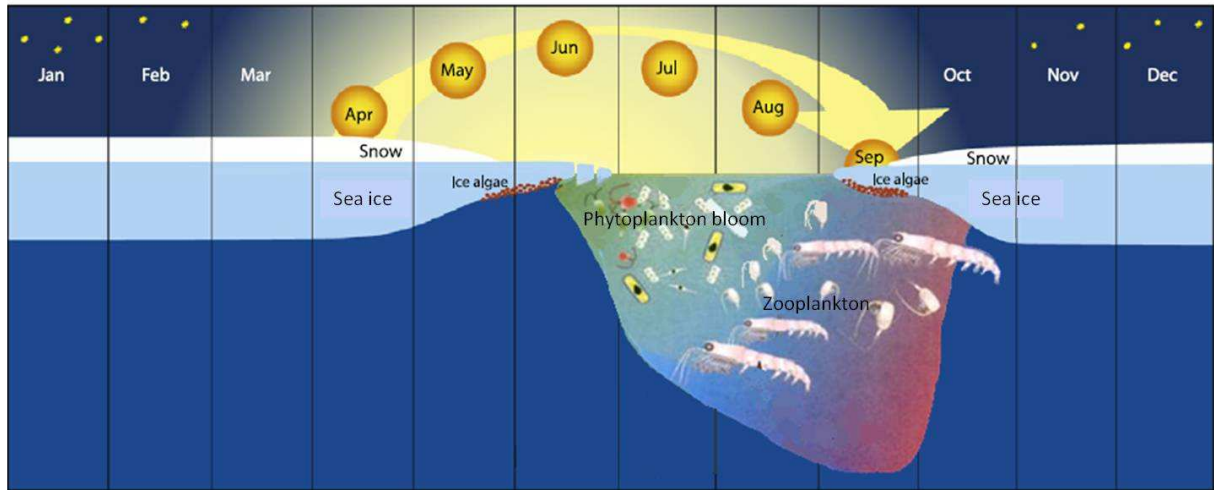


Figure 1. Seasonal cycle of the ice-influenced Arctic marine system. The figure illustrates the change in solar radiation and the melting of sea ice and snow, allowing sea ice algae and phytoplankton to bloom in late spring and summer. Also shown are key zooplankton grazers. Figure modified from Wassmann et al. (2004) and Wassmann (2011).

Primary production is thus constrained to a relatively short seasonal window during the spring-summer period in the Arctic, explaining why annual primary production is lower than at lower latitudes (Subba Rao and Platt 1984; Reigstad et al. 2002; Sakshaug 2004). However, this period is characterized by high biological activity, and a number of heterotrophic organisms rely heavily on the accumulated suspended biomass, which consists partly of Arctic zooplankton species.

1.2.2. Key Arctic species: Calanoid copepods

As a result of particularly good adaptation to a challenging environment, large calanoid copepods often contribute significantly to the total zooplankton biomass and most of the time dominate the meso-zooplankton population in Arctic and sub-Arctic areas (Søreide et al. 2008; Falk-Petersen et al. 2009; Svensen et al. 2011). These copepods are considered predominantly herbivorous and have a life cycle strategy characterized by the ability to synthesize and store high-calorific lipids in order to survive during periods devoid of phytoplankton (Kattner and Hagen 1995; Falk-Petersen et al. 2009). Other species in high-latitude systems have also developed this lipid storing ability, but the main calanoid copepods are by far the most efficient lipid synthesizers (Kattner and Hagen 1995; Hagen and Auel 2001). They are represented by three main species in the Arctic and in sub-Arctic areas, differing in their geographical distribution and life span (Falk-Petersen et al. 2009): the true

Arctic species *Calanus hyperboreus* and *Calanus glacialis* and the Atlantic species *Calanus finmarchicus* (cf. Fig. 2).

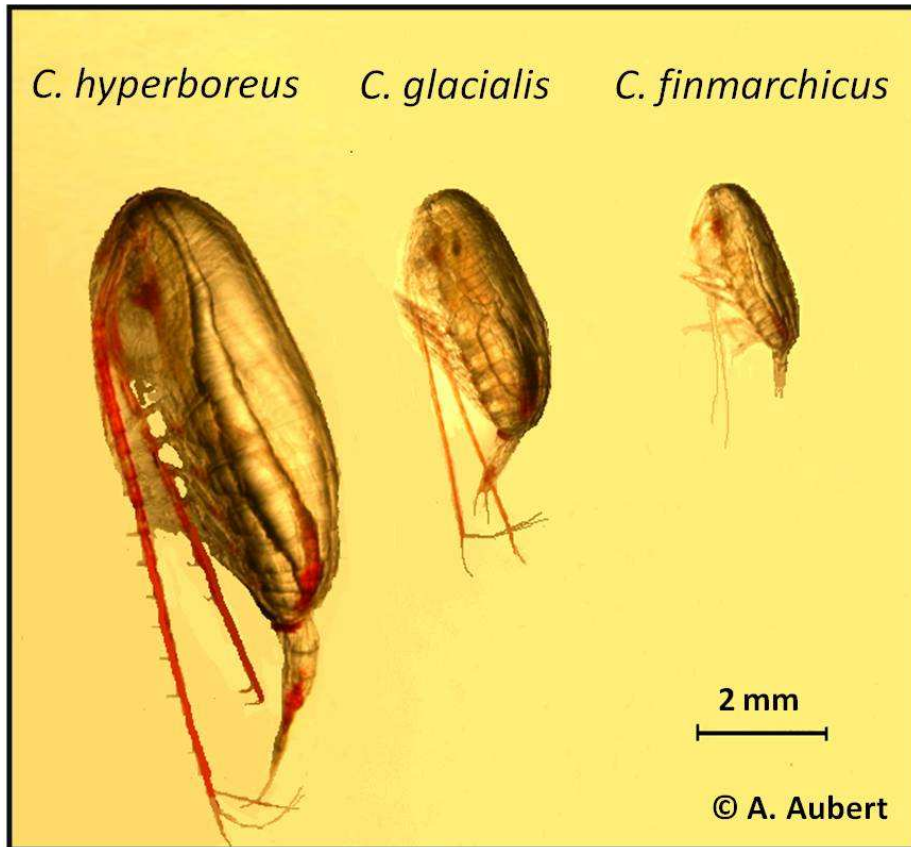


Figure 2. The three main calanoid copepod species present in the Arctic and sub-Arctic areas, from left to right: the large *Calanus hyperboreus*, *Calanus glacialis* and the smaller *Calanus finmarchicus*. All individuals are adult females.

Calanus hyperboreus is considered a deep-water species and is distributed mainly in the Greenland Sea, the Fram Strait, the Labrador Sea, Baffin Bay and the central Arctic Ocean Basins. It can also be found in shelf seas, such as the Norwegian Sea and the North Sea (Falk-Petersen et al. 2009). It is the largest of the three species and has the longest life span, ranging from 1 to 6 years depending on food conditions and habitat. *C. hyperboreus* produces lipids containing a higher proportion of long chain molecules compared to the two other species (Kattner and Hagen 1995; Hirche 1997; Falk-Petersen et al. 1999). The spawning occurs during winter at depth (Hirche and Niehoff 1996) and thus entirely relies on internal lipid reserves.

Calanus glacialis is a shelf species of smaller size and distributed throughout the Arctic Shelf seas. Its life span can range from 1 to 3 years, but a 2 years life span dominates (Tande et al,

1985; Kosobokova 1999). The spawning takes place prior to or during the Arctic spring bloom and ice algae appears to be an important food source (Niehoff et al. 2002; Hirche and Kosobokova 2003; Leu et al. 2011).

Calanus finmarchicus has its center of distribution in North Atlantic waters and can be found in high abundance in many locations influenced by Atlantic waters, such as parts of the southern and central Barents Sea or along the Norwegian coast (Aksnes and Blindheim 1996; Planque et al. 1997). Along with advected Atlantic water the species has also been reported occasionally in the central Arctic Ocean and in the pack ice region of the Greenland Sea (Smith 1990; Hirche and Kosobokova 2007; Madsen et al. 2008). It is a univoltine (one generation per year) species and spawns during or immediately after, the phytoplankton spring bloom. It overwinters at stage CV.

The productivity of these three species is particularly dependent on the short time window of primary production at the end of spring and summer. In the central Arctic Ocean, the three species alone account for 2/3 to 3/4 of the total mesozooplankton standing stock (Mumm et al. 1998; Auel and Hagen 2002). The role of these copepods in the lipid-driven Arctic food web is fundamental since, due to their abundance and high calorific value, they represent an important food input for a number of species at higher trophic levels (Falk-Petersen et al. 1999; Dahl et al. 2003; Falk-Petersen et al. 2009). *Calanus finmarchicus* for instance is a particularly fundamental food source for juvenile fish of commercially important species such as herring and cod (Cushing 1990; Beaugrand et al. 2003; Dommasnes et al. 2004).

1.2.3. Role of calanoid copepods in nutrient recycling and vertical export

During the Arctic autumn and winter, the large calanoid copepods overwinter at depth, in a state characterized by low metabolism, and they are considered not to feed (Båmstedt and Ervik 1984; Auel et al. 2003). In contrast, during the Arctic spring and summer, they graze on the intense primary production and invest part of this energy into lipid storage (Tande 1982; Conover and Huntley 1991; Falk-Petersen et al. 2009). Their grazing impact on the phytoplankton production can be significant (Nielsen and Hansen 1995; Carlotti and Radach 1996; Hansen et al. 1999). During blooms, calanoid copepods have been shown to consume 45 to 80% of primary production per day in Greenland waters (Nielsen and Hansen 1995) and

22 to 44 % of the daily primary production in terms of particulate organic carbon (POC) in the northern Barents Sea (Wexels Riser et al. 2008). The grazing of these copepods on primary production does not only represent a sequestration of material. It also acts on nutrient cycling via sloppy feeding and excretion which resupplies nutrients in the surface layers (Lehman, 1984; Sterner and Elser 2002). Copepods release nutrients in particulate form through fecal pellets, but also in dissolved form, mostly ammonia and phosphate, and trace elements, which can be directly used by autotrophs, thus promoting regenerated production (Mauchline 1998).

The copepods' release of dissolved substances has been shown to provide 50% of phytoplankton N and P requirements at several stations in east-Greenlandic and in Svalbard waters during summer (Alcaraz et al. 2010). Another study in the Canadian Arctic has shown that the dominant copepod species provided through excretion on average 40% of the NH_4^+ required by the phytoplankton (Harrison et al. 1985). In addition, fecal pellets supply nutrients to the upper mixed layer when they are degraded, although the mechanisms involved have not been extensively documented in the literature (but see Turner 2002 and references therein).

An important aspect concerning fecal pellets is that they constitute a fast pathway for vertical export of organic matter to the deep oceans. They can contribute significantly to the total POC export and also supply food to deep-sea benthic fauna (Suess 1980; Bathmann et al. 1987; Wassmann 1997). The relative importance of fecal pellets for POC export varies greatly but on average, they have been shown to contribute 20% of total POC flux from a compilation of sediments trap studies worldwide, reviewed by Wexels Riser (2007). Studies from the Arctic have shown that the contribution of fecal pellets is highly variable, ranging from close to 0 to 95% (Wexels Riser et al. 2002; Wexels Riser et al. 2007; Lalande et al. 2011), but on average ranges between 15 and 35% in the Barents Sea (Wexels Riser et al. 2008). The overall role of copepods on C, N and P cycling and export is summarized in Fig. 3.

While much work has been done to understand the quantitative role of calanoid copepod fecal pellets in vertical C export in the Arctic Ocean (Reigstad et al. 2000; Wexels Riser et al. 2010), relatively few investigations are available on the qualitative contribution to both nutrient recycling and particulate export at depth (Wexels Riser et al. 2007).

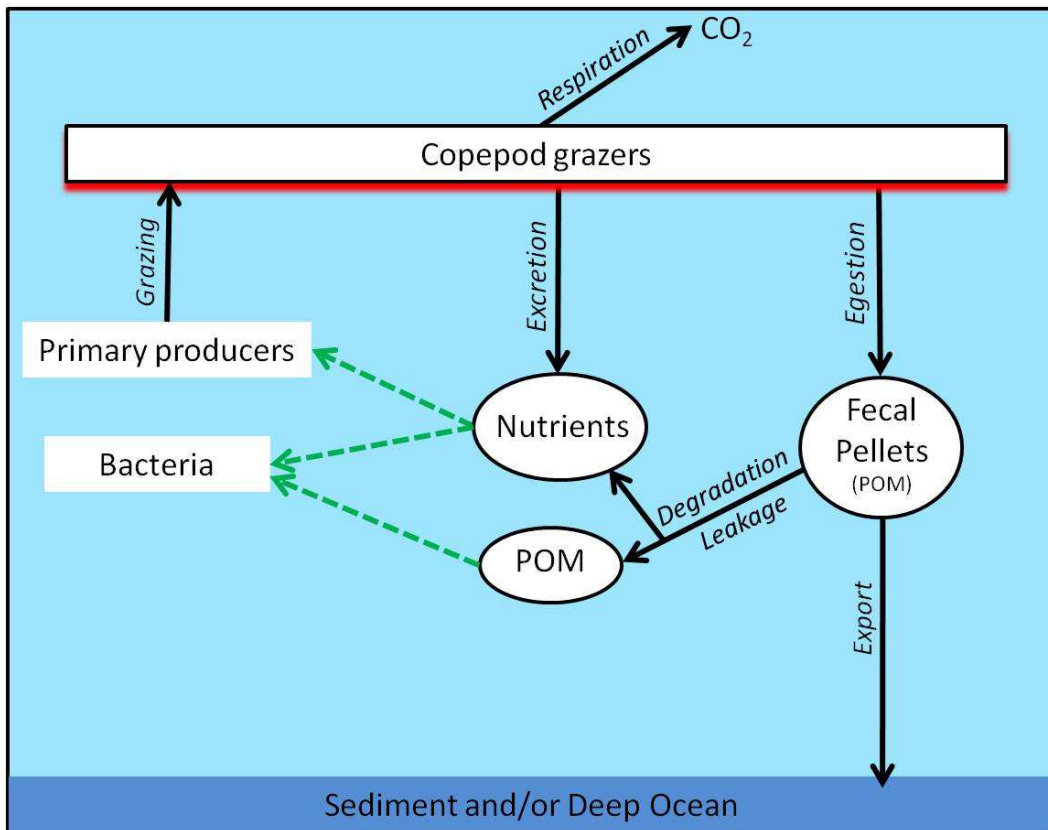


Figure 3. Conceptual model of copepod grazer-mediated nutrient cycling and vertical export. The green arrows represent flux of nutrients to the recipient organisms. POM is Particulate Organic Matter.

To the best of my knowledge, phosphorus has not been included in any of these studies done in the Arctic marine environment. Since fecal pellets play an important role in nutrient cycling and export, their C:N:P composition has to be considered.

1.2.4 Challenges for a stoichiometric approach

The most obvious difference in the body composition of high-latitude copepods, compared to organisms from lower latitudes, is their high proportion of storage lipids. For the three calanoid copepod species, *C. hyperboreus*, *C. glacialis* and *C. finmarchicus*, the lipid in the storage compartment consists mainly of wax esters and to a lesser extent of triacylglycerols. Both these lipids are composed of long-chain monounsaturated fatty acids and fatty alcohols (Hagen and Auel 2001; Scott et al. 2002; Falk-Petersen et al. 2009). These molecules are extremely C-rich: their C content is never <70% of their molar weight, and the storage lipids represent on average 50% of the copepod dry weight (and can be as much as 85%). Most of the body C is thus present in the lipid storage (Vogedes et al. 2010), which implies that lipid-

synthesizing copepods in high-latitude marine systems are characterized by high C:nutrient body ratios compared to lower latitude zooplankton (Tande 1982; Gismervik 1997). The body C content is not only higher, but also much more variable owing to the seasonal character of the lipid synthesis. Since lipids can be considered devoid of N and P (Walve and Larsson 1999; Ventura 2006), the body C:N and C:P ratios in these copepods are highly variable throughout the year. This means that high-latitude calanoid copepods do not maintain homeostasis in their elemental C:N:P body composition, which suggests difficulties for considering these zooplankton through stoichiometric approaches (Anderson and Hessen 1995). Models to study potential elemental limitation of *Calanus finmarchicus* have been developed (Mayor et al. 2009a; Mayor et al. 2009b), focusing on adult females, but these have not addressed the lipid compartment homeostatic deviation, nor considered phosphorus in their approaches. The lipid weight in terms of C has never been quantified for these copepods and this is addressed in the present study.

2. Aims and objectives

This thesis is dedicated to key lipid-synthesizing calanoid copepods in sub-Arctic and Arctic marine areas. The aim of the work was to describe their body composition, their interaction with primary producers and their role in nutrient recycling and export from a stoichiometric point of view. Ecological stoichiometry enables studying the qualitative interaction between these organisms and their food but also facilitates understanding of the role of these copepods in the C, N and P nutrient recycling and vertical export. Focus was placed on the period of highest variability in primary production, from the end of winter to late summer, when the copepod-producer interaction is intense. So far, elements as limitation factors have not been investigated for grazers of the Arctic ecosystem, and no studies exist that include P. Rapid climate changes and potential impacts on the Arctic ecosystem call for an improved understanding of growth and production-limiting factors of Arctic key species. The discussion includes an outlook onto the potential effects of these climate changes on copepod-food interaction in the Arctic.

The specific objectives were:

- 1) To characterize the C:N:P body composition of the three main lipid-synthesizing calanoid copepod species and the C:N:P composition of their food in sub-Arctic and Arctic marine ecosystems (**Paper I, II and additional unpublished data**)
- 2) To investigate the copepod-food interaction and to identify the limiting elemental factors for growth/reproduction of these copepods (**Paper I, II and additional unpublished data**).
- 3) To identify the role of copepod fecal pellets for C:N:P recycling and vertical export (**Paper I, II, III and additional unpublished data**)

3. Study areas

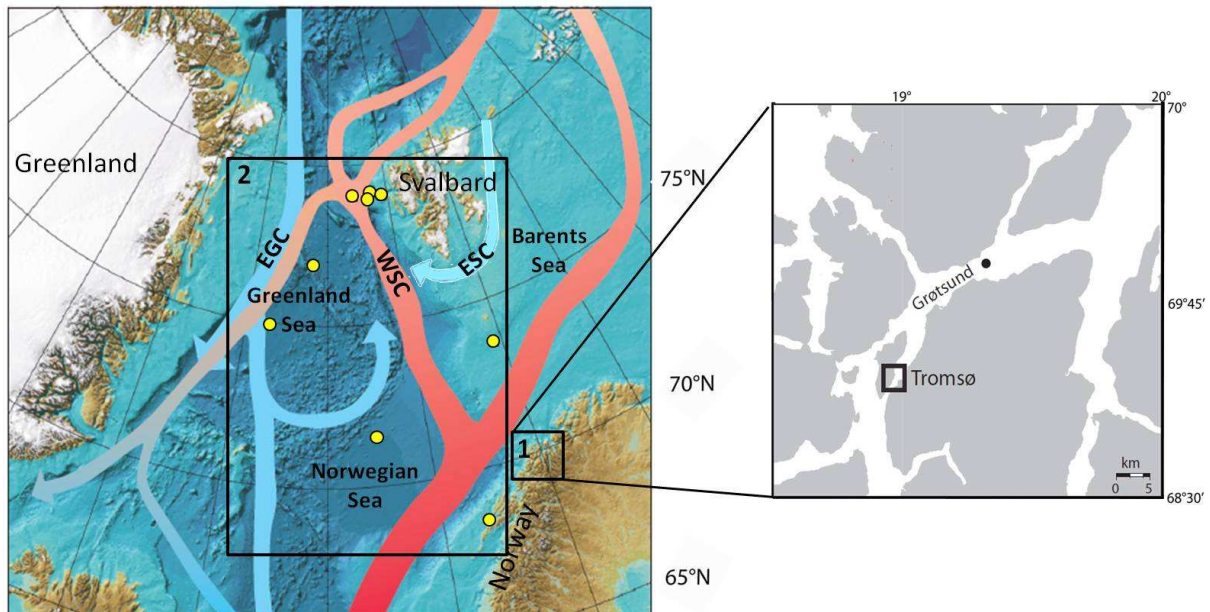


Figure 4. Map of the western section of the European Arctic Ocean with principal currents (arrows) and location of the stations visited (yellow dots). The warm West Spitsbergen Current (WSC) is in red and the cold East Greenland Current (EGC) and East Spitsbergen Current (ESC) in blue. The Grøtsund sound in northern Norway is indicated on the large map by the small black square (Area 1). The enlargement of this area close to Tromsø is presented on the right. Sampling took place over 4 months in the winter-spring period in Grøtsund (Paper I, Area 1) while snapshot sampling was carried out at several stations in the western European Arctic Ocean between Norway, the Greenland Sea and Svalbard during the spring-summer period (Paper II, III and additional data, Area 2).

3.1. Grøtsund, a sub-Arctic sound

The first objective was to characterize the C:N:P composition of the target grazers and of their food. In order to determine whether development stages and/or spring bloom progression have an influence on the stoichiometric ratios of the grazers, it was necessary to sample the same copepod species throughout the productive season and to obtain several measurements for each development stage over this season. A seasonal study also makes it possible to study inter-individual variability in lipid storage which is expected to greatly influence the body stoichiometry of the lipid-synthesizing individuals. It is difficult to conduct such a sampling from the open ocean for logistic reasons. However, north Norwegian fjords and sounds are easy to reach and observations throughout the year are therefore possible. In addition they present a number of characteristics similar to the Arctic and sub-Arctic open oceans. Two of

the three target copepod species are generally present in these areas (Pedersen and Tande 1992; Pedersen et al. 1995). The timing of the spring bloom has been shown to be similar with the southern Barents Sea and Svalbard fjords and the vernal phytoplankton composition is similar to the southern Barents Sea (Eilertsen et al. 1989; Eilertsen and Wyatt 2000; Degerlund and Eilertsen 2010). Grøtsund was chosen for a number of these reasons. This sub-Arctic sound is located in northern Norway, north-east of the city of Tromsø (69°47'N 19°19'E, Fig. 4). It is protected from Atlantic currents by the Norwegian coastal current and the circulation pattern is influenced by adjacent sounds (Svensen and Tande, 1999; Tande and Slagstad, 1992). Temperature typically ranges from 2.5°C in February to 6°C in June and the surface salinity is quite stable, between 33 and 35, staying close to 34 during the winter-spring and decreasing in May when freshwater runoff occurs (Havmiljødata programme, University of Tromsø). *Calanus finmarchicus* dominates the mesozooplankton biomass in this area (Tande 1982; Svensen and Tande 1999). It has been hypothesized that an overwintering population of this species exists at depth and it was shown that ontogenic development could be easily followed through the season (Tande and Hopkins 1981; Svensen and Tande 1999). A number of studies have been conducted in the area close to Grøtsund, focusing not only on primary production but also on the population development of *C. finmarchicus* (Eilertsen et al. 1981; Tande 1982; Eilertsen and Taasen 1984) and thus provide useful background information. The sampling in Grøtsund was carried out twice a month from the very beginning of the productive season, i.e. end of winter (end February), to the end of spring, in mid-May. Different stages of *C. finmarchicus* (Paper I), but also some *C. hyperboreus*, and their food were sampled for C:N:P composition analysis.

3.2. The western European Arctic Ocean

In order to describe the copepod-producer interaction in the open Arctic Ocean and study the role of copepod fecal pellets in nutrient recycling and vertical export, stations in the western European part of the Arctic Ocean (WEAO) were visited during two cruises (Fig. 4). The WEAO includes the northern Norwegian Sea, the Greenland Sea, the Fram Strait and the western Barents Sea. The large area covered (Area 2 in Fig. 4) increased the chance to encounter all of the three key copepod species. It enabled sampling at different phases of the spring phytoplankton bloom during the restricted time window provided by oceanographic cruises. The onset of the phytoplankton bloom is highly variable according to latitude in the Arctic Ocean (Leu et al. 2011). We wanted to sample different phases of the bloom because

they can potentially show different types of stoichiometric interaction between grazers and producers. The area covered also has the potential to exhibit stoichiometric differences among stations since there are large differences in nutrient concentrations, biochemical properties and food chain dynamics in different hydrographical regimes (Smith 1988). The area is characterized by a variety of hydrographic regimes, with two main opposing currents that together represent the most important water mass exchange with the Arctic Ocean through the deep Fram Strait. The most important input currents are the warm and highly-saline West Spitsbergen Current (WSC) which flows along the west coast of Svalbard and the cold East Spitsbergen Current (ESC) which originates from the northern Barents Sea (Aagaard and Greisman 1975; Schauer and Beszczynska-Moller 2009). The East Greenland Current (EGC) is the main outflow current and carries cold Arctic water and ice from the upper layer of the Arctic Ocean along the east Greenland shelf slope toward the North Atlantic (Aagaard and Greisman 1975; Aagaard and Carmack 1989). These currents are also responsible for different ice regimes (Aagaard and Carmack 1989), shaping the outburst of primary production in ice-covered and ice-influenced areas (Spindler 1994). The western part of the European Arctic Ocean, along the east Greenland shelf, is influenced by large input of sea ice from the Arctic Ocean, whereas in the eastern part, ice formation and retention is prevented by heat flux.

Two cruises were conducted in this part of the Arctic, allowing comparisons of the interaction of each individual copepod species with its food at different phases of the phytoplankton bloom (Paper II). The role of copepod fecal pellets for C:N:P recycling and vertical export was also investigated during the productive season at selected stations (Paper II, III).

4. Results and discussion

4.1. Characterization of C:N:P ratios

4.1.1. Key calanoid copepod grazers

The consideration of the interaction of calanoid copepod with their food by applying stoichiometry theory is important for ecosystem processes such as nutrient cycling and the structure of the food web. While the variable body C:N ratio is a known feature of the three key calanoid copepods characteristics of the sub-Arctic and Arctic marine regions (Kattner and Hagen 1995; Falk-Petersen et al. 2009), their C:P and N:P body ratios have so far not been measured. It is assumed that the lipid storage compartment is important in the variation of these ratios but this has not been measured neither. Knowledge of these ratios creates a baseline that permits calculations to study the elemental limitation of these grazers through food. The following part aims to characterize C:N:P composition of high-latitude calanoid copepods.

The specific objectives are:

- To describe the copepod C:N:P body ratios
- To identify the potential causes of variability in the copepod C:N:P body ratios
- To compare copepod C:N:P body ratios with those of other zooplankton

Table I (p. 16-17) presents the body C:N, C:P and N:P ratios for the three species *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* in various Arctic and sub-Arctic areas. The dry weights used to calculate the ratios for *C. glacialis* were based on the prosome length-DW relationship determined for this species in the present study ($DW=0.0145PL^{2.71}$, $R^2=0.77$). The body C:N ratios found ranged from 3 to 11.4 among the three species and were within the range of previously published ratios. Body C:P ratios of calanoid copepods are nearly nonexistent in the literature, and the measured ratios among the three copepod species exhibited large variations, from 38 to 333. It was not possible to test the differences in body C:N and C:P ratios among the species since the available data are too heterogeneous (different number of individuals per stage; different stages encountered among stations and species, different timing of sampling). If tested, the differences in body C:N and C:P ratios would rather reflect different levels of lipid storage than real inter-specific differences.

Table I. Body C:N, C:P (total and somatic (_s)) and N:P ratios for different development stages for the three species *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus*

Species	Stage	Season	Location	C:N	C:N _s	C:P	C:P _s	N:P	Reference
<i>Calanus hyperboreus</i>	Female	March to April	Grøtsund	4.3 -7.8	1.7-2.7	97-203	38-67	22-29	This study
		August	Fram Strait	9.0-11.3	-	-	-	-	This study
		April and October	Greenland Sea and WSC	3.8-8.5	-	-	-	-	Hirche 1997
	CV	April-May	Grøtsund	5.3-10.4	1.7-2.9	87-190	25-45	13-19	This study
		June	Fram Strait	9.7-10.4	2.7-3.0	261-333	75-94	25-34	Paper II
		August	Fram Strait	9.7-11.0	-	-	-	-	This study
		April and October	Greenland Sea and WSC	5.1-10.3	-	-	-	-	Hirche 1997
	CIV	March to May	Grøtsund	4.2-11.3	1.7-3.3	38-185	27-71	12-24	This study
		July and October	Greenland Sea and WSC	4.4-10.6	-	-	-	-	Hirche 1997
	CIII	End of April	Grøtsund	10.0	3.2	-	-	-	This study
Mixed	January to August	Amundsen Gulf	± 5-9	-	-	-	-	Forest et al. 2011	
<i>Calanus glacialis</i>	Female	August	Fram Strait	9.5-11.4	-	-	-	-	This study
		May	Isfjorden	4.0-5.0	-	48-73	-	14-18	This study
		April	West Barents Sea	6.1	-	-	-	-	Hirche & Kattner 1993
	CV	August	Fram Strait	6.9-10.0					This study
		June	Greenland Sea	6.8-9.9					This study
		June	Isfjorden	8.5-9.8	3.2-3.8	187-314	82-129	26-38	This study
		End of June	West Spitsbergen shelf	10.3-10.6	3.5-3.8	144-282	58-108	16-31	This study
	CIV	May	Isfjorden	5.2-7.1	3.3-3.4	66-102	30-57	15-17	This study
		May	Ice station	6.2-7.8	3.2-3.9	83-126	50-73	15.7-19	This study
	Mixed	January to August	Amundsen Gulf	3.5-12					Forest et al. 2011
	Nauplii	May	Isfjorden	4.2-4.4		38-39		10-11	This study
	Eggs	May	Isfjorden	4.5-4.9		47-66		11-17	This study
4.6								Hirche & Kattner 1993	

Species	Stage	Season	Location	C:N	C:N _s	C:P	C:P _s	N:P	Reference
<i>Calanus finmarchicus</i>	Female	February- May	Grøtsund	3.9-7.7	1.9-3.7	83-187	53-92	17-33	Paper I
		yearly	Balsfjord	~ 4-16	-	-	-	-	Tande 1982
	Male	February- May	Grøtsund	3.8-6.6	2.4-3.4	59-152	38-73	16-23	Paper I
	CV	February- May	Grøtsund	5.8-8.1	2.6-3.5	89-185	47-74	15-24	Paper I
		End of May	Lofoten coast	4.8-7.7	3.2-3.5	87-207	63-85	18-27	Paper II
		Early June	Nowegian Sea	6.1-9.5	2-3.5	130-231	42-86	21-24	Paper II
		Mid-June	West Spitsbergen Slope shelf	10.1-10.2	3.6-3.9	125-229	82-89	22-23	Paper II
		June	West Greenland Sea	7.6-9	2.7-3	147-252	52-81	19-28	Paper II
		End of June	West Barents Sea	5.7-6.3	-	134-143	-	22-23	Paper II
		Late November	Nova Scotia (Canada)	8.4	-	249	-	30	Mayzaud & Martin 1975
	CIV	April to Mid-May	Grøtsund	5.1-6	2.2-2.6	79-147	30-55	13 -24	Paper I
		yearly	Balsfjord	~ 6-13	-	-	-	-	Tande 1982
	Nauplii	April	Grøtsund	4.2-4.5	-	64-89	-	15-20	Paper I
	Eggs	April	Grøtsund	3 - 5.1	-	52-88	-	10-18	Paper I
<i>Calanus spp.</i>	Female	Yearly	Oslofjord	4.9-5.4	-	117-139	-	21-28	Gismervik 1997
	CV	Yearly	Oslofjord	8.6-11.6	-	131-325	-	18-28	Gismervik 1997

The body C:nutrient ratios in these animals are indeed a reflection of their lipid storage state: the positive relationship between the amount of wax ester in the lipid storage compartment and the body C:N ratio (assuming lipids consist of 100% wax esters) is clearly visible in Fig. 5.

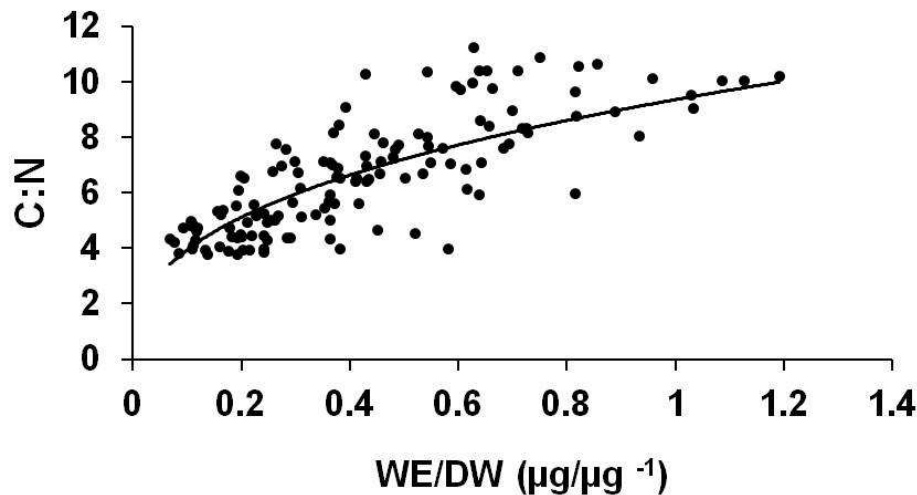


Figure 5. Body C:N ratio as a function of the amount of wax ester (WE) in the lipid storage compartment per unit dry weight (DW). The relationship is based on all C:N ratio measurements from this study for which the lipid sac was measured ($n=133$) and includes the three *Calanus* species and several development stages (female, male, CV and CIV).

The relationship between the body C:P ratio and the amount of wax ester was not tested since the amounts of C and P were measured in two different samples containing organisms which have variable amounts of lipid. Given that most of the body C is present in the lipid compartment, body C:P ratio is most likely driven by the lipid storage, which is a seasonal process (cf. Fig. 3 in Paper I). To enable comparison among species and to consider these copepods through a stoichiometric approach, body elemental ratios were calculated in the somatic tissues alone, after removal of the C of the lipid sac compartment (cf. methodology in Paper I). These new body ratios, $C:N_s$ and $C:P_s$, are also presented in Table I and ranged from 1.7 to 4.7 and from 25 to 129 respectively. For all measurements in the present study, the standard deviations of the C:N and C:P ratios were significantly lower (CN: $t_{224}=24$, $P=2.2*10^{-16}$; CP: $t_{254}=15.7$, $P=2.2*10^{-16}$) when the lipid storage compartment was removed. C:N decreased by a factor of 3.2 and C:P decreased by a factor of 2.7. Figure 6 presents the ratios in the three *Calanus* species. *C. glacialis* generally presented higher somatic $C:N_s$ and $C:P_s$ ratios than the two other species. Its body $C:N_s$ ratio was significantly higher than that of *C. hyperboreus*. The ratios obtained for *C. glacialis* emanate from the few truly Arctic stations and from two sampling dates. This is in contrast to data sets for the two other species,

which include numerous values from the sub-Arctic station Grøtsund over a long time span. The paucity of data might explain the slight tendency for *C. glacialis* to exhibit higher C:N_s and C:P_s. It is also possible that the C content of their lipid sac was slightly underestimated (which results in higher C:N_s and C:P_s). *C. glacialis* from ice-influenced locations feeds on ice algae (when present), which have been shown to contain longer C-chain molecules compared to other groups of phytoplankton (Falk-Petersen et al. 1998; Henderson et al. 1998). This might induce production of lipids with a higher proportion of C.

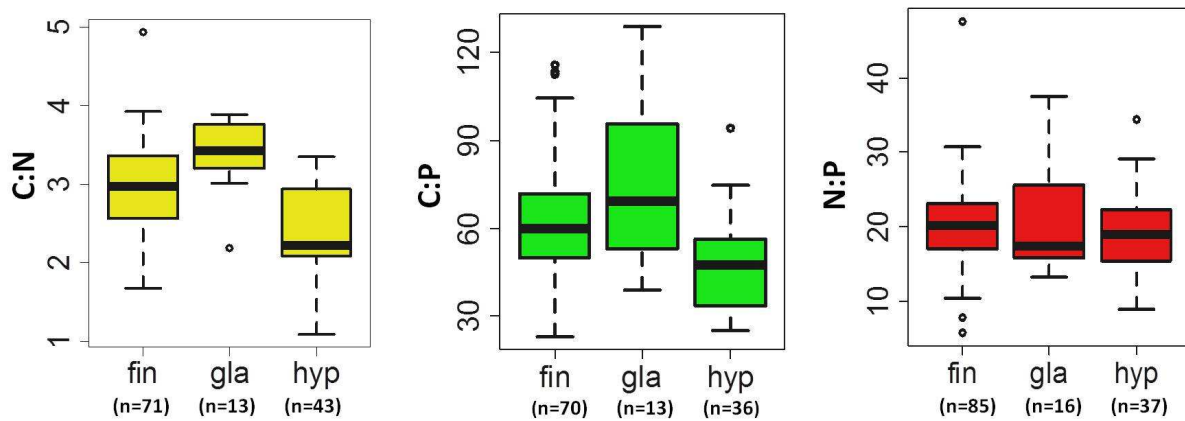


Figure 6. Somatic body C:N_s (in yellow), C:P_s (in green) and N:P (in red) ratios for the three *Calanus* species represented in boxplots (n=number of individuals). fin= *C. finmarchicus*, gla=*C. glacialis* and hyp=*C. hyperboreus*. Each boxplot gives the lower quartile (25% of data less than this value), the median, the upper quartile (25% of data greater than this value) and the whiskers show the minimum and the maximum. Circles denote outliers.

Body C:N_s and C:P_s ratios were lower in *C. hyperboreus* compared to *C. finmarchicus* but the differences were not significant. Lower body C:P_s indicates a higher relative amount of body P, and suggests a higher growth rate, according to the GRH. The high proportion of CIV stages in the samples of this *C. hyperboreus* might be responsible for this apparent discrepancy. Among the three *Calanus* species, the body N:P ratio ranged from 10 to 38, with most of the individuals having a ratio between 15 and 25. These values were in the range of the few N:P ratios measured for copepods from fjords in southern Norway (Gismervik 1997). No differences appeared among the three species for this ratio, which indicates that N and P are more strongly coupled in the body of copepods than are C and P or C and N. The variability exhibited among the somatic body ratios, free of lipid C, is dependent on the development stage and the seasonality (Paper I). However, these variations are small compared to the variations in total body C:N and C:P ratios. The present study thus shows

that high-latitude copepods tend to maintain a certain homeostasis in their body tissues (Paper I, II). This implies that lipid-synthesizing copepods should be treated through a two-compartment stoichiometric model, with the lipid storage pool as one entity and somatic tissues as a second (Paper I).

The lack of body C:P and N:P ratios measured for high-latitude zooplankton has previously prevented comparison among different species and different areas. These data are not only useful for stoichiometric food web interaction studies to be addressed later, but are important in light of a general understanding of stoichiometric variations among zooplankton (Gismervik 1997; Elser et al. 2000d). Removing the lipid compartment allows comparison of elemental ratios with other non lipid-synthesizing zooplankton. The somatic body C:P_s and N:P ratios of high-latitude calanoid copepods are similar to the ratios measured for freshwater zooplankton such as *Daphnia magna* (Main et al. 1997; Sterner and Elser 2002). Few data are available for the body C:P and N:P ratios of marine zooplankton (Elser and Hassett 1994). The body N:P ratios measured here present a larger range of values compared to ratios found for bulk copepod samples in the literature (Table I and Båmstedt 1986). However, the average body N:P ratio (20.1) was lower than those of copepods from Long Island Sound, the Sargasso Sea or the tropical Atlantic (Le Borgne 1978). This suggests that high-latitude copepods have, with regard to their body N:P ratio, a higher growth rate compared to copepods from lower latitudes. These data originate from the spring-summer season in the Arctic and sub-Arctic. It would be interesting to also obtain these ratios for the fall-winter season and test and compare the GRH in dormant (fall-winter) and active (spring-summer) individuals. No data on C:N:P ratios of other zooplankton groups from the Arctic are available in order to discuss the potential variations among Arctic taxa and regions.

C:N:P ratios of eggs and nauplii for the two species *C. finmarchicus* (Paper I) and *C. glacialis* are provided in Table II. To our knowledge, they are the first C:P and N:P ratios provided for these species for both eggs and nauplii. The C:N ratio of eggs was typical for copepods in the literature (Checkley 1980; Hirche and Kattner 1993) and the ratio in nauplii was similar between the two species. The C:P (both C:P and C:P_s) and N:P ratios were higher in females *C. finmarchicus* compared to the ratios of their eggs, indicating strong allocation of P to the eggs (Paper I).

Table II. C:N:P ratios (\pm standard deviation) of females *C. finmarchicus* and *C. glacialis*, of their eggs and nauplii stage I (hatched from the same batch of eggs).

Location	Date	Species	Stage	C:N	C:N _s	C:P	C:P _s	N:P
Grøtsund	Mid-April	<i>C. finmarchicus</i>	Female	4.6 \pm 0.7	2.5 \pm 0.1	162 \pm 62	82 \pm 17	33 \pm 8
			Egg	3.6 \pm 0.3	-	49 \pm 7	-	14 \pm 2
			Nauplius	4.4 \pm 0.1	-	77 \pm 12	-	17 \pm 2
Isfjorden (Svalbard)	Early May	<i>C. glacialis</i>	Female	4.5 \pm 0.5	2.6 \pm 0.6	63 \pm 17	45 \pm 9	16 \pm 2
			Egg	4.7 \pm 0.2	-	69 \pm 12	-	15 \pm 3
			Nauplius	4.3 \pm 0.1	-	45 \pm 1	-	10 \pm 1

Strong P allocation in eggs is an indication that P is an important element for the earliest stages of development when the growth rate is high (Carrillo et al. 2001). This difference in the N:P ratio was not exhibited by *C. glacialis* and suggests a stronger lipid allocation into eggs compared to *C. finmarchicus* (or allocation of longer C-chain lipids).

In summary, deviation from homeostasis in the body elemental composition of high-latitude calanoid copepods is clearly driven by lipid synthesis. Calanoid copepods maintain homeostasis in their somatic tissues with small variations according to season and ontogenic development. This implies that a two-compartment model, separating lipid storage and somatic tissues, needs to be considered for these lipid-synthesizing organisms. Stoichiometric principles only can be applied to their somatic tissues. Basic knowledge of the body elemental ratios can provide useful information on the organism's growth, ontogenic development or different sensitivity to limiting elements. The results suggest that high-latitude copepods have a high growth rate compared to zooplankton from other marine regions. The element P appears to be particularly important for *C. finmarchicus* during the earliest stages of development probably owing to their high growth rate. *C. glacialis* however seems to exhibit a different strategy for allocation of carbon and nutrients into eggs. The body C:N:P ratios of these key species of the Arctic and sub-Arctic ecosystems constitute a baseline against which to study stoichiometric interactions with their food.

4.1.2. Seston

Calanoid copepods are filter-feeders recognized to be mainly herbivorous during periods of high primary production (Falk-Petersen et al. 1987; Sargent and Falk-Petersen 1988; Graeve et al. 1994). They are considered indiscriminate and also feed on protozoa, detritus and bacteria which together with phytoplankton form the suspended organic particulate matter, or seston (Conover 1966; Cowles 1979; Levinsen et al. 2000). Elemental composition of seston is used as a proxy of food quality for zooplankton grazers (Elser and Hassett 1994) and knowledge on its fluctuation is imperative to study the stoichiometric grazer-seston interaction.

The specific objectives are:

- To determine C:N:P ratios in seston
- To identify the potential factors that shape seston C:N:P ratios

Table III presents C:N:P ratios of marine seston from the areas sampled in the present study (Paper I, II). Additional values from the literature for the Arctic Ocean and lower latitudes are also shown. The average ratios measured in Grøtsund were within the range of ratios measured in Norwegian fjords and along the coast of Norway. The ratios measured in the WEAO were in the lower range of values compared to lower-latitude marine systems, particularly for the C:N and C:P ratios. The seston N:P ratio is similar to those of the south-east Atlantic. The lower C:N and C:P ratios in seston indicate a higher relative proportion of N and P compared to C, supposedly reflecting better food quality for organisms feeding on seston (Sterner and Elser 2002).

In comparison with other data available for the Arctic Ocean, C:N ratios for seston measured in the WEAO were in the lower range, reflecting that low Arctic seston C:N ratios are not the rule. Higher values found on the north-east Greenland shelf by Daly et al. (1999) were also obtained during the period of intense production (June-August). This was explained by the dominance of nutrient-deficient diatoms indicating that nutrient limitation in phytoplankton seems to impact seston C:N ratio. This higher value found by Daly et al. (1999) might also be related to the station's location in the inner part of the east Greenland shelf, where the waters are known to be poor in inorganic nitrogen (Mauritzen et al. 2011). Thus, lower values found

during the same period (Paper II) in the WEAO may indicate good nutritional quality of seston. No seston C:P and N:P ratios were available from other Arctic Ocean studies for comparison. Large variations in these ratios can be expected since a high heterogeneity characterizes the Arctic Ocean in terms of inorganic nutrient concentrations, phytoplankton composition, water masses...

Table III. C:N:P ratios of marine seston (above 100 m depth) available from the literature and from the current work for Arctic, sub-Arctic areas and other marine regions for comparison (Arctic areas are indicated by *).

Area	C:N ± SD	C:P ± SD	N:P±SD	References
WEAO *	5.9 ± 0.9	100 ± 19	17.5 ± 3	Paper II, III
NE Greenland shelf *	8.9	-	-	Daly et al: 1999
Arctic Ocean *	5.8 - 12 (<53µm) 6.2 - 18.6 (>53µm)	-	-	Moran et al. 1997
Beaufort Sea *	5.9 - 9.5	-	-	Bates et al. 2005
South east Atlantic	6.7 ± 0.7	112 ± 29	17 ± 3	Sterner et al. 2008
Western Mediterranean Sea	8.3 ± 3.3	202 ± 65	26 ± 10	Sterner et al. 2008
Indian	6.5 ± 1.2	101 ± 37	15 ± 5	Sterner et al. 2008
Hawaii	7.2 ± 3.1	128 ± 29	19 ± 6	Sterner et al. 2008
Sea of Japan	9.3 ± 2.4	153 ± 99	16 ± 10	Sterner et al. 2008
Eastern North Pacific	6.0-7.0	154 - 427	22 - 61.5	Loh and Baur 2000
Southern Ocean	7.0	273	38	Loh and Baur 2000
Sub-tropical Pacific	6.6	158	24	Hannides et al. 2009
Grøtsund	7.2 ± 1.5	116 ± 30	17 ± 4	Paper I
Coast of Norway	7.6 ± 5	137 ± 82	19 ± 13	Sterner et al. 2008
Sub-Arctic Norwegian fjords	6.0 – 12.0	-	-	Reigstad 2000
Oslo fjord	9.2 ± 2.5	154 ± 49	17 ± 5	Sterner et al. 2008
South Norwegian coast	7.7 - 7.2 (means)	119 - 147 (means)	16 - 22 (means)	Frigstad et al. 2011

The present study shows that phytoplankton nutrient limitation to some extent drives seston C:N:P ratios (Paper II). The DIN:TP ratio which indicates a shift between N and P limitation of phytoplankton is used as a proxy of phytoplankton N/P limitation (Ptacnik et al. 2010). In the WEAO, despite of large geographical differences, the trend according to bloom stages observed in seston C:N and N:P ratios appears to reflect N/P phytoplankton limitation (Paper II). Seston N:P ratio was high during the early and peak bloom phases when phytoplankton was most likely P-limited (above Redfield), and lower during the late bloom phase when the phytoplankton was potentially limited by both N and P (Paper II). No trend could be observed

for the seston C:P ratio. The DIN:TP ratio was not measured in Grøtsund. In more southerly Norwegian fjords inorganic nutrients have been identified as a driver of seston C:N:P ratios (Frigstad et al. 2011) and shifts in phytoplankton limitation have also been observed (Paasche and Erga 1988). In the study by Paasche and Erga, N limitation was observed during peak bloom and P limitation during late bloom. The higher seston N:P ratios in Grøtsund during peak and late bloom potentially indicated P-limited phytoplankton populations. Shifts in the phytoplankton nutrient limitation can also reflect change in the composition of the phytoplankton population (Anderson et al. 2002; Mette et al. 2011). We did not investigate phytoplankton composition, but clearly more comprehensive seston C:N:P ratios studies should include this crucial information (Paper I, II, III).

The N/P phytoplankton limitation might impact seston C:N:P composition only during the period when primary producers dominate the seston fraction (Sterner and Elser 2002). Bloom stage was identified as a factor in the variation of seston quality, more specifically for the seston C:N ratio (Paper I, II), in agreement with the results of Frigstad et al. (2011). Grøtsund and the WEAO exhibited different patterns (Paper I, II). While the seston C:N ratio decreased from pre- to late bloom in Grøtsund, it increased from early to late bloom in the WEAO stations. The seston N:P variation also differed between the two areas. The ratio was higher during the peak and late bloom phases in Grøtsund compared to the pre- and early bloom phases. In contrast, the ratio was lower during late bloom in the WEAO compared to early and peak bloom (Paper I, II). The results from Grøtsund for the seston C:N and C:P ratios variation are similar to those presented by Frigstad et al. (2011) who used a large data set of seston C:N:P ratios through the year in the southern coast of Norway. They identified the main drivers of seston C:N:P ratios as water temperature, inorganic nutrients concentrations and certain characteristics of the water mass, mainly input of freshwater and water stratification (Frigstad et al. 2011). The different variations exhibited between Grøtsund and the WEAO might thus be explained by a number of these drivers since two radically different physical systems are compared: a sound and the open ocean. Different water masses in the Arctic have also been shown to be characterized by different inorganic N:P ratios which can impact the phytoplankton uptake (Damm et al. 2010) and thus the seston N:P ratio. Water masses and freshwater input are thus potential factors responsible for seston C:P and N:P ratios being higher at stations A and Ab (respectively in coastal Norway and in the Norwegian Sea) than at the other open ocean stations in the WEAO (Paper II). Seston POC and PON

concentrations were also tightly coupled (Paper I) while the seston C:P and N:P ratios were driven by particulate P (Paper I).

In summary, seston C:P and N:P ratios from the WEAO are the first to be reported for the Arctic Ocean. The values measured suggest that Arctic seston is of higher nutritive quality than seston in other marine regions. Seston C:N:P ratios have been shown to fluctuate in relation to several factors. The phytoplankton nutrient limitation (N and/or P limitation) has been shown to depend on the bloom stage and to drive the seston N:P ratio. Different variations in seston C:N:P ratios and phytoplankton limitation according to bloom phases between the two areas (Grøtsund and the WEAO) can be explained by differences in water masses, freshwater input and water properties such as salinity and nutrient concentrations

4.2. Copepod-seston interaction

Food needs to be of a sufficient quality in order to fulfill zooplankton feeding requirements, but must also be available in saturating amounts (Gulati and DeMott 1997; Sterner and Schulz 1998). Chl *a* is a proxy of food quantity (Vijverberg 1976), but also particulate C and N can be used (Checkley 1980). Consideration of the basic life traits and physiology of any organisms, including copepods, is important for understanding potential food limitation (Mitra and Flynn 2005). The introduction concludes that stoichiometric limitation calculations are based on the fact that consumers maintain homeostasis (Sterner and Elser 2002). In the following, the lipid-corrected body somatic ratios are used in these calculations (Paper I, II). Bloom development has been identified as one of the principal factors of variation for food quality (seston C:N:P ratios), but to a lesser extent also for the body somatic ratios (Paper I, II). In addition, phytoplankton, assumed to be the main food for calanoid grazers, varies dramatically in quantity with the seasons in the Arctic Ocean and sub-Arctic areas. The copepod-seston interaction is thus presented against a seasonal backdrop, per bloom stage, in the current work. The period from the early appearance of phytoplankton cells to the end of the spring bloom is divided into four distinct bloom phases: pre-bloom, early bloom, peak bloom and late bloom (Paper I, II). The bloom phase grouping allows comparison of different regions even though the timing of the bloom differs according to latitude in the Arctic Ocean and sub-Arctic marine regions (Fig. 7).

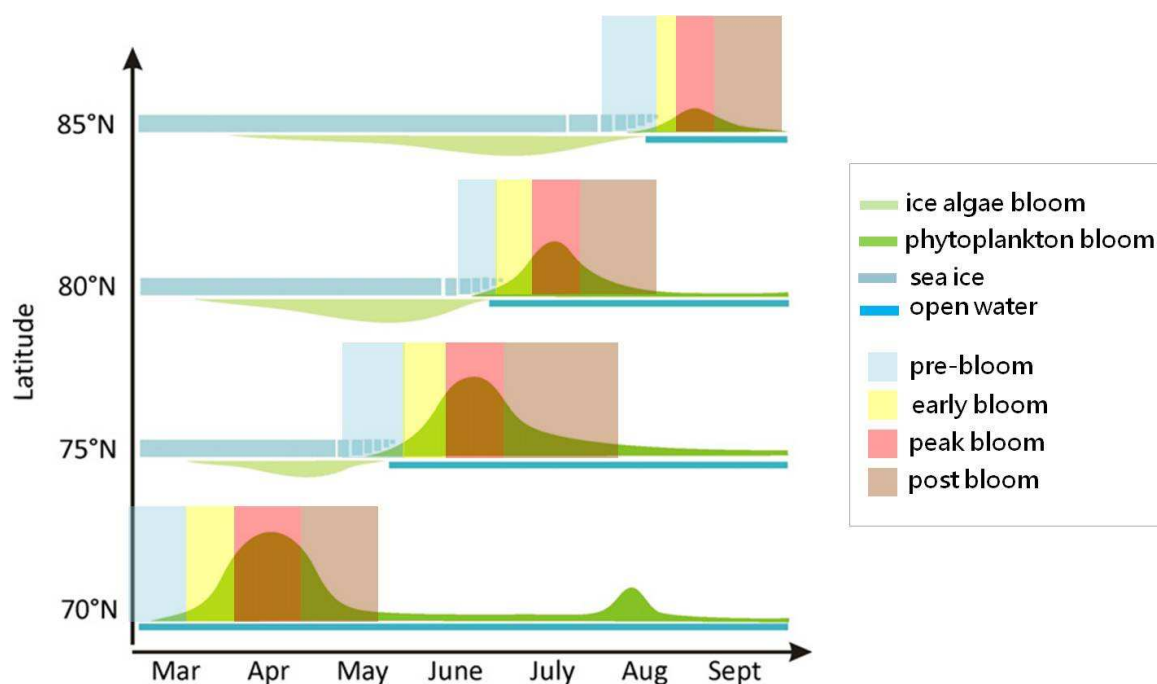


Figure 7. Conceptual overview of the timing of phytoplankton bloom in the WEAO and northern sub-Arctic along a latitudinal gradient (Tromsø Sound is represented by the 70°N scenario). Modified from Leu et al. (2011).

The specific objectives are:

- To assess elemental matching between the seston composition and calanoid copepod food requirements during the different bloom phases
- To reveal the main limiting elements (C, N, and P) for copepods in relation to their life cycle
- To assess potential parallel limitation in producers and their consumers

Pre-bloom

The pre-bloom conditions for *Calanus spp.* were investigated in Grøtsund (Paper I) but not in the WEAO. Overwintering stages of *C. finmarchicus* (adults and CV) were found active in the upper 100 m in Grøtsund. They used their lipid sac reserves heavily, indicating that they were most likely limited by food quantity rather than quality at this time. Indeed, calculation for metabolism maintenance showed that seston C concentration was too low to meet the copepods C requirements unless they were able to have a high clearance rate for this element (Paper I). The use of stored lipids to maintain their metabolism, was observed through a clear decrease in body C (Table III, Paper I) while body N also decreased (except in females),

indicating that proteins were used. The seston present might not have constituted adequate food in terms of quality; the high C:N and C:P ratios indicate that a large proportion of the seston consisted of C-rich detritus rather than C-rich nutritional compounds. Only adult stage female *C. finmarchicus* (in which there was no body N decrease and a smaller loss of storage lipids compared to males and CV) met their N and P requirements at this time showing that they fed on some type of food item rich in these elements. The species *C. hyperboreus* was not present during this bloom phase and appeared in the upper 50 m later in the season. This is a potential indication that this species, with a more flexible overwintering capacity compared to *C. finmarchicus*, did not ascend during the pre-bloom due to the lack of adequate food.

The situation might be different in the Arctic Ocean compared to sub-Arctic coastal areas such as Grøtsund. Indeed, the bloom does not occur until late April in the WEAO (Eilertsen 1993; Niehoff et al. 1999), but calanoid copepods present in the surface layer might have encountered earlier ice algae bloom and thus improvement in food conditions compared to the sub-Arctic areas. Ice algae have been shown to supply rich food for *Calanus* spp. (Søreide et al. 2010; Leu et al. 2011) and their C:N:P composition should be investigated.

Early bloom

The early bloom phase corresponds to the start of the exponential phase of the vernal phytoplankton bloom, prior to the peak of production. The food quantity was still low in terms of chl *a* and seston C, N, and P concentrations in Grøtsund (Paper I) while these concentrations were higher in the WEAO for this same phase of the bloom (Paper II). However, the increase in body C_s and N_s contents in *C. finmarchicus* adult stages and CV from the early bloom to the start of the peak bloom phase indicates that food quantity was no longer limiting in Grøtsund. This also indicates that copepods were able to increase their clearance rate to meet their C requirements. In the WEAO, *Calanus* CV individuals already had larger amounts of lipids than those in Grøtsund, which might be explained by previous feeding on ice algae (except for station in the Norwegian Sea, where no sea ice is present, and where the individuals sampled had the lowest lipid content among the WEAO stations). Grazers were most likely C-limited in both Grøtsund and in the WEAO during this bloom phase, unless they were able to achieve high assimilation efficiency (AE) for C (Fig. 8, Paper I, II). This is a general observation also for the peak bloom and late bloom phases for both areas; C limitation is the most likely scenario for these grazers according to the stoichiometric

calculations. Since most copepods, starting from the early bloom phase, are clearly investing their energy intake into lipids, it may seem counterintuitive that they can simultaneously be limited by C. This shows that the role of quality limitation in the context of C is not straightforward (Paper I). In addition, differences in C limitation were exhibited among stages in Grøtsund (Paper I) with adult stage females less subject to C limitation in this period. If they can achieve high AE for C, females would most likely be N-limited due to high N demand for egg production (Paper I). High AE for C is plausible during this period since food abundance in terms of chl *a* was low (Besiktepe and Dam 2002). Thus, with a high AE for C, male and stage CV copepods had food elemental requirements matching seston composition in Grøtsund (Fig. 8). In the WEAO, if C limitation is excluded, assuming higher AE for C compared to N, *Calanus* CV were N-limited (Fig. 8). Since we showed that primary producers were most likely P-limited during this bloom phase, primary and secondary production exhibited different nutrient limitations during early bloom in the WEAO (Paper II).

Peak bloom

The peak of the phytoplankton bloom observed in Grøtsund and in the WEAO was in agreement with the general knowledge of bloom timing and phytoplankton abundance in these areas (Paper I, II and citations therein). The bloom was dominated by the diatom *Chaetoceros socialis* in Grøtsund, and in the WEAO, phytoplankton information from some stations indicated dominance of small pennate diatoms. Food quantity was not limiting for *C. finmarchicus* at this period in Grøtsund, as seen by a clear investment in lipid storage, particularly in stage CV (Fig. 3 in Paper I). It might have been the same in the WEAO since the chl *a* concentrations were typical for the season and seston C concentrations were well above C requirements for CV stage *Calanus* spp. In addition, these individuals were investing in lipid storage (Paper II). However, the stoichiometric calculations revealed C limitation of the grazers, as during the early bloom phase (Fig. 8). In Grøtsund, the potential for grazers to be C-limited was stronger than during the early bloom phase. Stage CIV, which appeared in the surface layer in this period, was less likely to be C-limited compared to other stages (Paper I) and was potentially P-limited. This suggests that this earlier stage of development has higher P requirements in relation to investment in growth. If able to achieve high AE for C compared to N, copepod grazers could meet their elemental requirements by feeding on seston both in Grøtsund and in the WEAO. If not limited by C, N limitation would occur

(except for copepods at the Norwegian Sea station). For this bloom phase as well, copepods and primary producers exhibited different elemental limitations (cf. Fig. 8).

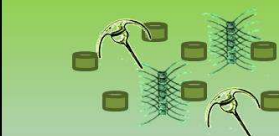
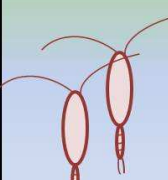

	early bloom	peak bloom	late bloom
	P (A)	P (A)	N & P (A)
Low AE for C 	C (A, sA)	C (A, sA)	C (A, sA)
	N CV (A)	N CV (A)	C F (sA)
High AE for C 	/ M, CV (sA)	/C F, M, CV (sA)	/C M, CV (sA)
	N F (sA)	P CIV (sA)	/N CIV (sA)

Figure 8. Elemental limitation of primary producers and copepods according to bloom phases based on the results of Paper I and Paper II. C, N, or P indicates the limiting element. “/” indicates that none of these elements are limiting and “/C” and “/N” indicate slight limitation for C and for N respectively. F: Female, M: Male, CV: Copepodite CV, CIV: Copepodite CIV. The letters in brackets indicate the region of study: A for Arctic and sA for sub-Arctic

Late bloom

The late bloom phase corresponds to the start of the bloom senescence, as seen in a decrease of the phytoplankton abundance in Grøtsund (Paper I). Copepods were building lipid storage from peak to post bloom in Grøtsund, except for stage CIV, and there was no evidence that they could be limited by food quantity during this period (Paper I). The chl *a* concentrations were still high at the stations sampled in the WEAO where nutrients started to be depleted in the surface layer (Paper II). Calculation of the body somatic ratios for this phase, only available in Grøtsund, showed that copepods were C-limited, even with a high AE for C, with the exception of stage CIV (for which a high AE for C will lead to slight N limitation, cf. Fig. 8). In the WEAO, the lower body N:P ratios of copepods indicated a higher proportion of P-associated compounds in the body, potentially in relation to a higher protein synthesis. A change of metabolism might be linked to the preparation for descent at depth at that time and such a hypothesis would need further consideration. C limitation of the grazers should be less likely than during the earlier bloom phases in the WEAO, contrary to Grøtsund, since the

seston C:N ratios were higher in the WEAO during late bloom (Paper II). Low seston C:N ratios in Grøtsund and high ratios in the WEAO, might be driven partly by the phytoplankton composition, as indicated previously. In Grøtsund, this could be triggered by the higher abundance of flagellates, but also of protozooplankton which have been shown to increase toward the end of the spring bloom in Balsfjord (Lutter et al. 1989). In general the higher seston C:N ratio observed could be linked to a higher fraction of C-rich detritus as a result of rapid degradation in the surface layers where bacterial activity is high (Paper II and citations therein).

In summary, the elemental limitation (C, N and P) of copepod grazers, in relation to seston food composition, varies according to development stages, with C limitation being the most likely scenario. During the pre-bloom phase, food quantity appears to be limiting, but this limitation might be less constraining for the copepods in areas where ice algae are available prior to the phytoplankton bloom. From the peak bloom phase, food quantity no longer appears to be limiting. C is the most likely element to limit the calanoid copepods unless their C assimilation efficiency is high. In this case, N limitation would occur, particularly for females during the period of egg production. Only development stage CIV was shown to be subject to P limitation in relation to higher growth rate. The seston composition and the contribution of the different seston fractions should be further considered since it might affect the grazers' elemental limitation over the course of the spring bloom.

4. 3. C:N:P ratios of copepod fecal pellets

The particulate matter egested by calanoid copepods is packed in the form of cylindrical fecal pellets which increases its capacity to be exported at depth (Honjo and Roman 1978; Turner and Ferrante 1979). At the same time, bacterial degradation and physical mechanisms realized by the zooplankton themselves (coprophagy or coprorexy) render the fecal pellets potential sources of nutrients for other organisms in the upper mixed layer and thus contribute to nutrient recycling (Noji et al. 1991; Wexels Riser et al. 2007). While several studies have quantified the role of fecal pellets in the flux of particulate C in the ocean (Part 1.2.3 and citations therein), little is known about their contribution to nutrient (N and P) export and recycling. No data concerning the overall C:N:P ratios of pellets or the factors that impact

their relative elemental compositions are available. Since copepods maintain body homeostasis and seston food quantity and composition vary, variations can also be expected in the elemental composition of copepod fecal pellets.

The specific objectives are:

- To clarify the effect of food quality and quantity on the C:N:P ratios of copepod fecal pellets
- To assess the role of the fecal pellets in C, N and P export at depth and for nutrient recycling in the upper mixed layer

4.3.1. Copepod food: Sources of variation

The C:N ratios of fecal pellets from *C. finmarchicus* and *C. hyperboreus* (Paper I, II, III) were in the range of previously published values for marine copepods (Morales 1987; Gonzalez and Smetacek 1994). There is a general assumption that food concentration does not have an effect on the elemental ratio of copepod fecal pellets, at least for C:N (Small et al. 1983; Morales 1987). The fecal pellet C:N ratios were not correlated to the food concentration (chl *a* or seston C and N concentrations) neither in Grøtsund through the bloom stages (Paper I) nor among the WEAO stations (Paper II). Thus, food quantity appears not to influence the C:N ratio of copepod fecal pellets. The same was observed for the C:P and N:P ratios of the fecal pellets, which ranged from 28 to 179 and 4 to 19, respectively (Paper I, II, III).

Effects of food quality on fecal pellet C:N:P ratios have been reported. The C:N ratios of pellets of tropical and subtropical copepods were linearly related to the C:N ratios of their food (Checkley and Entzeroth 1985) and a model relating food and copepod fecal pellets C:N ratio has been constructed by Anderson (1994). However, the relation for tropical copepods shown by Checkley and Entzeroth (1985) is thought not to be valid for lipid-synthesizing copepods. No relationship was found between the C:N ratio of the seston (food) and that of the fecal pellets produced by *Calanus* spp. in Grøtsund and in the WEAO (Paper I, II). The C:N ratio of fecal pellets was generally higher compared that of the seston in both areas (Fig. 8), in agreement with the general pattern described in the literature (Morales 1987; Anderson 1994). Higher assimilation efficiency for N compared to C has been shown (Landry et al. 1984; Checkley and Entzeroth 1985) and could explain this pattern; however, we showed that

higher C assimilation would be more beneficial for the metabolism and development of these high-latitude copepods. Conversely, the C:P ratio and more especially the N:P ratio of copepod fecal pellets were lower than those of the seston (Fig. 9), both in Grøtsund and in the WEAO (except at two stations for the C:P ratio), suggesting higher assimilation efficiency for C and N as compared to P.

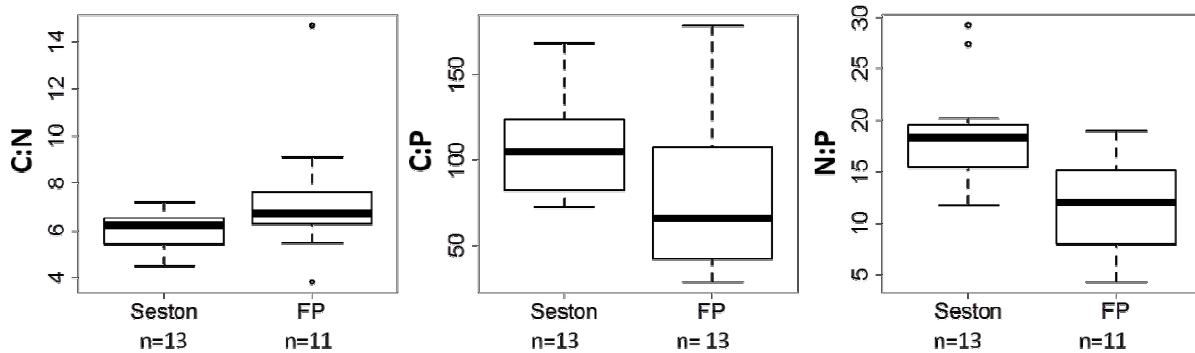


Figure 9. C:N, C:P and N:P ratios of fecal pellets of *Calanus* spp. based on results of Paper I, II and III and additional data for *C. glacialis* (cf. Appendix). Seston stoichiometric ratios are from the depth of maximum chl a concentration. Each boxplot gives the lower quartile (25% of data less than this value), the median, the upper quartile (25% of data greater than this value) and the whiskers show the minimum and the maximum. n=number of individuals. Circles denote outliers.

Both the C:P and N:P ratios of fecal pellets revealed temporal variation similar to that of the seston C:P and N:P ratios in Grøtsund (Paper I). A comparable observation was also made in the WEAO (Paper II), showing that food elemental quality to some extent influences the C:P and N:P ratios of copepod fecal pellets.

A small experiment was conducted with *C. glacialis* CIV fed with an algal culture of *Porosira glacialis* (Bacillariophyceae). Individuals were separated in two beakers and each group received either algae grown under nutrient-replete conditions (F2 medium) or algae grown in depleted medium (F10). No difference could be observed in the C:N:P ratios of the two algal cultures. However, microscopic observations revealed numerous highly pigmented phytoplankton cells in the culture run under F10 medium. The fecal pellets produced based on the two cultures had similar C:N ratios, which were higher (8) than that of the algal cultures (5), in agreement with previous results. Interestingly, the different feeding regimes gave rise to significant differences in the C:P and N:P ratios of the fecal pellets. In the pellets produced by copepods fed algae grown under low-nutrient conditions, both ratios were nearly half of those found in the pellets from those fed with nutrient-replete algae. This small experiment

suggests that not only the elemental composition of the food but also other aspects of its composition impact the elemental composition of fecal pellets. These are preliminary results, but highlight the need for a better understanding of fecal pellet elemental composition in relation to food uptake.

4.3.2. Contribution to nutrient cycling and vertical export

The contribution of copepod fecal pellets to vertical flux of organic particles was measured at three of the stations in the WEAO (Paper III). At these stations, *Calanus* spp. fecal pellets were clearly the dominating fraction of the exported fecal material. The vertical export of POC and PON were within the range of previously measured rates during summer in the regions (Paper III and citations therein). The vertical TPP export ranged from 2 to 10 mg TPP m⁻²d⁻¹ and this figure is to the best of our knowledge the first ever reported from the Arctic Ocean. Copepod fecal pellets were shown to make an average contribution of 10% of the vertical POC and PON exports. This is lower than the low mean contribution ($\pm 15\%$) of fecal pellets to vertical POC flux in the Barents Sea (Wexels Riser et al. 2008). This could be explained by the important presence of fecal pellets from krill and appendicularians (larger than the copepod pellets) in the study of Wexels Riser et al. (2008). An important feature observed in the present work, and shown here for the first time, is that fecal pellets made a higher contribution to vertical TPP export than to POC and PON exports, with a mean contribution of 17% (Paper III). If we consider copepod food as consisting mostly of phytoplankton or phytoplankton-based detritus, the present results show that calanoid copepod fecal pellets constitute an important pathway channeling P from the autotrophs to the deeper ocean during the productive season. In shallower areas, shelf, or coastal marine regions, the process should be particularly considered since it could constitute a source of P for benthic communities.

In addition to being an important contributor to vertical TPP export, fecal pellets produced by the three species of *Calanus* had lower N:P and mostly lower C:P ratios than the corresponding ratios for seston (Paper I, II, III, Fig. 9, Appendix). Compared to the seston composition in the upper mixed layer, this indicates that calanoid copepods tend to supply, through egestion, particulate material enriched in P. This is potentially a result of C or N limitation, implying a higher relative retention of these elements compared to P in the body

(Paper I, II, Sterner and Elser 2002). It is also possible that it reflects superfluous feeding as proposed by Beklemishev (1962), which implies a high organic content in fecal pellets when phytoplankton abundance is high.

This P-rich fecal material was moreover shown to have the potential to be retained in the upper layer of the water column during the productive season in the WEAO. The fecal pellets contribution to TPP fluxes, but also to vertical POC and PON fluxes, was indeed attenuated, particularly within the upper 60 m of the water column at several stations (Fig. 4 in Paper III). The contribution of copepod fecal pellets to the vertical TPP flux was not measured in the sub-Arctic Grøtsund sound. However, it has been shown that copepod fecal pellets are more likely to be retained than exported in the upper mixed layer in areas close to Grøtsund, where krill fecal pellets can dominate the sinking fecal material (Reigstad et al. 2000; Wexels Riser et al. 2010). The higher relative content of P in the fecal pellets compared to the seston in Grøtsund and the potential for a high retention of pellets in the upper layer indicate that a large fraction of P could potentially be remineralized. Different mechanisms can be responsible for the retention of fecal pellets: degradation through coprophagy and/or coprorhexy exerted by zooplankton organisms but also degradation by bacteria (Noji et al. 1991; Turner 2002). In the WEAO, the highest P retention efficiency was observed at the stations in peak bloom condition (station 74) where the macrozooplankton biomass was highest and dominated by large *C. hyperboreus* (Paper III). Thus, higher retention was potentially the result of zooplankton being more numerous, and thus more likely to encounter the large *C. hyperboreus* fecal pellets in the upper mixed layer. Bacterial degradation also plays a role in the retention but it is difficult to discuss its importance. Recent studies underlined that the microbial loop is more important than previously assumed in the Arctic marine regions (Lovejoy et al. 2002; Sherr et al. 2003; Seuthe et al. 2011). In the Arctic Ocean, bacteria might be of greater importance for fecal pellet degradation during the post bloom phase and late summer seasons, when its production become nearly as important as primary production, as shown in a fjord of Svalbard (Iversen and Seuthe 2011). This pattern is expected to be enhanced by lower inorganic nutrient concentrations and fewer fecal pellets (Paper II), which might increase the degradation of fecal pellets exerted by more numerous and potentially nutrient or C- limited bacteria. Copepod fecal pellets thus have the potential to provide an important source of nutrients to the pelagic microbial food web and may therefore rather enhance carbon and nutrient recycling than export them vertically.

Several other factors can affect the retention efficiency of fecal pellets in the upper mixed layer. During the productive season, a station in the Barents Sea showed that storm events can reduce the P retention in the surface layer by reducing the stability of the upper mixed layer (Paper III). Phytoplankton species differ both in terms of elemental composition (Geider and Laroche, 2002) and physical properties such as shape and density, which may potentially alter the elemental ratios and proportion of fecal material that can be exported. The type of cells eaten by the copepods has been shown to change the fecal pellets' density and sinking speed and thus the likelihood that they will be degraded pelagically. For instance the copepod *Acartia tonsa* produces smaller fecal pellets with a higher density and slower sinking speed when fed with heterotrophic flagellates and dinoflagellates than when fed with diatoms or ciliates (Feinberg and Dam 1998). In the Arctic marine regions, the proportion of heterotrophic flagellates as compared to diatoms has been shown to increase during the summer season (Iversen and Seuthe 2011), most likely implying changes in fecal pellet density and sinking speed. Studying the fecal pellet dynamics and bacteria production jointly is necessary in order to determine whether these changes will increase or decrease fecal pellet degradation.

In summary, it has been shown that while food quantity does not seem to affect the elemental composition of fecal pellets, food quality does. While the C:N ratio of fecal pellets is generally higher than that of the seston, their C:P and N:P ratios vary in relation to the seston stoichiometric ratios. The C:P and N:P ratios of fecal pellets tend to be lower than the C:P and N:P ratios of seston, which indicates that copepod fecal pellets are rich in P and have the potential to supply P both for export and recycling. During a period of intense primary production in the WEAO, copepod fecal pellets contributed more to vertical TPP export (mean of 17%) than to POC and PON export (about 10%). At the same time, the contribution of fecal pellets to these fluxes was attenuated in the surface layers, particularly for the TPP flux. This indicates that P-rich fecal pellets do indeed export P at depth but also contribute to the retention of P in the surface layer during the productive season in the WEAO. Retention of fecal pellets may be more pronounced during the late bloom phase when nutrients are depleted and bacterial production and water column stratification are enhanced.

5. Climate change perspectives for the copepod-seston interaction in the western European Arctic Ocean

A better understanding of the food requirements of Arctic key species contributes to the general comprehension of how ecosystems function. However, efforts to understand the Arctic ecosystem are particularly crucial since this is the part of the world that is most strongly subject to rapid climate change. Indeed, the Arctic marine regions are experiencing a warming which is 2 to 4 times faster than the world average (Screen and Simmonds 2010). In addition, some Arctic marine ecosystems are highly productive. A loss of key species such as calanoid copepods is thus expected to have large implications for the food web interactions and structure but also for the export and recycling of organic matter that is mediated by these species (Frank et al. 2005).

One of the most important impacts of warming in the Arctic marine regions is the melting of sea ice, which constitutes the main driver for computer models (Serreze and Francis 2006; Arrigo et al. 2008). Available models predict an increase of annual primary production in the central Arctic Ocean, whereas productivity is expected to decrease in the large southern regions of the WEAO (Slagstad et al. 2011; Wassmann 2011; Wassmann and Reigstad 2011). Predictions for 2045-2055 have been made by the European Union ATP project (Fig. 10). In the WEAO, the annual primary production is expected to increase only on the east Greenland shelf (Fig. 10B). Increased water column stratification, caused by surface warming and sea ice melt, is among the factors responsible for the lower predicted primary production in the WEAO (Wassmann 2011; Ellingsen et al., unpublished data). Since ice melt will occur earlier in the year, the period of phytoplankton production may be longer, thus extending the period of food production for copepods. However, an earlier ice melt would influence not only the timing of the phytoplankton bloom but also ice algae bloom, and might lead the timing of copepod migration in the water column to mismatch this earlier ice algae bloom (Leu et al. 2011; Wassmann 2011).

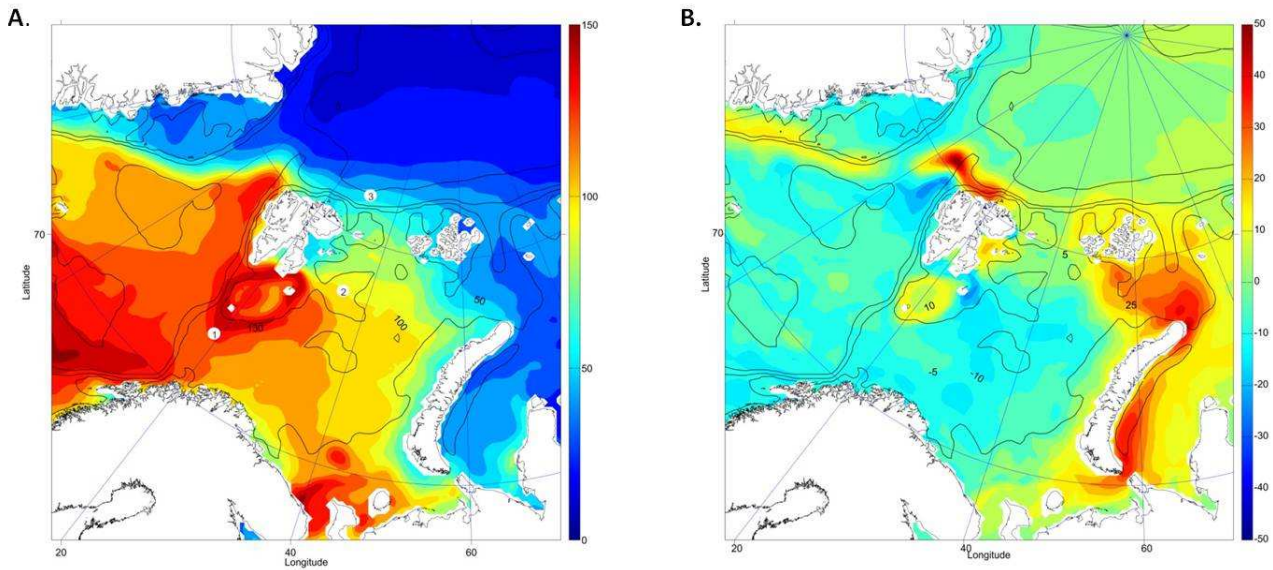


Figure 10. A. Average annual primary production ($\text{g C m}^{-2} \text{y}^{-1}$) for the period 2001-2010. B. Predictions on the relative annual changes in primary production for the period 2045-2055. (Unpublished ATP project data from the physically-biologically coupled SINMOD model, courtesy of I. Ellingsen et al.).

The potential changes in food quality are more difficult to predict. In terms of stoichiometry, an increase in PAR in the stratified surface layer would increase C fixation by the autotrophic cells, which in combination with lower predicted nutrient concentrations would result in increased C:nutrient ratios in phytoplankton (Van de Waal et al. 2010). Higher C:nutrient ratios render C limitation less likely for the copepods while nutrient limitation, N or P, could be more frequent. However, the way C is assimilated and used in the body of these copepods needs to be better elucidated before clear predictions can be made. Duarte et al. (2012) predict a shift from a diatom-dominated regime to a regime dominated by smaller forms (picoplankton) in the Arctic Ocean. Instead of being a CO_2 sink, this ocean may act as a CO_2 source to the atmosphere in the future. Yet, it is difficult to predict the impact of such changes on seston stoichiometry. Long C-chain molecules are present in essential fatty acids of diatoms, but also in *Phaeocystis*, and other flagellates can be eaten by calanoid copepods and used for lipid synthesis (Lee et al. 2006; Leu et al. 2011). A change in seston composition toward picoplankton dominance may lead to a decrease in the availability of long C-chain fatty acids with negative repercussions for calanoid copepods and their lipid synthesis. This comes in addition to the increased chances for copepods to miss the ice algae bloom mentioned earlier.

Clearly, calanoid copepod's food will fluctuate in quantity, but also in composition according to Duarte et al. (2012). These changes are expected to be abrupt rather than smooth in the Arctic marine regions. Since the elemental composition of fecal pellets is shown to be linked to some extent to that of seston (Paper I, II), the organic export and nutrient recycling will also be affected. Other factors such as temperature are also involved. Arctic copepod species such as *C. glacialis* are more sensitive to temperature increase than *C. finmarchicus* for instance: increased temperatures reduce *C. glacialis*' survival rate (U. Grote, unpublished data). *C. glacialis* starved for 20 days and exposed to different temperatures (2.5, 5 and 7.5°C), showed a tendency toward increased use of their stored lipids with increasing temperatures (A. B. Aubert, unpublished data). This can be explained by a higher C demand in relation to higher respiration at higher temperatures, as proposed by Hirche (1987). Thus, while potential higher C:N ratio in phytoplankton should be beneficial for copepods' increased C requirements in a warming Arctic, the decrease of specific long C-chain compounds in the phytoplankton may affect their ability to synthesize lipids.

In summary, the copepod-seston interaction is most likely to change in the warming Arctic. While early life stages of *Calanus* spp. may experience a mismatch with the ice algal bloom, phytoplankton will be available during a longer period of the year in the WEAO, albeit in lower quantities. The composition of seston is also expected to change from a diatom-dominated regime to picoplankton dominance, with expected repercussions for the lipid storage ability of copepods. Changes in the food composition and quantity would also have effects on the fecal pellet composition and thus on the export and recycling of nutrients. Direct effects of warming on copepod physiology are also to be expected, such as potential increase of respiratory demands and decreased survival rate.

6. Conclusions and perspectives

This thesis addressed the characterization of the C:N:P composition and elemental requirements of lipid-synthesizing calanoid copepods in planktonic, marine high-latitude ecosystems. It also investigated the role copepods play in vertical C:N:P export and recycling via egestion of fecal pellets. The results presented here highlight the need to apply a two-compartment approach when studying elemental limitations imposed on high-latitude copepods by stoichiometric imbalances, with lipid storage and somatic tissues separated (Paper I). The calculated somatic ratios show that these copepods may be able to invest into C-rich lipid storage even at times when they are C-limited. This apparent paradox calls for a better understanding of how C is assimilated by these copepods, but also of how C is linked with specific biochemical compounds. Study of the links between elements and the biochemical compounds would help us understand several characteristics of the growth and development of these species. Phosphorus appears to be of importance in the ontogeny of the copepods (Paper I). Factors such as development stage and bloom phase should be considered in future studies since they influence the somatic ratios.

This work considers Arctic and sub-Arctic marine organisms (specifically lipid-synthesizing copepods) for the first time by applying stoichiometric theory. It sheds light upon the large gap in stoichiometric information from the Arctic marine regions. Yet, calanoid copepods are only one component of planktonic ecosystems of the High North, and the stoichiometry of other Arctic taxa should also be studied to understand their food requirements better. A larger data set would allow comparisons with organisms from different biomes, and may confirm whether high-latitude calanoid copepods have a higher growth rate compared to those from lower latitudes, as suggested by their lower somatic body C:P and N:P ratios.

The results presented here also illustrate the importance of considering stoichiometric ratios of the particulate matter on which copepods feed in order to study their elemental food limitation. These ratios are also considered in the fecal pellets the copepods produce, and which contribute to vertical C export. The stoichiometric ratios including P of seston and fecal pellets are among the first reported from the Arctic Ocean. We showed that copepod fecal pellets contribute significantly to P export via vertical transport during the Arctic productive season, with a larger contribution to P export than to C and N export (Paper III). At the same time, a fraction of these fecal pellets is recycled in the upper layers. Since fecal pellets are

enriched in P compared to seston (lower C:P and N:P ratios), degradation of pellets in the water column therefore has a potential to re-supply P to the productive surface layer. The data were collected from the western European Arctic Ocean and a sub-Arctic marine region, and more measurements are needed to verify if the observed trends apply to other Arctic marine areas and other seasons. Indeed, since fecal pellet C:P and N:P ratios have been shown to fluctuate in conjunction with the ratios of seston, we can expect seasonal changes in these ratios. More experimental work should be conducted in order to understand the link between the C:N:P ratios of both the food and fecal pellets of copepods inhabiting the Arctic marine regions. In particular, factors related to potential changes in climate will affect primary production in the future Arctic and need our attention.

This thesis should inspire future studies in the field of Arctic stoichiometry. Acquiring stoichiometric data is important at the scale of zooplankton physiology and ecology and for vertical export of C, N and P. In addition, there is a need for ecological data and studies that can be integrated in theoretical frameworks (Elser and Hamilton 2007). Ecological stoichiometry has been shown to be a powerful means of addressing ecological problems and can be applied to different types of ecosystems. However, studies implying stoichiometric consideration are still rare in Arctic marine ecosystems. Hence, stoichiometry is a useful tool in the effort to build predictive models, particularly in the Arctic, where the effects of climate change are the greatest.

Acknowledgements

Jumping back to my childhood, I remember those late evenings in front of my Earth globe when I was always amazed by the diversity of our planet, and by the huge contribution of the blue Ocean. Some years later, it turned out that I wanted to study oceanology; I was particularly interested by coral reefs and lagoons, as a result of a Polynesian influence in the family. Always heading to southern countries while starting my adult life, it never came to mind to visit and study Polar Regions. It was not because I did not want to, but simply because I never thought about it. Thus, when the first opportunity to go to the Arctic came, it appeared so intriguing, and I have to say scary, as well (-60°C?!?), that I decided that I could not miss this chance. This was how the wish to know more about this ecosystem started. So, first, I am giving a tribute to the Arctic, a really special place on the planet where I feel I have been really lucky to go.

A PhD thesis can be an extremely solitary journey at some points, but when walking at night, you can always perceive those bright stars which guide your way. These “benchmarks” have been my supervisors, Paul Wassmann and Tobias Tamelander, to who I would like to express my sincere gratitude. Thanks Paul for insisting so much while I had to decide whether to live in the Côte d’Azur in Villefranche-sur-Mer or up the Arctic circle, in Tromsø, for the coming 3 years of my life! ;-) Working with polar science living in a polar place makes a difference. Thank to both you for guiding me through the long and self-catering process of understanding what doing science really is. Thank you for your time and patience.

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Far from eyes but not far from heart, I want to express my sincere gratitude to my family, especially mum, dad and brother but also to my greatest fan ever, my grand-mother. I love you.

I hate to break promises and this is the reason of the following line:

“A big step for me, a small one for Humanity” ;-)

And more seriously and philosophically, I am ending here borrowing Newton’s mind:

“I do not know what people will think about me. For my part, I have the feeling that I was a kid playing on the beach and finding here and there a prettier shell than ordinary, while the large ocean of Truth remains unexplored in front of me.”

Anaïs Aubert

Appendix

C:N:P ratios of seston (\pm standard deviation) and fecal pellets produced by *Calanus glacialis* stage CIV sampled on 8th of May 2010 at an ice-covered station on the west coast of Svalbard.

	C:N	C:P	N:P
Seston	4.5 \pm 1	72 \pm 4	17 \pm 4
Fecal pellet (<i>C. glacialis</i> CIV)	7.8	93	12

References

- Aagaard, K., Carmack, E.C., 1989. The role of sea-ice and other fresh-water in the Arctic circulation. *J. Geophys. Res-Oceans* 94, 14485-14498. doi 10.1029/JC094iC10p14485
- Aagaard, K., Greisman, P., 1975. Toward new mass and heat budgets for the Arctic Ocean. *J. Geophys. Res.* 80, 3821-3827. doi 10.1029/JC080i027p03821
- Aksnes, D.L., Blindheim, J., 1996. Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. *Ophelia* 44, 7-28.
- Alcaraz, M., Almeda, R., Calbet, A., Saiz, E., Duarte, C.M., Lasternas, S., Agusti, S., Santiago, R., Movilla, J., Alonso, A., 2010. The role of Arctic zooplankton in biogeochemical cycles: respiration and excretion of ammonia and phosphate during summer. *Polar Biol.* 33, 1719-1731. doi 10.1007/s00300-010-0789-9
- Andersen, T., 1997. *Pelagic Nutrient Cycles: Herbivores as sources and sinks*. Ecol. Stu. 129, Springer
- Anderson, D., Glibert, P., Burkholder, J., 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuar. Coasts* 25, 704-726. doi 10.1007/bf02804901
- Anderson, T.R., 1994. Relating C:N ratios in zooplankton food and fecal pellets using a biochemical model. *J. Exp. Mar. Biol. Ecol.* 184, 183-199. doi 10.1016/0022-0981(94)90004-3
- Anderson, T.R., Hessen, D.O., 1995. Carbon or nitrogen limitation in marine copepods. *J. Plankton Res.* 17, 317-331.
- Anderson, T. R., Hessen, D. O., Elser, J.J, Urabe, J., 2005. Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers. *Am. Nat.* 165, 1-15.
- Arrigo, K.R., Van, D.G., Pabi, S., 2008. Impact of a shrinking Arctic ice cover on marine primary production. *Geophys. Res. Lett.* 35. doi L1960310.1029/2008gl035028
- Auel, H., Klages, M., Werner, I., 2003. Respiration and lipid content of the Arctic copepod *Calanus hyperboreus* overwintering 1 m above the seafloor at 2300 m water depth in the Fram Strait. *Mar. Biol.* 143, 275-282. doi 10.1007/s00227-003-1061-4
- Auel, H.A., Hagen, W.H., 2002. Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. *Mar. Biol.* 140, 1013-1021. doi 10.1007/s00227-001-0775-4

- Båmstedt, U. 1986. Chemical composition and energy content. In CoMer, E.D.S., and O'Hara, S.C.M., eds. The biological chemistry of marine copepods. Clarendon Press, Oxford, pp. 1-58.
- Båmstedt, U., Ervik, A., 1984. Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* (Copepoda, Calanoida) overwintering on the west coast of Norway. J. Plankton Res. 6, 843-857.
- Bates, N.R., Hansell, D.A., Bradley Moran, S., Codispoti, L.A., 2005. Seasonal and spatial distribution of particulate organic matter (POM) in the Chukchi and Beaufort Seas. Deep-Sea Res Pt II 52,3324-3343.
- Bathmann, U.V., Noji, T.T., Voss, M., Peinert, R., 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May June 1986 Mar. Ecol. Prog. Ser. 38, 45-51. doi 10.3354/meps038045
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C. 2003. Plankton effect on cod recruitment in the North Sea. Nature 426, 661-664.
- Beklemishev, C. W., 1962. Superfluous feeding of marine herbivorous zooplankton. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 153, 108-113.
- Besiktepe, S., Dam, H.G., 2002. Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. Mar. Ecol. Prog. Ser. 229, 151-164. doi 10.3354/meps229151
- Carlotti, F., 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.
- Carmack, E., McLaughlin, F., 2011. Towards recognition of physical and geochemical change in Subarctic and Arctic Seas. Prog. Oceanogr. 90, 90-104. doi 10.1016/j.pocean.2011.02.007
- Carrillo, P., Villar-Argaiz, M., Medina-Sánchez, J.M., 2001. Relationship between N:P ratio and growth rate during the life cycle of calanoid copepods: an in situ measurement. J. Plankton Res. 23, 537-547. doi 10.1093/plankt/23.5.537
- Checkley, D.M., 1980. The egg production of a marine planktonic copepod in relation to its food supply: Laboratory studies Limnol. Oceanogr. 25, 430-446.
- Checkley, D.M., Entzeroth, L.C., 1985. Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen-cycle. J. Plankton Res. 7, 553-568.

- Conover, R.J., 1966. Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.* 11, 338-345.
- Conover, R.J., Huntley, M., 1991. Copepods in ice-covered seas-Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *J. Marine Syst.* 2, 1-41.
- Cowles, T.J. 1979. Feeding response of copepods from the Peru upwelling system: food size selection *J. Mar. Res.* 37, 601-622.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: An update of the match mismatch hypothesis. *Adv. Mar. Biol.* 26, 249-293.
- Dahl, T.M., Falk-Petersen, S., Gabrielsen, G.W., Sargent, J.R., Hop, H., Millar, R.M., 2003. Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar: a trophic study from an Arctic fjord. *Mar. Ecol. Prog. Ser.* 256, 257-269. doi 10.3354/meps256257
- Daly, K.L., Wallace, D.W.R, Smith, W.O., Skoog, A., Lara, R., Gosselin, M., Falck, E., Yager, P.L., 1999. Non-Redfield carbon and nitrogen cycling in the Arctic: Effects of ecosystem structure and dynamics. *J.Geophys. Res-Oceans* 104, 3185-3199.
- Damm, E., Helmke, E., Thoms, S., Schauer, U., Nothig, E., Bakker, K., Kiene, R.P., 2010. Methane production in aerobic oligotrophic surface water in the central Arctic Ocean. *Biogeosciences* 7, 1099-1108.
- Degerlund, M., Eilertsen, H., 2010. Main Species characteristics of phytoplankton spring blooms in NE Atlantic and Arctic Waters (68–80° N). *Estuaries Coasts* 33, 242-269. doi 10.1007/s12237-009-9167-7.
- DeMott, W.R., Gulati, R.D., Siewertsen, K., 1998. Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnol. Oceanogr.* 43, 1147-1161.
- Dommasnes, A., Melle, W., Dalpadado, P., Ellertsen, B., 2004. Herring as a major consumer in the Norwegian Sea. *ICES J. Mar. Sci.* 61, 739-751. doi 10.1016/j.icesjms.2004.04.001
- Duarte, C.M., Agustí, S., Wassmann, P., Arrieta, J.M., Alcaraz, M., Coello, A., Marba, N., Hendriks, I.E., Holding, J., Garcí'a-Zarandona, I., Kritzberg, E., Vaque, E., 2012. Tipping elements in the Arctic marine ecosystem. In *The Arctic in the Earth system perspective: The role of tipping points*, ed. Wassmann, P., Lenton, T.M. *Ambio*. doi:10.1007/s13280-011-0224-7
- Eilertsen, H.C., 1993. Spring blooms and stratification. *Nature* 363, 24-24.

- Eilertsen, H.C., Schei, B., Taasen, J.P., 1981. Investigation of the plankton community of Balsfjorden, northern Norway- The phytoplankton 1976-1978. Abundance, species composition and succession. *Sarsia* 66, 129-141.
- Eilertsen, H.C., Taasen, J.P., 1984. Investigations on the plankton community of Balsfjorden, Northern Norway - the Phytoplankton 1976-1978. Environmental factors, dynamics of growth, and primary production. *Sarsia* 69, 1-15.
- Eilertsen, H.C., Taasen, J.P., Weslawski, J.M., 1989. Phytoplankton studies in the fjord of West Spitzbergen: physical environment and production in spring and summer. *J. Plankton Res.* 11, 1245-1260.
- Eilertsen, H.C., Wyatt, T., 2000. Phytoplankton models and life history strategies. *S. Afr. J. Marine Sci.* 22, 323-338.
- Elser, O., Dobberfuhl D.R., Dowling, T.E., 2000a. The evolution of ecosystem processes: growth rate and elemental stoichiometry of a key herbivore in temperate and arctic habitats. *J. Evolution. Biol.* 13, 845-853. doi 10.1046/j.1420-9101.2000.00215.x
- Elser, J.J., Dobberfuhl, D.R., MacKay, N.A., Schampel, J.H., 1996. Organism size, life history, and N:P stoichiometry. *Bioscience* 46, 674-684.
- Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H., Sterner, R.W., 2000b. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408, 578-580.
- Elser, J.J., Hamilton, A., 2007. Stoichiometry and the new biology: The future is now. *Plos Biol.* 5, 1403-1405.
- Elser, J.J., Hassett, R.P., 1994. A stoichiometric analysis of the zooplankton-phytoplankton interaction in marine and fresh-water ecosystems. *Nature* 370, 211-213.
- Elser, J.J., O'Brien W.J., Dobberfuhl, D.R., Dowling, T.E., 2000c. The evolution of ecosystem processes: growth rate and elemental stoichiometry of a key herbivore in temperate and arctic habitats. *J. Evolution. Biol.* 13, 845-853.
- Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., Harrison, J.F., Hobbie, S.E., Odell, G.M., Weider, L.W. 2000d. Biological stoichiometry from genes to ecosystems. *Ecol. Lett.* 3, 540-550. doi 10.1111/j.1461-0248.2000.00185.x
- Falk-Petersen, S., Hop, H., Budgell, W.P., Hegseth, E.N., Korsnes, R., Løyning, T.B., Børre, Ørbæk, J., Kawamura, T., Shirasawa, K., 2000. Physical and ecological processes in the marginal ice zone of the northern Barents Sea during the summer melt period. *J. Marine Syst.* 27, 131-159. doi 10.1016/s0924-7963(00)00064-6

- Falk-Petersen, S., Mayzaud, P., Kattner, G., Sargent, J., 2009. Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.* 5, 18-39.
- Falk-Petersen, S., Pedersen, G., Kwasniewski, S., Hegseth, E.N., Hop, H., 1999. Spatial distribution and life-cycle timing of zooplankton in the marginal ice zone of the Barents Sea during the summer melt season in 1995. *J. Plankton Res.* 21, 1249-1264.
- Falk-Petersen, S., Sargent, J.R., Henderson, J., Hegseth, E.N., Hop, H., Okolodkov, Y.B. 1998. Lipids and fatty acids in ice algae and phytoplankton from the Marginal Ice Zone in the Barents Sea. *Polar Biol.* 20, 41-47. doi 10.1007/s003000050274
- Falk-Petersen, S., Sargent, J.R., Tande, K.S. 1987. Lipid composition of zooplankton in relation to the sub-arctic food web. *Polar Biol.* 8, 115-120. doi 10.1007/bf00297065
- Feinberg, L.R., Dam, H.G., 1998. Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* 175, 87-96. doi 10.3354/meps175087
- Forest, A., Galindo, V., Darnis, G., Pineault, S., Lalande, C., Tremblay, J.R., Fortier, L., 2011. Carbon biomass, elemental ratios (C:N) and stable isotopic composition (¹³C, ¹⁵N) of dominant calanoid copepods during the winter-to-summer transition in the Amundsen Gulf (Arctic Ocean). *J. Plankton Res.* 33, 161-178. doi 10.1093/plankt/fbq103
- Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621-1623. doi 10.1126/science.1113075
- Frigstad, H., Andersen, T., Hessen, D.O., Naustvoll, L.J., Johnsen, T.M., Bellerby, R.G.J., 2011. Seasonal variation in marine C:N:P stoichiometry: can the composition of seston explain stable Redfield ratios? *Biogeosciences* 8, 2917-2933. doi 10.5194/bg-8-2917-2011
- Geider, R.J., La Roche, J., 2002. Redfield revisited: variability of C : N : P in marine microalgae and its biochemical basis. *Eur. J. Phycol.* 37, 1-17.
- Gismervik, I., 1997. Stoichiometry of some marine planktonic crustaceans. *J. Plankton Res.* 19, 279-285.
- Gonzalez, H.E., Smetacek, V., 1994. The possible role of the cyclopoid copepod *Oithona* in retarding the vertical flux of zooplankton fecal material. *Mar. Ecol. Prog. Ser.* 113, 233-246. doi 10.3354/meps113233
- Graeve, M., Kattner, G., 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. doi Doi: 10.1016/0022-0981(94)90213-5

- Gulati, R.D., DeMott, W.R., 1997. The role of food quality for zooplankton: remarks on the state-of-the-art, perspectives and priorities. *Freshwater Biol.* 38, 753-768.
- Hagen, W., Auel, H., 2001. Seasonal adaptations and the role of lipids in oceanic zooplankton. *Zoology* 104, 313-326. doi 10.1078/0944-2006-00037
- Hannides, C. C. S., Landry, M. R., Benitez-Nelson, C. R., Styles R. M., Montoya J. P., Karl D. M., 2009. Export stoichiometry of migrant-mediated flux of phosphorus in the North Pacific Subtropical Gyre. *Deep-Sea Res Pt I* 56, 73-88.
- Hansen, A.S., Nielsen, T.G., Levinsen, H., Madsen, S.D., Thingstad, T.F., Hansen, B.W., 2003. Impact of changing ice cover on pelagic productivity and food web structure in Disko Bay, West Greenland: A dynamic model approach. *Deep-Sea Res. Pt. I* 50, 171-187. doi 10.1016/s0967-0637(02)00133-4
- Hansen, B.W., Nielsen, T.G., Levinsen, H., 1999. Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. III. Mesozooplankton. *Aquat. Microb. Ecol.* 16, 233-249. doi 10.3354/ame016233
- Harrison, W.G., Head, E.J.H., Conover, R.J., Longhurst, A.R., Sameoto, D.D., 1985. The distribution and metabolism of urea in the eastern Canadian Arctic. *Deep-Sea Res.* 32, 23-42. doi 10.1016/0198-0149(85)90015-9
- Harvey, H.W., 1926. Nitrate in the sea. *J. Mar. Biol. Assoc. U.K.* 14, 71-88. doi doi:10.1017/S0025315400007141
- Hassett, R.P., Cardinale, B., Stabler, L.B., Elser, J.J., 1997. Ecological stoichiometry of N and P in pelagic ecosystems: Comparison of lakes and oceans with emphasis on the zooplankton-phytoplankton interaction. *Limnol. Oceanogr.* 42, 648-662.
- Hecky, R.E., Campbell, P., Hendzel, L.L., 1993. The Stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. *Limnol. Oceanogr.* 38, 709-724.
- Henderson, R.J., Hegseth, E.N., Park, M.T. 1998. Seasonal variation in lipid and fatty acid composition of ice algae from the Barents Sea. *Polar Biol.* 20, 48-55. doi 10.1007/s003000050275
- Hessen, D.O., Agren, G.I., Anderson, T.R., Elser, J.J., De Ruiter, P.C., 2004. Carbon, sequestration in ecosystems: The role of stoichiometry. *Ecology* 85, 1179-1192.
- Hessen, D.O., Leu, E., Faerovig, P.J., Petersen, S.F., 2008. Light and spectral properties as determinants of C:N:P-ratios in phytoplankton. *Deep-Sea Res. Pt. II* 55, 2169-2175.
- Hessen DO, Lyche A (1991) Interspecific and Intraspecific Variations in Zooplankton Element Composition. *Archiv Fur Hydrobiologie* 121: 343-353

- Hirche, H.J., Kosobokova, K., 2007. Distribution of *Calanus finmarchicus* in the northern North Atlantic and Arctic Ocean: Expatriation and potential colonization. *Deep-Sea Res. Pt II* 54, 2729-2747. doi 10.1016/j.dsr2.2007.08.006
- Hirche, H.J., Niehoff, B., 1996. Reproduction of the Arctic copepod *Calanus hyperboreus* in the Greenland Sea: Field and laboratory observations. *Polar Biol.* 16, 209-219. doi 10.1007/bf02329209
- Hirche, H.J., 1987. Temperature and plankton .2. Effect on respiration and swimming activity in copepods from the Greenland Sea. *Mar. Biol.* 94, 347-356.
- Hirche, H.J., 1997. Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Mar. Biol.* 128, 607-618. doi 10.1007/s002270050127
- Hirche, H.J., 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. doi 10.1007/bf00349773
- Hirche, H.J., Kosobokova, K., 2003. Early reproduction and development of dominant calanoid copepods in the sea ice zone of the Barents Sea : Need for a change of paradigms? *Mar. Biol.* 143, 769-781. doi 10.1007/s00227-003-1122-8
- Ho, T.Y., Quigg, A., Finkel, Z.V., Milligan, A.J., Wyman, K., Falkowski, P.G., Morel, F.M.M., 2003. The elemental composition of some marine phytoplankton. *J. Phycol.* 39, 1145-1159.
- Honjo, S., Roman, M.R., 1978. Marine copepod fecal pellets: Production, preservation and sedimentation *J. Mar. Res.* 36, 45-57.
- Hugh, C., 1911. "Richter, Jeremias Benjamin". *Encyclopædia Britannica* (11th ed.). Cambridge University Press.
- Iversen, K.R., Seuthe, L., 2011. Seasonal microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): I. Heterotrophic bacteria, picoplankton and nanoflagellates. *Polar Biol.* 34, 731-749. doi 10.1007/s00300-010-0929-2
- Kattner, G., Hagen, W., 1995. Polar herbivorous copepods: Different pathways in lipid biosynthesis *Ices J. Mar. Sci.* 52, 329-335. doi 10.1016/1054-3139(95)80048-4
- Kosobokova, K.N., 1999. The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. *Polar Biol.* 22, 254-263. doi 10.1007/s003000050418
- Kuijper, L.D.J., Kooi, B.W., Anderson, T.R., Kooijman, S., 2004. Stoichiometry and food-chain dynamics. *Theor. Popul. Biol.* 66, 323-339.

- Lalande, C., Bauerfeind, E., Nothig, E.M., 2011. Downward particulate organic carbon export at high temporal resolution in the eastern Fram Strait: Influence of Atlantic Water on flux composition. *Mar. Ecol. Prog. Ser.* 440, 127-136. doi 10.3354/meps09385
- Landry, M.R., Hassett, R.P., Fagerness, V., Downs, J., Lorenzen, C.J. 1984. Effect of food acclimation on assimilation efficiency of *Calanus pacificus*. *Limnol. Oceanogr.* 29, 361-364.
- Le Borgne, R., 1978. Evaluation de la production secondaire planctonique en milieu océanique par la méthode des rapports C/N/P. *Oceanol. Acta* 1, 107-118.
- Lee, R.F., Hagen, W., Kattner, G., 2006. Lipid storage in marine zooplankton. *Mar. Ecol. Prog. Ser.* 307, 273-306. doi 10.3354/meps307273
- Lehman, J.T., 1984. Grazing, nutrient release, and their impacts on the structures of phytoplankton communities. In: Meyers, D.G., & Strickler, J.R. (Eds) *Trophic Interactions within Aquatic Ecosystems* (pp 49-72). AAAS Selected Symposium 85, Westview Press, Boulder
- Leu, E., Søreide, J.E., Hessen, D.O., Falk-Petersen, S., Berge, J., 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Prog. Oceanogr.* 90, 18-32. doi 10.1016/j.pocean.2011.02.004
- Levinsen, H., Turner, J.T., Nielsen, T.G., Hansen, B.W., 2000. On the trophic coupling between protists and copepods in arctic marine ecosystems. *Mar. Ecol. Prog. Ser.* 204, 65-77.
- Logan, J., Joern, A., Wolessky, W., 2004. Control of CNP homeostasis in herbivore consumers through differential assimilation. *B. Math. Biol.* 66, 707-725. doi 10.1016/j.bulm.2003.10.008
- Loh, A.N., Bauer, J.E., 2000. Distribution, partitioning and fluxes of dissolved and particulate organic C, N and P in the eastern North Pacific and Southern Oceans. *Deep-Sea Res. I.* 47, 2287-2316.
- Lovejoy, C., Legendre, L., Martineau, M.J., Bacle, J., Von Quillfeldt, C.H., 2002. Distribution of phytoplankton and other protists in the North Water. *Deep-Sea Res. Pt. II* 49, 5027-5047. doi 10.1016/s0967-0645(02)00176-5
- Lutter, S., Taasen, J.P., Hopkins, C.C.E., Smetacek, V., 1989. Phytoplankton dynamics and sedimentation processes during spring and summer in Balsfjord, Northern Norway. *Polar Biol.* 10, 113-124. doi 10.1007/bf00239156

- Madsen, S.J., Nielsen, T.G., Tervo, O.M., Soderkvist, J., 2008. Importance of feeding for egg production in *Calanus finmarchicus* and *C. glacialis* during the Arctic spring. Mar. Ecol. Prog. Ser. 353, 177-190. doi 10.3354/meps07129
- Main, T.M., Dobberfuhl, D.R., Elser, J.J., 1997. N:P stoichiometry and ontogeny of crustacean zooplankton: A test of the growth rate hypothesis. Limnol. Oceanogr. 42, 1474-1478.
- Makino, W., Cotner, J.B., Sterner, R.W., Elser, J.J., 2003. Are bacteria more like plants or animals? Growth rate and resource dependence of bacterial C:N:P stoichiometry. Funct. Ecol. 17, 121-130. doi 10.1046/j.1365-2435.2003.00712.x
- Mauchline, J., 1998. The biology of calanoid copepods. Academic Press
- Mauritzen, C., Hansen, E., Andersson, M., Berx, B., Beszczynska-Moller, A., Burud, I., Christensen, K.H., Debernard, J., De Steur, L., Dodd, P., Gerland, S., Godoy, O., Hansen, B., Hudson, S., Hoydalsvik, F., Ingvaldsen, R., Isachsen, P.E., Kasajima, Y., Koszalka, I., Kovacs, K.M., Koltzow, M., LaCasce, J., Lee, C.M., Lavergne, T., Lydersen, C., Nicolaus, M., Nilsen, F., Nost, O.A., Orvik, K.A., Reigstad, M., Schyberg, H., Seuthe, L., Skagseth, O., Skardhamar, J., Skogseth, R., Sperrevik, A., Svensen, C., Soiland, H., Teigen, S.H., Tverberg, V., Riser, C.W., 2011. Closing the loop: Approaches to monitoring the state of the Arctic Mediterranean during the International Polar Year 2007-2008. Prog. Oceanogr. 90, 62-89. doi 10.1016/j.pocean.2011.02.010
- Mayor, D.J., Anderson, T.R., Pond, D.W., 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. doi DOI: 10.1016/j.jmarsys.2008.12.019
- Mayor, D.J., Anderson, T.R., Pond, D.W., Irigoien, X., 2009b. Limitation of egg production in *Calanus finmarchicus* in the field: A stoichiometric analysis. J. Mar. Syst. 78, 511-517. doi DOI: 10.1016/j.jmarsys.2008.12.020
- Mayzaud, P., Martin, J.L.M., 1975. Some Aspects of biochemical and mineral composition of marine plankton. J. Exp. Mar. Biol. Ecol. 17, 297-310.
- Mette, E.M., Vanni, M.J., Newell, J.M., Gonzalez, M.J., 2011. Phytoplankton communities and stoichiometry are interactively affected by light, nutrients, and fish. Limnol. Oceanogr. 56, 1959-1975. doi 10.4319/lo.2011.56.6.1959

- Mitra, A., Flynn, K.J., 2005. Predator–prey interactions: Is ‘ecological stoichiometry’ sufficient when good food goes bad? *J. Plankton Res.* 27, 393-399. doi 10.1093/plankt/fbi022
- Morales, C.E., 1987. Carbon and nitrogen content of copepod fecal pellets: Effect of food concentration and feeding behavior *Mar. Ecol. Prog. Ser.* 36, 107-114. doi 10.3354/meps036107
- Moran, S.B., Ellis, K.M., Smith, J.N., 1997. $^{234}\text{Th}/^{238}\text{U}$ disequilibrium in the central Arctic Ocean: implications for particulate organic carbon export. *Deep-Sea Res.* 44 (8), 1593-1606.
- Mumm, N., Auel, H., Hanssen, H., Hagen, W., Richter, C., Hirche, H.J., 1998. Breaking the ice: large-scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises. *Polar Biol.* 20, 189-197. doi 10.1007/s003000050295
- Niehoff, B., Klenke, U., Hirche, H.J., Irigoien, X., Head, R., Harris, R., 1999. A high frequency time series at Weathership M, Norwegian Sea, during the 1997 spring bloom: The reproductive biology of *Calanus finmarchicus*. *Mar. Ecol. Prog. Ser.* 176, 81-92.
- Niehoff, B., Madsen, S.D., Hansen, B.W., Nielsen, T.G., 2002. Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. *Mar. Biol.* 140, 567-576. doi 10.1007/s00227-001-0731-3
- Nielsen, S.L., Enriquez, S., Duarte, C.M., SandJensen, K., 1996. Scaling maximum growth rates across photosynthetic organisms. *Funct. Ecol.* 10, 167-175. doi 10.2307/2389840
- Nielsen, T., Hansen, B., 1995. Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. *Mar. Ecol. Prog. Ser.* 125, 239-257. doi 10.3354/meps125239
- Noji, T.T., Estep, K.W., Macintyre, F., Norrbin, F., 1991. Image analysis of fecal material grazed upon by three species of copepods: Evidence for coprorhexy, coprophagy and coprochaly. *J. Mar. Biol. Ass. U.K.* 71, 465-480. doi doi:10.1017/S0025315400051717
- Paasche, E., Erga, S.R., 1988. Phosphorus and nitrogen limitation of phytoplankton in the inner Oslo fjord (Norway) *Sarsia* 73, 229-243.
- Partington, J.R., 1948. The Concepts of Substance and Chemical Element. *Chymia* 1, 109-121.

- Pedersen, G., Tande, K., Ottesen, G.O., 1995. Why does a component of *Calanus finmarchicus* stay in the surface waters during the overwintering period in high latitudes? ICES J. Mar. Sci. 52, 523-531. doi 10.1016/1054-3139(95)80066-2
- Pedersen, G., Tande, K.S., 1992. Physiological plasticity to temperature in *Calanus finmarchicus*. Reality or artefact? J. Exp. Mar. Biol. Ecol. 155, 183-197. doi 10.1016/0022-0981(92)90062-f
- Persson, J., Fink, P., Goto, A., Hood, J.M., Jonas, J., Kato, S., 2010. To be or not to be what you eat: Regulation of stoichiometric homeostasis among autotrophs and heterotrophs. Oikos 119, 741-751. doi 10.1111/j.1600-0706.2009.18545.x
- Planque, B., Hays, G.C., Ibanez, F., Gamble, J.C., 1997. Large scale spatial variations in the seasonal abundance of *Calanus finmarchicus*. Deep-Sea Res. Pt. I 44, 315-326. doi 10.1016/s0967-0637(96)00100-8
- Proshutinsky, A.Y., Polyakov, I.V., Johnson, M.A., 1999. Climate states and variability of Arctic ice and water dynamics during 1946–1997. Polar Res. 18, 135-142. doi 10.1111/j.1751-8369.1999.tb00285.x
- Ptacnik, R., Andersen, T., Tamminen, T., 2010. Performance of the Redfield ratio and a family of nutrient limitation indicators as thresholds for phytoplankton N vs. P Limitation. Ecosystems 13, 1201-1214. doi 10.1007/s10021-010-9380-z
- Redfield, A.C., 1958. The biological control of chemical factors in the environment. Am. Sci. 46, 230A-221.
- Reigstad, M., 2000. Plankton community and vertical flux of biogenic matter in north Norwegian fjords: Regulating factors, temporal and spatial variations. PhD thesis. University of Tromsø.
- Reigstad, M., Wassmann, P., Ratkova, T., Arashkevich, E., Pasternak, A., Oygarden, S., 2000. Comparison of the springtime vertical export of biogenic matter in three northern Norwegian fjords. Mar. Ecol. Prog. Ser. 201, 73-89.
- Reigstad, M., Wassmann, P., Wexels Riser, C., Øygarden, S., Rey, F., 2002. Variations in hydrography, nutrients and chlorophyll *a* in the marginal ice-zone and the central Barents Sea. J. Mar. Syst. 38, 9-29. doi 10.1016/s0924-7963(02)00167-7
- Reiners, W. A., 1986. Complimentary models for ecosystems. Am. Nat. 127, 59-73.
- Revelle, R., 1995. Alfred C. Redfield 1890-1983. In Biographical Memoirs V.67. The National Academies Press, Washington, 315-329.

- Sakshaug, E., 2004. Primary and secondary production in the Arctic Seas, in: Stein, R., and MacDonald, R., (Ed.) (2004). The organic carbon cycle in the Arctic Ocean. Springer, Berlin, pp. 57-81
- Sargent, J.R., Falk-Petersen, S., 1988. The lipid biochemistry of calanoid copepods. *Hydrobiologia* 167-168, 101-114. doi 10.1007/bf00026297
- Schauer, U., Beszczynska-Moller, A., 2009. Problems with estimation and interpretation of oceanic heat transport - conceptual remarks for the case of Fram Strait in the Arctic Ocean. *Ocean. Sci.* 5, 487-494.
- Scott, C.L., Kwasniewski, S., Falk-Petersen, S., Sargent, J.R., 2002. Species differences, origins and functions of fatty alcohols and fatty acids in the wax esters and phospholipids of *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* from Arctic waters. *Mar. Ecol. Prog. Ser.* 235, 127-134. doi 10.3354/meps235127
- Screen, J.A., Simmonds, I., 2010. The central role of diminishing sea ice in recent Arctic temperature amplification. *Nature* 464, 1334-1337. doi 10.1038/nature09051
- Serreze, M., Francis, J., 2006. The Arctic amplification debate. *Climatic Change* 76, 241-264. doi 10.1007/s10584-005-9017-y
- Seuthe, L., Iversen, K.R., Narcy, F., 2011. Microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): II. Ciliates and dinoflagellates. *Polar Biol.* 34, 751-766. doi 10.1007/s00300-010-0930-9
- Sherr, E.B., Sherr, B.F., Wheeler, P.A., Thompson, K., 2003. Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. *Deep-Sea Res. Pt I* 50, 557-571. doi 10.1016/s0967-0637(03)00031-1
- Slagstad, D., Ellingsen, I.H., Wassmann, P., 2011. Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: An experimental simulation approach. *Prog. Oceanogr.* 90, 117-131. doi 10.1016/j.pocean.2011.02.009
- Small, L.F., Fowler, S.W., Moore, S.A., Larosa, J., 1983. Dissolved and fecal pellet carbon and nitrogen release by zooplankton in tropical waters. *Deep-Sea Res.* 30, 1199-1220. doi 10.1016/0198-0149(83)90080-8
- Smith, S., 1990. Egg production and feeding by copepods prior to the spring bloom of phytoplankton in Fram Strait, Greenland Sea. *Mar. Biol.* 106, 59-69. doi 10.1007/bf02114675
- Smith, S.L., 1988. Copepod in Fram Strait un summer: Distribution, feeding and metabolism. *J. Mar. Res.* 46, 145-181. doi 10.1357/002224088785113720

- Søreide, J.E., Falk-Petersen, S., Hegseth, E.N., Hop, H., Carroll, M.L., Hobson, K.A., Blachowiak-Samolyk, K., 2008. Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. *Deep-Sea Res. Pt. II* 55, 2225-2244. doi 10.1016/j.dsr2.2008.05.024
- Søreide, J.E., Leu, E.V.A., Berge, J., Graeve, M., Falk-Petersen, S., 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob. Change Biol.* 16, 3154-3163. doi 10.1111/j.1365-2486.2010.02175.x
- Spindler, M., 1994. Notes on the biology of sea ice in the Arctic and Antarctic. *Polar Biol.* 14, 319-324. doi 10.1007/bf00238447
- Sterner, R., Schulz, K., 1998. Zooplankton nutrition: Recent progress and a reality check. *Aquat.Ecol.* 32, 261-279. doi 10.1023/a:1009949400573
- Sterner, R.W., 1995. Elemental stoichiometry of species in ecosystems. Chapman & Hall Inc, New York
- Sterner, R.W., Andersen, T., Elser, J.J., Hessen, D.O., Hood, J.M., McCauley, E., Urabe, J., 2008. Scale-dependent carbon:nitrogen:phosphorus seston stoichiometry in marine and freshwaters. *Limnol Oceanogr* 53, 1169-1180.
- Sterner, R.W., Elser, J.J., 2002. Ecological stoichiometry : the biology of elements from molecules to the biosphere. Princeton Univ. Press, Princeton, NJ [u.a.]
- Subba Rao, D.V., Platt, T., 1984. Primary production of Arctic waters. *Polar Biol.* 3, 191-201. doi 10.1007/bf00292623
- Suess, E., 1980. Particulate organic carbon flux in the oceans: Surface productivity and oxygen utilization. *Nature* 288, 260-263.
- Surhone, L., Tennoe, M. T., Henssonow, S.F., 2010. Stoichiometry. Betascript publishing. 80 p.
- Svensen, C., Seuthe, L., Vasilyeva, Y., Pasternak, A., Hansen, E., 2011. Zooplankton distribution across Fram Strait in autumn: Are small copepods and protozooplankton important? *Prog. Oceanogr.* 91, 534-544. doi 10.1016/j.pocean.2011.08.001
- Svensen, C., Tande, K., 1999. Sex change and female dimorphism in *Calanus finmarchicus*. *Mar. Ecol. Prog. Ser.* 176, 93-102.
- Szabadváry, F., 1993. History of analytical chemistry. Gordon and Breach science publishers.
- 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., Hassel, A., Slagstad, D., 1985. Gonad maturation and possible life cycle strategies in *Calanus finmarchicus* and *Calanus glacialis* in the northwest part of the Barents Sea. In: Gray, J.S., Christiansen, M.E., editors. Marine biology of Polar regions and effects of stress on marine organisms. New York, Chichester: Wiley and Sons. 141-55.
- Tande, K.S., Hopkins, C.C.E., 1981. Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: The genital system in *Calanus finmarchicus* and the role of gonad development in overwintering strategy. Mar. Biol. 63, 159-164. doi 10.1007/bf00406824
- Tande, K.S., Slagstad, D., 1992. Regional and interannual variations in biomass and productivity of the marine copepod, *Calanus finmarchicus*, in sub-Arctic environments. Oceanol. Acta 15, 309-321.
- Touratier, F., Legendre, L., Vezina, A., 1999. Model of copepod growth influenced by the food carbon:nitrogen ratio and concentration, under the hypothesis of strict homeostasis. J. Plankton Res. 21, 1111-1132. doi 10.1093/plankt/21.6.1111
- Turner, J.T., 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquat. Microb. Ecol. 27, 57-102. doi 10.3354/ame027057
- Turner, J.T., Ferrante, J.G., 1979. Zooplankton fecal pellets in aquatic ecosystems BioScience 29, 670-677. doi 10.2307/1307591
- Urabe, J., 1993. N-cycling and P-cycling coupled by grazers activities: Food quality and nutrient release by zooplankton. Ecology 74, 2337-2350.
- Urabe, J., Elser, J.J., Kyle, M., Yoshida, T., Sekino, T., Kawabata, Z., 2002. Herbivorous animals can mitigate unfavourable ratios of energy and material supplies by enhancing nutrient recycling. Ecol. Lett. 5, 177-185.
- Van de Waal, D.B., Verschoor, A.M., Verspagen, J.M.H., Van Donk, E., Huisman, J., 2010. Climate-driven changes in the ecological stoichiometry of aquatic ecosystems. Front. Ecol. Environ. 8, 145-152. doi 10.1890/080178
- Van Nieuwerburgh, L., Wänstrand, I., Snoeijs, P., 2004. Growth and C:N:P ratios in copepods grazing on N- or Si-limited phytoplankton blooms. Hydrobiologia 514, 57-72.
- Ventura, M., 2006. Linking biochemical and elemental composition in freshwater and marine crustacean zooplankton. Mar. Ecol. Prog. Ser. 327, 233-246.
- Vijverberg, J., 1976. The effect of food quantity and quality on the growth, birth-rate and longevity of *Daphnia hyalina* Leydig. Hydrobiologia 51, 99-108. doi 10.1007/bf00009824

- Vogedes, D., Varpe, O., Søreide, J.E., Graeve, M., Berge, J., Falk-Petersen, S., 2010. Lipid sac area as a proxy for individual lipid content of arctic calanoid copepods. *J. Plankton Res.* 32, 1471-1477. doi 10.1093/plankt/fbq068
- Walve, J., Larsson, U., 1999. Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: Implications for nutrient recycling. *J. Plankton Res.* 21, 2309-2321.
- Wassmann, P., 1997. Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. *Hydrobiologia* 363, 29-57 doi 10.1023/a:1003113403096
- Wassmann, P., 2011. Arctic marine ecosystems in an era of rapid climate change. *Prog. Oceanogr.* 90, 1-17. doi 10.1016/j.pocean.2011.02.002
- Wassmann, P., Bauernfeind, E., Fortier, M., Fukuchi, M., Hargrave, B., Moran, B., Noji, Th., Nöthig, E.-M., Peinert, R., Sasaki, H., Shevchenko, V., 2004. Particulate organic carbon flux to the sea floor. In: Stein, R., Macdonald, R.M. (Eds.), *The organic carbon cycle in the Arctic Ocean*. Springer-Verlag, Heidelberg–Berlin– New York, pp. 101–138.
- Wassmann, P., Duarte, C.M., Agusti, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. *Glob. Change Biol.* 17, 1235-1249. doi 10.1111/j.1365-2486.2010.02311.x
- Wassmann, P., Reigstad, M., 2011. Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. *Oceanography* 24, 220-231.
- Wexels Riser, C., 2007. Fate of zooplankton fecal pellets in marine ecosystems: export or retention? PhD thesis. University of Tromsø
- Wexels Riser, C.W., Reigstad, M., Wassmann, P., 2010. Zooplankton-mediated carbon export: A seasonal study in a northern Norwegian fjord. *Mar. Biol. Res.* 6, 461-471. doi 10.1080/17451000903437067
- Wexels Riser, C., Reigstad, M., Wassmann, P., Arashkevich, E., Falk-Petersen, S., 2007. Export or retention? Copepod abundance, fecal pellet production and vertical flux in the marginal ice zone through snap shots from the northern Barents Sea. *Polar Biol.* 30, 719-730. doi 10.1007/s00300-006-0229-z
- Wexels Riser, C., Wassmann, P., Olli, K., Pasternak, A., Arashkevich, E., 2002. Seasonal variation in production, retention and export of zooplankton fpellets in the marginal ice zone and central Barents Sea. *J. Mar. Syst.* 38, 175-188. doi 10.1016/s0924-7963(02)00176-8

Wexels Riser, C., Wassmann, P., Reigstad, M., Seuthe, L., 2008. Vertical flux regulation by zooplankton in the northern Barents Sea during Arctic spring. *Deep-Sea Res. Pt II* 55, 2320-2329. doi 10.1016/j.dsr2.2008.05.006

Paper I

Aubert, A.B., Svensen, C., Hessen, D., Tamelander, T., 2012. CNP stoichiometry of a lipid-synthesising calanoid copepod, *Calanus finmarchicus*, from winter to spring bloom in a sub-Arctic sound. Journal of Marine Systems. doi 10.1016/j.jmarsys.2012.09.004

Paper II

Aubert, A.B., Tamelander, T., (manuscript). Stoichiometric approach to elemental limitation of pelagic producers and grazers during the Arctic summer.

Submitted to Marine Ecology Progress Series.

Paper III

Tameler, T., Aubert, A. B., Wexels Riser, C., 2012. Export stoichiometry and contribution of copepod faecal pellets to vertical flux of particulate organic carbon, nitrogen and phosphorus. *Marine Ecology Progress Series*, 459, 17-28.

