

Variation in the seston C:N ratio of the Arctic Ocean and pan-Arctic shelves

Helene Frigstad^{a, b, c, *}, Tom Andersen^d, Richard G.J. Bellerby^{a, b, e}, Anna Silyakova^{a, b}, Dag O. Hessen^d

^a Uni Bjerknes Centre, Uni Research, Allégaten 55, 5007 Bergen, Norway

^b Bjerknes Centre for Climate Research, Allégaten 55, 5007 Bergen, Norway

^c Geophysical Institute, University of Bergen, Allégaten 70, 5007 Bergen, Norway

^d Department of Biology, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo, Norway

^e Norwegian Institute for Water Research (NIVA, Thormøhlensgate 53D, 5006, Bergen, Norway)

*: Corresponding author : Helene Frigstad, tel.: + 47 99 26 40 02 ; email address : helene.frigstad@uni.no

Abstract:

Studying more than 3600 observations of particulate organic carbon (POC) and particulate organic nitrogen (PON), we evaluate the applicability of the classic Redfield C:N ratio (6.6) and the recently proposed Sterner ratio (8.3) for the Arctic Ocean and pan-Arctic shelves. The confidence intervals for C:N ranged from 6.43 to 8.82, while the average C:N ratio for all observations was 7.4. In general, neither the Redfield or Sterner ratios were applicable, with the Redfield ratio being too low and the Sterner ratio too high. On a regional basis, all northern high latitude regions had a C:N ratio significantly higher than the Redfield ratio, except the Arctic Ocean (6.6), Chukchi (6.4) and East Siberian (6.5) Seas. The latter two regions were influenced by nutrient-rich Pacific waters, and had a high fraction of autotrophic (i.e. algal-derived) material. The C:N ratios of the Laptev (7.9) and Kara (7.5) Seas were high, and had larger contributions of terrigenous material. The highest C:N ratios were in the North Water (8.7) and Northeast Water (8.0) polynyas, and these regions were more similar to the Sterner ratio. The C:N ratio varied between regions, and was significantly different between the Atlantic (6.7) and Arctic (7.9) influenced regions of the Barents Sea, while the Atlantic dominated regions (Norwegian, Greenland and Atlantic Barents Seas) were similar (6.7–7). All observations combined, and most individual regions, showed a pattern of decreasing C:N ratios with increasing seston concentrations. This meta-analysis has important implications for ecosystem modelling, as it demonstrated the striking temporal and spatial variability in C:N ratios and challenges the common assumption of a constant C:N ratio. The non-constant stoichiometry was believed to be caused by variable contributions of autotrophs, heterotrophs and detritus to seston, and a significant decrease in C:N ratios with increasing Chlorophyll *a* concentrations supports this view. This study adds support to the use of a power function model, where the exponent is system-specific, but we suggest a general Arctic relationship, where $POC = 7.4 PON^{0.89}$.

Highlights

► Largest meta-analysis to date of seston C:N ratios in Arctic and pan-Arctic shelves ► Average ratio 7.4, with confidence intervals ranging from 6.4 to 8.8 for different regions ► In general, Redfield ratio (6.6) too low and Sterner ratio (8.3) too high ► Significant difference between regions, recommending the use of regional ratios ► Decreasing C:N ratios with increasing concentrations; non-constant stoichiometry

Keywords: Arctic ; Carbon ; Nitrogen ; Stoichiometry ; Redfield ratio

1. Introduction

The Arctic Ocean make up around 3% of the total area of the world oceans, with over 50% of the total area comprised of relatively shallow continental shelves that encompass the Arctic Ocean proper (Jakobsson et al., 2004). Some of these Arctic shelves are among the most productive in the World Ocean (Sakshaug, 2004), and the Arctic Ocean is disproportionately important in the global carbon (C) cycle with up to 14% of the global CO₂ uptake (Bates and Mathis, 2009). Most temperate and high-latitude shelves act as net sinks of atmospheric CO₂ (Chen and Borges, 2009), which can subsequently be transported out of the surface layers and sequestered on long time scales (Thomas et al., 2004). This “continental shelf pump” is considered especially important on Arctic shelves, due to the wide extent, regionally high productivity and formation of dense water (Anderson et al., 2010; Kivimae et al., 2010). The sea ice cover in the Arctic Ocean has decreased over the last decades (Perovich and Richter-Menge, 2009), which could stimulate primary production through an increase in solar radiation. However, nutrient availability is limited due to strong vertical stratification (Tremblay et al., 2002), which might increase due to higher river run-off with climate change (Peterson et al., 2002). In addition, it has been proposed that warming will increase the respiration rates and decrease the potential these regions have to act as CO₂ sinks (Vaquer-Sunyer et al., 2010). Whether the oceanic CO₂ sink in the Arctic Ocean will increase or decrease in the future due to the effects of climate change on ice-cover, stratification and metabolic balance is still under scrutiny (Bates and Mathis, 2009; Duarte et al., 2012; Hill et al 2013).

The cycles of C and the major nutrients, nitrogen (N) and phosphorus (P), are linked through the uptake and remineralization of marine autotrophs. The Redfield ratio (C:N:P = 106:16:1 (atomic ratio)) describes the relationship between C, N and P in the suspended particulate organic matter (seston hereafter) and in the dissolved inorganic fraction (Redfield, 1958; Redfield et al., 1963), and a fixed Redfield ratio has for simplicity been widely adopted in ecosystem modelling. There are, however, debates about the general applicability of a constant ratio between C and nutrients (Arrigo, 2005; Karl et al., 2001), and both model selection and variability in C:N-ratios may have profound impact on simulations of C and N-flux in marine food-webs (Anderson et al., In Press). Indeed, model studies have shown improved performance with a variable elemental stoichiometry (Christian, 2005; Klausmeier et al., 2004). Increasing the C:N ratio of autotrophs in ecosystem models can have substantial effects on the uptake of CO₂ and C-sequestration (assuming higher C:N in the material exported below the winter mixed layer), and thus increase the drawdown of atmospheric CO₂ (Schneider et al., 2004, Oschlies et al., 2008).

Sterner et al. (2008) recently performed the largest meta-analysis of C:N:P stoichiometry in aquatic systems (including both oceanic and freshwater samples) to date. However, their study did not include data from high latitudes. They found variable stoichiometry between C:N:P when analysing the data on smaller spatial scales (e.g. between ocean basins), which violates the assumption of a *constant* ratio between the elements. A revised global ratio of C:N:P = 166:20:1 (atomic ratio) was proposed, which correspond to a C:N ratio of 8.3 (henceforth the Sterner ratio).

Autotrophs have a large plasticity in their uptake of nutrients and C, and can adjust their C fixation (mediated by photosynthesis) and nutrient uptake according to cellular requirements and ambient conditions (Berman-Frank and Dubinsky, 1999; Sterner and Elser, 2002). Higher C:nutrient ratios have been shown with progressive nutrient limitation over the season (Sambrotto et al., 1993, Kortzinger et al., 2001, Falck and Anderson, 2005) and in mesocosm experiments with higher pCO₂ (Bellerby et al., 2008). Autotrophs do generally not have homeostatic elemental regulation (Sterner and Elser, 2002), and thus elemental flexibility in the autotrophs themselves argues against constant C:N-ratios in seston. Seston is often dominated by non-autotroph fractions, and apparent stable Redfield ratios may emerge from a balancing of sestonic fractions with contrasting C:nutrient ratios (Frigstad et al., 2011; Hessen et al., 2003).

Historically, oceanographic data from Arctic shelves have been limited in space and time due to the distant location and often difficult weather and ice conditions. This has led to a fragmented understanding of the biogeochemical properties and cycling of the Arctic Ocean, such that the need for a “pan-Arctic” approach has been emphasized (Carmack and Wassmann, 2006). We present the largest compilation to date of suspended particulate organic carbon (POC) and particulate organic nitrogen (PON) from the northern high latitudes, in order to evaluate the variability of C:N ratios across the Arctic Ocean and pan-Arctic shelves. We have not included particulate organic phosphorus (POP) in this study, partly because the data on this element is scarce, and also because most ecosystem models operate with either C or N as the main element. However, given the key role of P in biological processes, we strongly recommend the inclusion of this element in future monitoring. The aim of this study is twofold, firstly to evaluate the applicability of the Redfield and Sterner ratios in the northern high latitudes, and secondly to test the assumption of constant C:N ratios by use of regression modelling. This has important implications for the C and N cycles, including effects on air-sea gas exchange, export production and sequestration of C on long (>100 years) time scales. The C:nutrient ratio in seston also has important implications for higher trophic levels, because a reduction in nutrient per unit C (i.e. reduced food *quality*) can impact growth and reproduction not only of herbivores, but also higher trophic levels (Malzahn et al., 2010; Sterner and Elser, 2002). The physical and biological systems of the Arctic Ocean are expected to be greatly affected by climate change, and a synthesis of sestonic C:N ratios can be useful for simulating to what extent the Arctic Ocean and pan-Arctic shelves will act as net sinks or sources of C in the future.

2. Methods

2.1. Data

Observations of POC and PON were gathered from published sampling campaigns north of 60°, comprising a total of 3672 observations from ten individual research programs (see overview in Table 1). Only observations shallower than 200 meters depth were included in the study. The observations were divided into regions (see Fig. 1 and Table 2) following the definitions in Jakobsson et al. (2004). The following regions were identified: Norwegian Sea (NS), Greenland Sea (GS), Atlantic Barents Sea (BA_t), Arctic Barents Sea (BA_r), Kara Sea (KS), Laptev Sea (LS), East Siberian Sea (ESS), Chukchi Sea and adjacent slope (CSS) and the Arctic Ocean (AO); the

acronyms will be used in tables and figures, henceforth). The Northeast Water Polynya (NEW) and North Water Polynya (NOW) were also treated as separate regions, due to the unique turbulence regimes (Smith et al., 1990). The Barents Sea was divided into an Arctic and an Atlantic region, due to the strong effect of the Polar Front on the hydrography and biology of the region (Loeng, 1991). Two stations north of Svalbard were included in the Arctic Barents Sea region, because they were on the relatively shallow Barents Sea shelf and thus more similar to the Arctic Barents Sea stations than the open Arctic Ocean stations.

POC and PON were measured by standard analytical methods in all studies, and the protocols are described in the references given in Table 1. The average C:N ratio of protein in organisms is 2.7 and protein can comprise up to 75% of body mass of the various sestonic components (Sterner and Elser, 2002, and references therein). We have applied a C:N of 3 as a conservative lower theoretical bound for the C:N ratio in organic material, and thus observations in the original datasets with a C:N ratio lower than 3 were removed ($n = 113$). From the two polynya studies there were observations with a C:N higher than 50 ($n = 44$), these were predominantly when the PON concentration was very low ($< 0.05 \mu\text{mol L}^{-1}$) suggesting that the very high C:N ratios were due to measurements errors, and these observations were removed from the database.

Around 2400 of the observations included measurements of Chlorophyll *a* (Chl *a*), yet there were no measurements available for the Kara, Laptev, East Siberian and Chukchi Seas. For the NOW polynya and the Arctic Ocean around 60% of the observations included Chl *a* measurements.

2.2. Statistical analyses

All statistical analyses were performed using the R statistical software (R Development Core Team, 2012). Due to non-normal distributions (as tested with the Shapiro-Wilk test of normality) significant differences in C:N ratios between regions were tested with a non-parametric Kruskal-Wallis Rank Sum test (Hollander and Wolfe, 1973), with the confidence level set to 95%. To test the significance of the relationship between the C:N ratio and Chl *a* we used a linear model on log-transformed data (shown in Fig. 5). Note that we did not use a model II regression (as described below), because we were not interested in the value of the intercept and/or slope, but the significance of the relationship (which can not be tested in a standardized major axis (SMA) regression).

Both POC and PON are affected by biological and observational sources of stochasticity, with no clear indication which of them should be considered the dependent and independent variable (Laws and Archie, 1981; McArdle, 2003). In such cases using ordinary least squares regression can underestimate the slope of the linear relationship between the variables, such that it is recommended to use model II methods for linear regression (e.g. Legendre and Legendre, 1998). In this study, the R package *lmodel2* was used to calculate SMA regressions (Legendre, 2011). The SMA regressions with 95% confidence intervals (CI) on log (POC) against log (PON) are shown in Fig. 6.

Following the arguments of Sterner et al. (2008), the C:N ratios can deviate from “constancy” in two mathematically different ways. The first is:

$$\text{Model 1: } POC = a * PON * e \quad (1)$$

$$\text{Log-log space: } \log POC = \log a + \log PON + \log e$$

Where in model 1 the variation comes from the random error term e , while a represents the proportionality factor (e.g. 6.6 for Redfield C:N). In this case the C:N ratio is constant over the whole range of concentrations of POC and PON (given that e is small compared to a). In log-log space this model would have a slope = 1. An alternative model, where the ratio between the elements might change as the concentrations increase or decrease is:

$$\text{Model 2: } POC = a * PON^b * e \quad (2)$$

$$\text{Log-log space: } \log POC = \log a + b \log PON + \log e$$

Model 2 is a power function model, where the relationship between $\log(POC)$ and $\log(PON)$ is still linear, however the slope does not have to equal 1. Significant deviations from a slope = 1 in log-log space indicates that the ratio varies over the range of the seston concentrations, and a log-log SMA slope < 1 implies that the ratio of C:N decreases with increasing concentrations of POC and PON. The SMA slopes with 95% CI are shown in Fig. 7. The anti-log of the intercept will estimate the C:N ratio, when PON equals $1 \mu\text{mol L}^{-1}$ (given significant non-constant relationship), and the C:N ratios with 95% CI are given in Table 3. Significant deviations from the Redfield and Sterner ratios were assumed when the 95% CI did not overlap with the respective ratio.

3. Results

The largest dataset on high latitude C:N to date provided good coverage of the Arctic Ocean proper and the pan-Arctic shelves (Fig. 1), and a good representation of all latitudes north of 65° (Fig. 2). Most observations (around 2800) were in the upper 50 metres of water column, spanning the productive season in this region (from March to October) and were collected over twelve years (Fig. 2).

The concentrations of POC and PON (Fig. 3) ranged over two orders of magnitude from the low productivity regimes of the Arctic Ocean to the spring bloom in the Arctic section of the Barents Sea. The C:N ratios (Fig. 3, lower panel) also showed large variability, both within and between individual regions. The C:N ratios with 95% CI are given in Table 3, and the average C:N ratio for all observations combined was 7.4, while the 95% CI for the individual regions spanned 6.43 to 8.82. All C:N ratios were significantly higher than the Redfield ratio, except the Arctic Ocean and the East Siberian and Chukchi Seas. The East Siberian and Chukchi Seas were the only two regions that had a C:N ratio significantly lower than the Redfield ratio. The C:N ratios were highest in the NOW and NEW polynyas, and these were higher and not different from the Sterner ratio, respectively. All other regions had C:N ratios significantly lower than the Sterner ratio.

There were significant differences between regions, also when excluding the NEW and NOW polynyas (Kruskal-Wallis test: Chi-squared = 189, df = 8, $p < 0.001$). The Atlantic and Arctic region of the Barents Sea were also significantly different (Kruskal-Wallis test: Chi-squared = 15, df = 1, $p < 0.001$), while the Atlantic-

influenced regions of the Norwegian, Greenland and Atlantic Barents Seas did not differ significantly (Kruskal-Wallis test: Chi-squared = 5, df = 2, $p = 0.080$).

There was monthly and inter-annual variation in the C:N ratios within the different regions (Fig.4), and all regions except the Laptev and East Siberian Seas were sampled in more than one year. There was considerable seasonal variations in the C:N ratio within the different regions, however, in general, the observations taken in different years overlapped.

There was a significant decreasing trend of C:N ratio with increasing Chl *a* (Fig 5), however the relationship had limited predictive power (log-transformed linear model: $R^2 = 0.09$, $F(1, 2371) = 224$, $p = <0.001$). The C:N ratio was higher at low Chl *a*, and decreased towards the Redfield ratio at higher Chl *a* concentrations.

The constancy of the C:N ratios across the range of seston concentrations was tested by a SMA regression (Fig. 6), and all ratios showed significant deviations from constancy except the Atlantic sector of the Barents Sea and the East Siberian Sea (SMA slopes in Fig. 7). All observations combined and all individual regions, except the Laptev Sea, had a log SMA slope significantly < 1 , showing that the C:N ratio decreased with increasing seston concentration.

4. Discussion

4.1. The Redfield and Sterner ratios in the Arctic

This meta-analysis presents the first compilation of seston C:N ratios in the Arctic and pan-Arctic shelves. We found that neither the Redfield nor the Sterner ratio were in general applicable for the Arctic, with the Redfield ratio being too low and the Sterner ratio too high. In addition, the significant differences in C:N ratios between regions suggests that it is more appropriate to use data-based regional ratios, rather than uniform global ratios in ecosystem models and budget studies in the Arctic.

The high latitude regions experience strong seasonal variability in light, nutrients and temperature, and especially the short growing season, strong stratification created by ice melt, low temperatures and low incident radiation separate them from the temperate regimes (Carmack et al., 2006; Macdonald et al., 2004). In addition, as some phytoplankton could be C-limited at present CO₂ concentrations (Riebesell et al., 1993), it is possible that there could be higher C:nutrient ratios in colder Arctic waters (with higher solubility of CO₂) compared to warmer tropical waters (Weiss et al., 1979). This could potentially explain the higher C:N ratio we observe in Arctic waters relative to the Redfield ratio, which was primarily based on temperate and tropical data (Redfield, 1934). However, low pCO₂ values have been observed in several Arctic studies (Arthun et al., 2012; Bellerby et al., 2012), which indicate that there must be other and unknown mechanisms at work.

The global sestonic C:N ratio proposed by Sterner et al. (2008) was based on a compilation of all available datasets containing POC, PON and POP, and included both freshwater and oceanic samples. The median ratios for coastal (7.5) and offshore oceans (6.6) habitats were substantially lower than the freshwater samples (9.5 and 8.5 for small and large lakes, respectively). The global ratio of 8.3 was

significantly higher than all the Arctic regions, except the NOW and NEW polynyas, west and east of Greenland, respectively.

In this meta-analysis, we found no consistent shift in the C:N ratio with latitude (data not shown), contrary to what has been reported for lakes (Dobberfuhl and Elser, 2000) and terrestrial vegetation (Reich and Oleksyn, 2004). However, our study included no real temperate regions (majority of observations were north of the Arctic Circle), and as discussed in Sect. 4.2 we believe the variations in C:N ratios were more related to the biogeochemical properties of the individual regions.

There was pronounced seasonal variation within the regions, and the two research programs that sampled consistently over several months (NOW and SBI; Table 1), reported higher C:N ratios towards the end of the productive season (Mei et al., 2005, Bates et al., 2005). This C overconsumption (Toggweiler, 1993) was in both abovementioned studies accredited production of N-rich material in spring when the nutrient supply was replete, and C-rich production later in the season when the nutrient pool was depleted or significantly drawn-down.

The C:N ratios for the different regions are based on data sampled between March and October (with the highest number of observations in June and July; Fig. 2). For example, the Arctic Ocean and the Kara, Laptev and East Siberian Seas have only been sampled during one or two months of the year. The lack of seasonal sampling reflects the restraints due to the accessibility and difficult weather and ice conditions in the region, implying that the averages given in this study might change as a result of improved seasonal sampling in the future.

4.2. Pan-Arctic variations in the C:N ratio

The C:N ratios in the NOW (8.7) and NEW (8.0) polynyas were the highest in this meta-analysis. Polynyas are essentially areas of open water surrounded by sea-ice, and can sustain intense sea-ice production and dense water formation (from brine rejection) in winter (Smith et al., 1990). Daly et al. (1999) reported a seston C:N ratio of 8.9 in the NEW polynya in 1992, and accredited the high C content to nutrient limitation and predominance of diatoms with a C-rich mucilaginous sheath (*Chaetoceros socialis*), while detritus (with high C:N ratios) was found to have little impact on the overall sestonic C:N ratio. The high seston C:N ratio in the NOW polynya during 1998 was associated with high irradiance and nitrate limitation (Mei et al., 2005). Nevertheless, the high C:N ratios of these two regions are striking, especially given that the two polynyas are known to function quite differently (e.g. Berreville et al., 2008). One possible similarity is that due to their ice-free nature, primary production can start early and be sustained over a longer growing season than the rest of the Arctic. This could imply that nutrient limitation can be severe for a major part of the growth season, thereby increasing the C:N ratios due to nitrate limitation, which is also highlighted in the two polynya studies (Daly et al., 2009; Mei et al., 2005).

The C:N ratios varied significantly between regions, even when not including the two polynya studies. The C:N ratio varied substantially over relatively short distances, and we found that the C:N ratio in the Arctic dominated Barents Sea was significantly higher than in the Atlantic Barents Sea (7.9 vs. 6.7). Significant differences between the Atlantic and Arctic Barents Sea were also found for the C:N ratio in the material

exported out of the euphotic zone by Tamelander et al. (2013) and Olli et al. (2002). The Barents Sea can be characterized as a deep inflow shelf, where significant modification of the inflowing Atlantic water occurs before entering the Arctic Ocean (Carmack and Wassmann, 2006). The inflow of Atlantic waters is high, but the Polar Front separates the primarily Atlantic regime of the southern Barents Sea from the Arctic water influenced regime of the northern Barents Sea (Loeng, 1991). The Atlantic region of the Barents Sea is characterized by deeper mixing and smaller phytoplankton cells compared to the salinity-stratified and diatom dominated regime of the Arctic Barents Sea (Reigstad et al., 2002). In contrast, the three regions primarily influenced by Atlantic water (i.e. the Norwegian, Greenland and Atlantic Barents Sea) did not show significant differences in the C:N ratios between regions.

While the C:N ratios varied considerably between regions, only the East Siberian and Chukchi Seas had C:N ratios significantly lower than the Redfield ratio, with averages of 6.5 and 6.4, respectively. The primary production in the Chukchi Sea is spatially variable, but regionally the rates of primary production are among the highest recorded for the World Ocean (Grebmeier et al., 2006). The production is fuelled by inflow of nutrient-rich Pacific waters across the Bering Strait, which occurs throughout most of the year (Woodgate et al., 2005). An influence of Pacific waters was also found in the eastern part of the East Siberian Sea during the International Siberian Shelf Study in 2008 (Sanchez-Garcia et al., 2011), from which most of the observations from the Siberian shelves in this study were sourced (ISSS; Table 1). The Pacific influenced waters in the East Siberian Sea had higher rates of primary production and around equal contributions of algal and terrestrial sources to the POC stock (Sanchez-Garcia et al., 2011). It therefore appears that the lower than Redfield C:N ratios in the Chukchi and East Siberian shelves were connected to nutrient-rich Pacific derived waters, which increased the fraction of algal-derived seston, especially compared to the Laptev and Kara Seas.

The C:N ratios in the nearby Laptev (7.9) and Kara (7.5) Seas were high, and the three major Arctic rivers (Yenisei, Lena and Ob) drain into these shelves, with annual discharges around 750 and 1500 km³, respectively (Rachold et al., 2004, and references therein). The rivers carry large amounts of organic C (plant material and eroded soils) to the Arctic Ocean. This terrigenous C flux mediated by river-inflow was found to dominate the POC pool in the Laptev and western region of the East Siberian Sea (Sanchez-Garcia et al., 2011). Coastal erosion of ice-rich deposits is also important to the total C load in the East Siberian and Laptev Seas (Rachold et al., 2004). In the Kara Sea, Hessen et al. (2010) found that over 90% of the C was in dissolved organic form and mostly of terrigenous origin. We hypothesize that this terrestrial-derived C from rivers and coastal erosion contributes to the high C:N ratios observed for the Laptev and Kara shelves in this study. In addition, the terrigenous C was found to be subject to relatively fast degradation and contribute to outgassing of CO₂ from the ocean to the atmosphere (Sanchez-Garcia et al., 2011). This outgassing is expected to increase in the future, because of permafrost thawing and intensification of coastal erosion due to sea-ice loss and sea-level rise (Macdonald et al., 2004), which represents a potential positive feedback on atmospheric CO₂ concentrations.

The C:N ratio for the Arctic Ocean (6.6) was not different from the Redfield ratio. Results from the Arctic Ocean Section in 1994 (AOS; Table 1) showed that the ice-covered Arctic Ocean was about a factor of 10 more productive than previously believed (English, 1961; Wheeler et al., 1996). Both the AOS and Arctic Ocean

Expedition (AOE; Table 1) crossed the predominantly ice-covered Arctic Ocean, and observed non-depleted nutrients and a relatively shallow euphotic layer (Olli et al., 2007; Wheeler et al., 1997). Both studies emphasize that even though the rates of primary production were moderate, the autochthonous production alone was not sufficient to support the relative high abundances of bacteria and mesozooplankton. This suggests that the central Arctic Ocean in part is dependent on supply of dissolved organic material from the more productive shelf-regions and river run-off, and that the high grazing pressure (partly advected from the shelves) contributes to net heterotrophy and to the apparent oligotrophic nature of the Arctic Ocean (Olli et al., 2007).

4.3. Dynamic coupling between C and N

In all but two regions, a systematic shift in the C:N ratio with seston concentrations was found, which means that a constant ratio (e.g. 6.6) between the elements did not hold true, as evidenced by the rejection of the unit slope hypothesis for the SMA regressions. Slopes <1 , meaning that the C:N ratio decreased with increasing seston concentrations, was found for all regions, except the Laptev Sea. This is in support of Tamelander et al. (2013), where using the same SMA method, they found significant departures from a constant C:N ratio in the exported material for several regions in the Eurasian Arctic.

Sterner et al. (2008) found a scale-dependence in the elemental ratios, where a constant ratio (albeit above the Redfield ratios) linked the elements at larger regional scales. However, at smaller regional scales the seston elemental ratios were found to decrease with increasing seston concentrations, as was also found in this study. The increase in nutrient content (i.e. lower C to nutrient ratios) at higher productivity was in the study by Sterner et al. (2008) attributed changing nutrient use efficiency (e.g. Vitousek, 1982). This is an alternative to the constant Redfield model, where other factors (such as light or micronutrients) become limiting when any given nutrient is present in high concentrations. Following Sterner & Elser (2002), autotrophs with high growth ratio to nutrient demand will be favoured under low nutrient availability. However, as the nutrient levels increases, plants with high growth rate to light demand will be favoured, as the increased biomass inevitably will lead to increased self-shading. Therefore, the system appears to be less efficient (measured as the production of a unit C per unit nutrient), because the critical competitive trait has shifted from nutrient utilization efficiency to light utilization efficiency.

We propose an alternative explanation for the decrease in C:N ratios with increasing seston concentrations, namely that the composition of seston changes. High C:N ratios were found at low Chl *a* concentrations, while the C:N ratios was lower and approached the Redfield ratio when the Chl *a* concentrations increased (Fig. 5). Frigstad et al. (2011) applied a regression of POC on Chl *a* and demonstrated that the seston composition (i.e. the fractions of autotrophs, heterotrophs and detritus) has important consequences for the resulting C:N (and even more so the C:P) ratios. In general, the autotrophic material had lower C:N ratios, while the ratios in the non-autotrophic material was higher and above the Redfield ratios. At low Chl *a* the influence of the autotrophic material on the total seston C:N ratio will be small, and other sestonic fractions, such as heterotrophic and detrital (both marine and terrestrial-derived), will have a larger impact on the resulting C:N ratio of seston as a whole, thereby increasing the C:N ratios. While at high Chl *a* concentration the

influence of the autotrophs on the seston C:N ratio is high, resulting in lower C:N ratios. Thus, there can be a systematic decrease in the C:N ratio as the Chl a concentrations increases, which results in non-constant C:N ratio over the range of POC and PON. The only region where the C:N ratio increased with increasing seston concentrations was the Laptev Sea, which is characterized by a strong contribution of terrigenous POC, due to high river loading and coastal erosion (Sanchez-Garcia et al. (2011)).

The non-constant C:N ratio demonstrated in this study has important implications for the modelling of these elements. Most ecosystem models in the northern high latitudes assume a fixed ratio between C and the limiting nutrient (usually N) regardless of the productivity or nutrient supply (Tian et al., 2003; Walsh et al., 2005; Wassmann et al., 2006). Our study corroborates on the recommendation by Sterner et al. (2008), to apply a power function model instead of a linear relationship (i.e. $POC = 6.6 PON$). The mixture of SMA slopes in this study (i.e. Fig. 7) suggests that the exponent in the power function model (b in eq. 2) will be system-dependent. Based on all observations the POC vs. PON relationship was best described by $POC = 7.4 PON^{0.89}$, where the ratio would be $POC:PON = 7.4 PON^{-0.11}$. Thus, a 100-fold increase in the concentration of PON (as was the approximate range in seston concentrations) would give a relative C:N change of $100^{-0.11} = 0.60$, which is equivalent to a 40% decrease in the C:N ratio from the lowest to highest PON concentration in this study.

The extent to which deviations from fixed sestonic C:N ratios reflects physiological status in the autotrophs (i.e. changed nutrient use efficiency) or variable proportions of autotrophs, heterotrophs and detritus in seston, has implications for the parameterization of this process in models. In the former case, C-uptake in autotrophs based on fixed C:N is clearly an oversimplification, but in either case variable elemental ratios will impact the C-transfer efficiency in the food webs, because of the effect of food quality up the trophic ladder (Malzahn et al., 2010; Sterner and Elser, 2002), and as such calls for closer attention.

References

- Anderson, L.G., Tanhua, T., Bjork, G., Hjalmarsson, S., Jones, E.P., Jutterstrom, S., Rudels, B., Swift, J.H., Wahlstrom, I., 2010. Arctic ocean shelf-basin interaction: An active continental shelf CO₂ pump and its impact on the degree of calcium carbonate solubility. *Deep-Sea Res Pt I* 57, 869-879.
- Anderson, T., Hessen, D.O., Mitra, A., Mayor, D.J., Yool, A., In Press. Sensitivity of secondary production and export flux to choice of trophic transfer formulation in marine ecosystem models. *J Marine Syst.*
- Arrigo, K.R., 2005. Marine microorganisms and global nutrient cycles. *Nature* 437, 349-355.
- Arthun, M., Bellerby, R.G.J., Omar, A.M., Schrum, C., 2012. Spatiotemporal variability of air-sea CO₂ fluxes in the Barents Sea, as determined from empirical relationships and modeled hydrography. *J Marine Syst* 98-99, 40-50.

Bates, N.R., Hansell, D.A., Moran, S.B., 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.

Bates, N.R., Mathis, J.T., 2009. The Arctic Ocean marine carbon cycle: evaluation of air-sea CO₂ exchanges, ocean acidification impacts and potential feedbacks. *Biogeosciences* 6, 2433-2459.

Bellerby, R.G.J., Schulz, K.G., Riebesell, U., Neill, C., Nondal, G., Heegaard, E., Johannessen, T., Brown, K.R., 2008. Marine ecosystem community carbon and nutrient uptake stoichiometry under varying ocean acidification during the PeECE III experiment. *Biogeosciences* 5, 1517-1527.

Bellerby, R.G.J., Silyakova, A., Nondal, G., Slagstad, D., Czerny, J., de Lange, T., Ludwig, A., 2012. Marine carbonate system evolution during the EPOCA Arctic pelagic ecosystem experiment in the context of simulated Arctic ocean acidification. *Biogeosciences Discussions* 9, 15541-15565.

Berman-Frank, I., Dubinsky, Z., 1999. Balanced growth in aquatic plants: Myth or reality? Phytoplankton use the imbalance between carbon assimilation and biomass production to their strategic advantage. *Bioscience* 49, 29-37.

Berreville, O.F., Vezina, A. F., Thompson, K. R., Klein, B., 2008. Exploratory data analysis of the interactions among physics, food web structure, and function in two Arctic polynyas. *Can J Fish Aquat Sci* 65, 1036 - 1046.

Cai, W.J., Chen, L.Q., Chen, B.S., Gao, Z.Y., Lee, S.H., Chen, J.F., Pierrot, D., Sullivan, K., Wang, Y.C., Hu, X.P., Huang, W.J., Zhang, Y.H., Xu, S.Q., Murata, A., Grebmeier, J.M., Jones, E.P., Zhang, H.S., 2010. Decrease in the CO₂ Uptake Capacity in an Ice-Free Arctic Ocean Basin. *Science* 329, 556-559.

Carmack, E., Barber, D., Christensen, J., Macdonald, R., Rudels, B., Sakshaug, E., 2006. Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. *Prog Oceanogr* 71, 145-181.

Carmack, E., Wassmann, P., 2006. Food webs and physical-biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. *Prog Oceanogr* 71, 446-477.

Chen, C.T.A., Borges, A.V., 2009. Reconciling opposing views on carbon cycling in the coastal ocean: Continental shelves as sinks and near-shore ecosystems as sources of atmospheric CO₂. *Deep-Sea Res Pt II* 56, 578-590.

Christian, J.R., 2005. Biogeochemical cycling in the oligotrophic ocean: Redfield and non-Redfield models. *Limnol Oceanogr* 50, 646-657.

Cochran, K., Fortier, L., Melling, H., 2007. P. Radisson 18RD19980404 (NOW98, Northwater Polynya) cruise data from the 1998 cruise. CARINA Data Set, <http://cdiac.ornl.gov/ftp/oceans/CARINA/P.Radisson/NOW98/>, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee.

- 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.
- Dobberfuhl, D.R., Elser, J.J., 2000. Elemental stoichiometry of lower food web components in arctic and temperate lakes. *J Plankton Res* 22, 1341-1354.
- Duarte, C. M., Agusti, S., Wassmann, P., Arrieta, J. M., Alcaraz, M., Coello, A., Marba, N., Hendriks, I., Holding, J., Garcia-Zarandona, I., Kritzberg, E., Vaque, D., 2012. Tipping elements in the Arctic marine ecosystem. *AMBIO* 41, 44-55.
- English, T.S., 1961. Some biological observations in the central North Polar Sea. Drift Sta. Alpha 1957-1958. *Arctic Intsitute of North America* 13, 8-80.
- 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.
- Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Prog Oceanogr* 71, 331-361.
- Hessen, D.O., Andersen, T., Brettum, P., Faafeng, B.A., 2003. Phytoplankton contribution to sestonic mass and elemental ratios in lakes: Implications for zooplankton nutrition. *Limnol Oceanogr* 48, 1289-1296.
- Hessen, D.O., Carroll, J., Kjeldstad, B., Korosov, A.A., Pettersson, L.H., Pozdnyakov, D., Sorensen, K., 2010. Input of organic carbon as determinant of nutrient fluxes, light climate and productivity in the Ob and Yenisey estuaries. *Estuar Coast Shelf S* 88, 53-62.
- Hill, V. J., Matrai, P. A., Olson, E., Suttles, S., Steele, M., Codispoti, L. A., Zimmerman, R. C., 2013. Synthesis of integrated primary production in the Arctic Ocean: II. In situ and remotely sensed estimates. *Prog Oceanogr* 110, 107-125.
- Hollander, M., Wolfe, D.A., 1973. *Nonparametric Statistical Methods*. John Wiley & Sons, New York, USA.
- Jakobsson, M., Grantz, A., Kristoffersen, Y., Macnab, R., 2004. Bathymetry and Physiogeography of the Arctic Ocean and its Constituent Seas, in: Stein, R., Macdonald, R.W. (Eds.), *The Organic Carbon Cycle in the Arctic Oceans*. Springer, Berlin, Germany, pp. 1-5.
- Johnson, K., Wallace, D.W.R., Neill, C., Schneider, B., Deming, J., 2007. Polar Sea 32L919930718, NEWP93 cruise data from the 1993 cruises. CARINA Data Set, <http://cdiac.ornl.gov/ftp/oceans/CARINA/PolarSea/NEWP93/>, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee.
- Karl, D.M., Bjorkman, K.M., Dore, J.E., Fujieki, L., Hebel, D.V., Houlihan, T., Letelier, R.M., Tupas, L.M., 2001. Ecological nitrogen-to-phosphorus stoichiometry at station ALOHA. *Deep-Sea Res Pt II* 48, 1529-1566.

- Kivimae, C., Bellerby, R.G.J., Fransson, A., Reigstad, M., Johannessen, T., 2010. A carbon budget for the Barents Sea. *Deep-Sea Res Pt I* 57, 1532-1542.
- Klausmeier, C.A., Litchman, E., Levin, S.A., 2004. Phytoplankton growth and stoichiometry under multiple nutrient limitation. *Limnol Oceanogr* 49, 1463-1470.
- Laws, E.A., Archie, J.W., 1981. Appropriate Use of Regression-Analysis in Marine Biology. *Mar Biol* 65, 13-16.
- Legendre, P., 2011. *Imodel2: Model II Regression*.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier, Amsterdam.
- Loeng, H., 1991. Features of the Physical Oceanographic Conditions of the Barents Sea. *Polar Res* 10, 5-18.
- Macdonald, R.W., Sakshaug, E., Stein, R., 2004. The Arctic Ocean: Modern Status and Recent Climate Change, in: Stein, R., Macdonald, R.W. (Eds.), *The Organic Carbon Cycle in the Arctic Oceans*. Springer, Berlin, Germany, pp. 6-21.
- Malzahn, A.M., Hantzsche, F., Schoo, K.L., Boersma, M., Aberle, N., 2010. Differential effects of nutrient-limited primary production on primary, secondary or tertiary consumers. *Oecologia* 162, 35-48.
- McArdle, B.H., 2003. Lines, models, and errors: Regression in the field. *Limnology and Oceanography* 48, 1363-1366.
- Mei, Z.P., Legendre, L., Tremblay, J.E., Miller, L.A., Gratton, Y., Lovejoy, C., Yager, P.L., Gosselin, M., 2005. Carbon to nitrogen (C : N) stoichiometry of the spring-summer phytoplankton bloom in the North Water Polynya (NOW). *Deep-Sea Res Pt I* 52, 2301-2314.
- Miller, L.A., Yager, P., Fortier, L., Melling, H., 2007. P. Radisson 18RD19990827 (NOW99, Northwater Polynya) cruise data from the 1999 cruises. CARINA Data Set, <http://cdiac.ornl.gov/ftp/oceans/CARINA/P.Radisson/NOW99/>, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee.
- Olli, K., Riser, C.W., Wassmann, P., Ratkova, T., Arashkevich, E., Pasternak, A., 2002. Seasonal variation in vertical flux of biogenic matter in the marginal ice zone and the central Barents Sea. *J Marine Syst* 38, 189-204.
- Olli, K., Wassmann, P., Reigstad, M., Ratkova, T.N., Arashkevich, E., Pasternak, A., Matrai, P.A., Knulst, J., Tranvik, L., Klais, R., Jacobsen, A., 2007. The fate of production in the central Arctic Ocean - Top-down regulation by zooplankton expatriates? *Prog Oceanogr* 72, 84-113.
- Perovich, D.K., Richter-Menge, J.A., 2009. Loss of Sea Ice in the Arctic. *Annu Rev Mar Sci* 1, 417-441.
- Peterson, B.J., Holmes, R.M., McClelland, J.W., Vorosmarty, C.J., Lammers, R.B., Shiklomanov, A.I., Shiklomanov, I.A., Rahmstorf, S., 2002. Increasing river discharge to the Arctic Ocean. *Science* 298, 2171-2173.

R Development Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rachold, V., Eicken, E., Gordeev, V.V., Grigoriev, M.N., Hubberten, H.-W., Lisitzin, A.P., Shevchenko, V.P., Schirrmeister, L., 2004. Modern Terrigenous Organic Carbon Input to the Arctic Ocean, in: Stein, R., Macdonald, R.W. (Eds.), *The Organic Carbon Cycle in the Arctic Oceans*. Springer, Berlin, Germany, pp. 33-54.

Redfield, A.C., 1958. The Biological Control of Chemical Factors in the Environment. *Am Sci* 46, 205-221.

Redfield, A.C., Ketchum, B., Richards, F., 1963. The influence of organisms on the composition of sea-water, in: Hill, M. (Ed.), *The Sea*. Interscience, New York, USA.

Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *P Natl Acad Sci USA* 101, 11001-11006.

Reigstad, M., Wassmann, P., Riser, C.W., Oygarden, S., Rey, F., 2002. Variations in hydrography, nutrients and chlorophyll a in the marginal ice-zone and the central Barents Sea. *J Marine Syst* 38, 9-29.

Rey, F., Noji, T.T., Miller, L.A., 2000. Seasonal phytoplankton development and new production in the central Greenland Sea. *Sarsia* 85, 329-344.

Sakshaug, E., 2004. Primary and Secondary Production in the Arctic Seas, in: Stein, R., Macdonald, R.W. (Eds.), *The Organic Carbon Cycle in the Arctic Oceans*. Springer, Berlin, Germany, pp. 57-81.

Sanchez-Garcia, L., Alling, V., Pugach, S., Vonk, J., van Dongen, B., Humborg, C., Dudarev, O., Semiletov, I., Gustafsson, O., 2011. Inventories and behavior of particulate organic carbon in the Laptev and East Siberian seas. *Global Biogeochem Cy* 25.

Smith, S.D., Muench, R.D., Pease, C.H., 1990. Polynyas and Leads - an Overview of Physical Processes and Environment. *J Geophys Res-Oceans* 95, 9461-9479.

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 University Press, Princeton, New Jersey.

Sterner, R.W., Elser, J.J., Fee, E.J., Guildford, S.J., Chrzanowski, T.H., 1997. The light:nutrient ratio in lakes: The balance of energy and materials affects ecosystem structure and process. *Am Nat* 150, 663-684.

Tamelander, T., Reigstad, M., Olli, K., Slagstad, D., Wassmann, P., 2013. New production regulates export stoichiometry in the ocean. *PLoS ONE* 8.

Thomas, H., Bozec, Y., Elkalay, K., de Baar, H.J.W., 2004. Enhanced open ocean storage of CO₂ from shelf sea pumping. *Science* 304, 1005-1008.

Tian, R.C., Deibel, D., Thompson, R.J., Rivkin, R.B., 2003. Modeling of climate forcing on a cold-ocean ecosystem, Conception Bay, Newfoundland. *Mar Ecol-Prog Ser* 262, 1-17.

Tremblay, J.E., Gratton, Y., Fauchot, J., Price, N.M., 2002. Climatic and oceanic forcing of new, net, and diatom production in the North Water. *Deep-Sea Res Pt II* 49, 4927-4946.

Trimble, S.M., Baskaran, M., 2005. The role of suspended particulate matter in Th-234 scavenging and Th-234-derived export fluxes of POC in the Canada Basin of the Arctic Ocean. *Mar Chem* 96, 1-19.

Vaquer-Sunyer, R., Duarte, C. M., Santiago, R., Wassmann, P., Reigstad, M., 2010. Experimental evaluation of planktonic respiration response to warming in the European Arctic Sector. *Polar Biol* 33, 1661-1671.

Vitousek, P., 1982. Nutrient Cycling and Nutrient Use Efficiency. *Am Nat* 119, 553-572.

Wallace, D.W.R., Deming, J., 2007. Polar Sea 32L919920715, NEWP92 cruise data from the 1992 cruises. CARINA Data Set, <http://cdiac.ornl.gov/ftp/oceans/CARINA/PolarSea/NEWP92/>, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee.

Walsh, J.J., Dieterle, D.A., Maslowski, W., Grebmeier, J.M., Whitley, T.E., Flint, M., Sukhanova, I.N., Bates, N., Cota, G.F., Stockwell, D., Moran, S.B., Hansell, D.A., McRoy, C.P., 2005. A numerical model of seasonal primary production within the Chukchi/Beaufort Seas. *Deep-Sea Res Pt II* 52, 3541-3576.

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

Wheeler, P.A., Gosselin, M., Sherr, E., Thibault, D., Kirchman, D.L., Benner, R., Whitley, T.E., 1996. Active cycling of organic carbon in the central Arctic Ocean. *Nature* 380, 697-699.

Wheeler, P.A., Watkins, J.M., Hansing, R.L., 1997. Nutrients, organic carbon and organic nitrogen in the upper water column of the Arctic Ocean: implications for the sources of dissolved organic carbon. *Deep-Sea Res Pt II* 44, 1571-+.

Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005. A year in the physical oceanography of the Chukchi Sea: Moored measurements from autumn 1990-1991. *Deep-Sea Res Pt II* 52, 3116-3149.

Acknowledgements

We would like to express our gratitude to all the people who have sampled and analysed the data, under frequently very challenging conditions. Most of the datasets were made available by the investigator directly, and we thank Kalle Olli (AOE and ALV), Marit Reigstad (ALV), Patricia Wheeler (AOS), Fransisco Rey (ESOP) and Örjan Gustafsson (ISSS) for contributing data. The SBI data were retrieved from NCAR/EOL (<http://data.eol.ucar.edu>) under sponsorship of the National Science

Foundation. The data from the polynya studies were retrieved from the CARINA database (<http://cdiac.ornl.gov/ftp/oceans/CARINA/>), and have the following attributions: NEW 1992 (Wallace and Deming, 2007), NEW 1993 (Johnson et al., 2007), NOW 1998 (Cochran et al., 2007) and NOW 1999 (Miller et al., 2007). This research was supported by EU FP7, through projects MEECE (212085), EURO-BASIN (264933) and GreenSeas (265294). The manuscript profited from comments by Raymond Sambrotto and Tobias Tamelander, who were opponents during HF's PhD defence (where an earlier version of this work was included). We also wish to thank one anonymous reviewer. This is publication number A422 from the Bjerknes Centre for Climate Research.

Tables

Table 1. Overview of research programs included in study.

Program	Location	N	Reference
ALV	Atlantic and Arctic Barents Sea	142	(Olli et al., 2002)
AOE	Transect Barents Sea to North Pole	216	(Olli et al., 2007)
AOS	Transect Chukchi Sea to North Pole	140	(Wheeler et al., 1997)
AWS	Transect into Canadian Basin	16	(Trimble and Baskaran, 2005)
ESOP	Norwegian and Greenland Seas	532	(Rey et al., 2000)
ISSS	Eurasian Arctic shelves	233	(Sanchez-Garcia et al., 2011)
NEW	Northeast Water Polynya	1302	(Daly et al., 1999)
NOW	North Water Polynya	569	(Tremblay et al., 2002)
SBI	Chukchi and Beaufort Seas	237	(Bates et al., 2005)
Yenisei	Kara Sea	9	(Hessen et al., 2010)

Table 2. Overview of regions.

Acronym	Region	N
All	All regions	3672
NOW	North Water Polynya	1302
NEW	Northeast Water Polynya	569
NS	Norwegian Sea	157
GS	Greenland Sea	294
BAt	Atlantic Barents Sea	139
BAr	Arctic Barents Sea	119
KS	Kara Sea	31
LS	Laptev Sea	77
ESS	East Siberian Sea	118
CSS	Chukchi Sea and slope	611
AO	Arctic Ocean	255

Table 3. C:N ratio with 95% CI (calculated as anti-log of intercept in SMA regressions in Fig. 6). For all regions, except the BAt and ESS, the C:N ratio is given for the reference concentration of 1 $\mu\text{mol N L}^{-1}$ (due to the non-constant relationship between POC and PON).

	CI 2.5%	C:N	CI 97.5%
Redfield	-	6.6	-
Sterner	-	8.3	-
All obs	7.32	7.38	7.45
NOW	8.59	8.71	8.82
NEW	7.54	8.03	8.57
NS	6.94	6.99	7.04
GS	6.81	6.95	7.10
BAt	6.73	6.74	6.75
BAr	7.81	7.94	8.07
KS	7.00	7.46	7.89
LS	7.73	7.86	7.98
ESS	6.45	6.47	6.48
CSS	6.39	6.44	6.50
AO	6.43	6.59	6.77

Figures

Figure 1. Map of the Arctic Ocean with adjacent marginal shelf seas. The different research programs are shown with colours and symbols (see Table 1), and the regions are encircled and labelled with bold and underlined acronym (see Table 2).

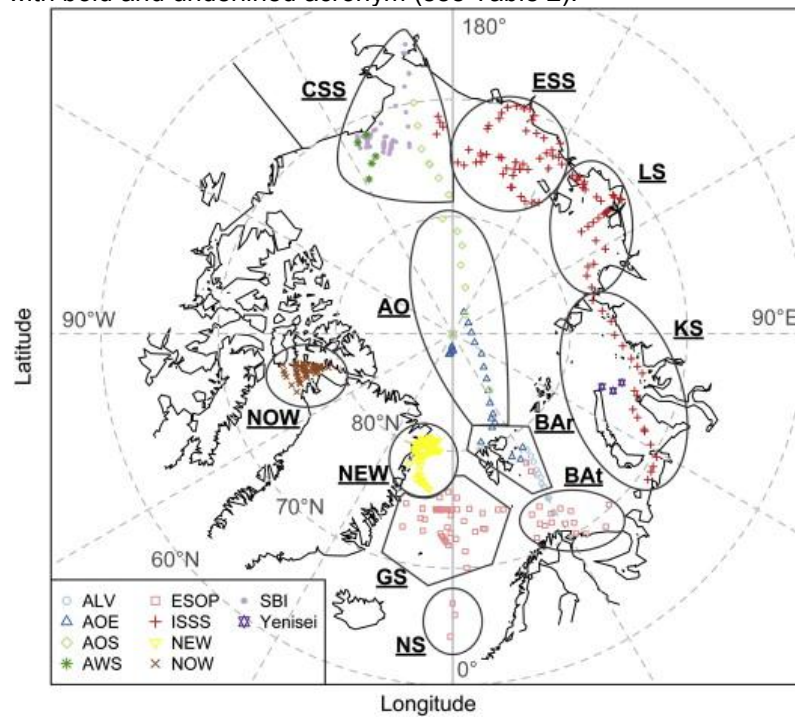


Figure 2. Panel of the distribution of observations with latitude, depth, month and year.

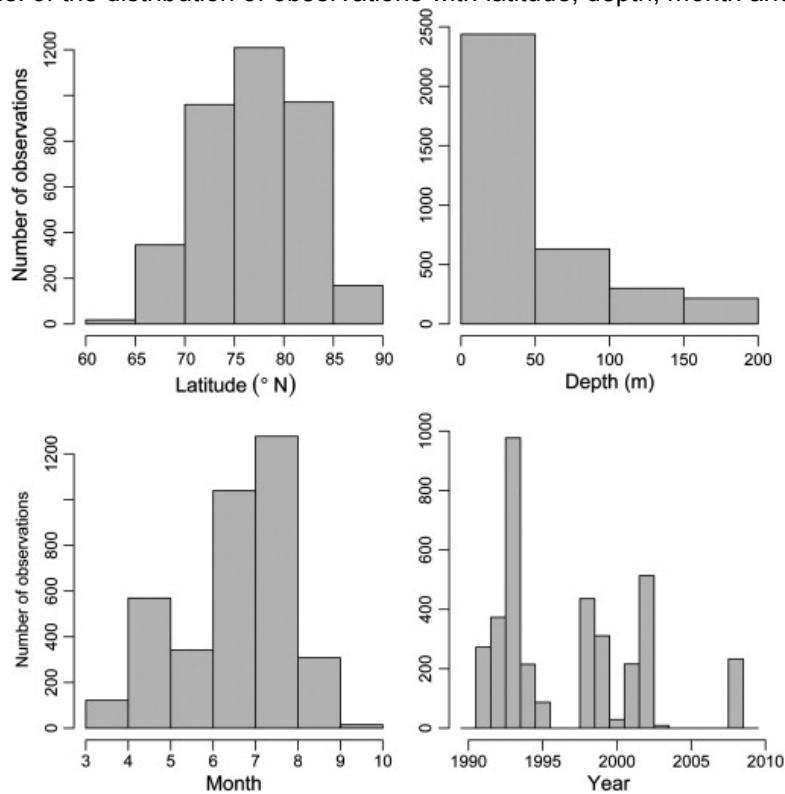


Figure 3. Box-and-whisker plot showing the concentrations of POC and PON and the C:N ratio for the different regions. The dashed and dotted red lines are the Redfield (6.6) and Sterner (8.3) C:N ratios, respectively.

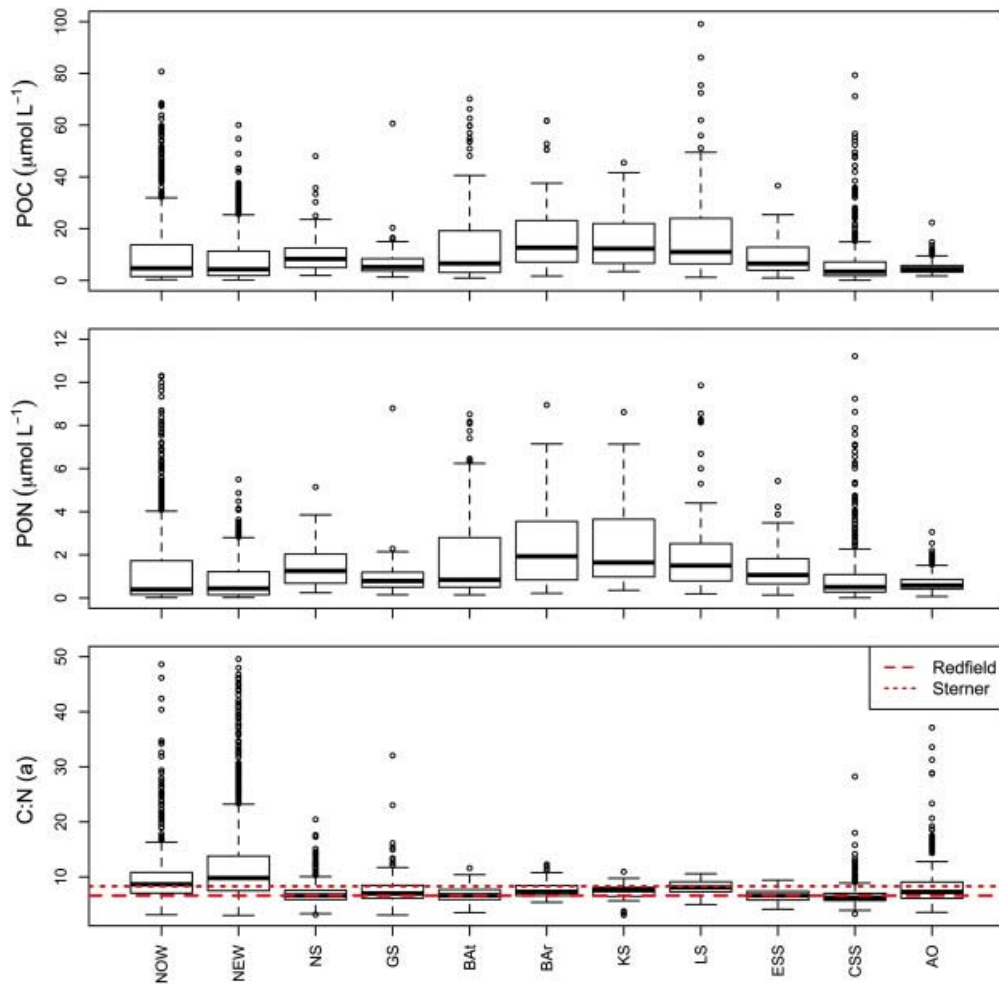


Figure 4. Panel showing the monthly variation in the C:N ratio across regions, the observations are colour coded according to year (see legend). Note the range on the y-axis, which is varied to emphasize the monthly variation within the regions.

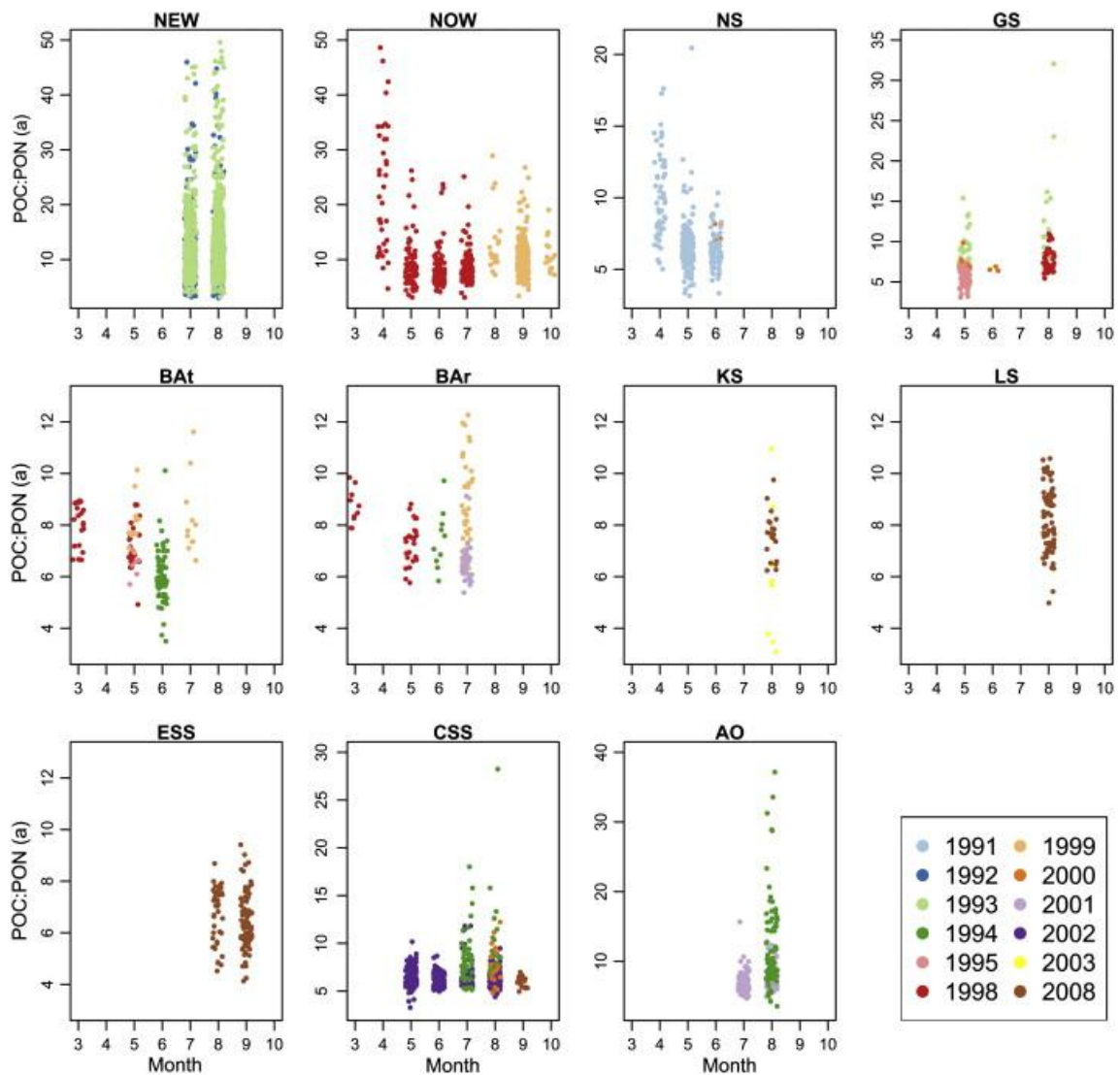


Figure 5. Plot of log (C:N) against log (Chl a) concentration with a significant log-transformed linear model (solid red line), 95% CI (dash-dotted red line) and prediction intervals (dotted dark red line).

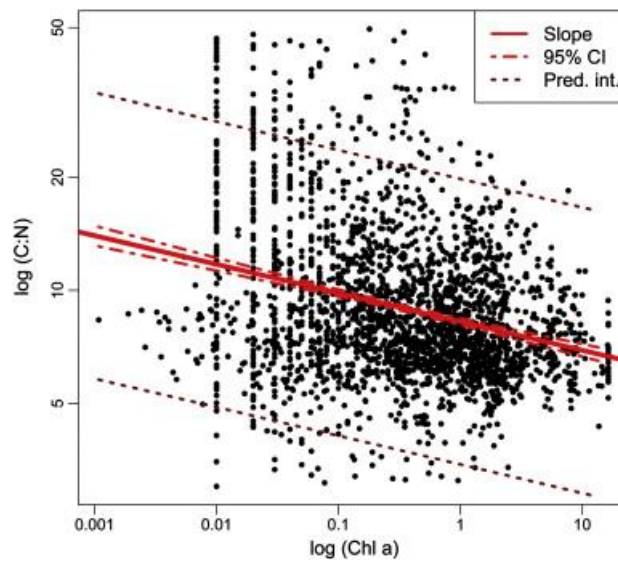


Figure 6. SMA regression of log (POC) against log (PON) concentrations for all observations combined and individually for the 11 regions, also shown is the Redfield ratio (dashed black line), SMA slope (solid red line) and 95% CI (dash-dotted red line).

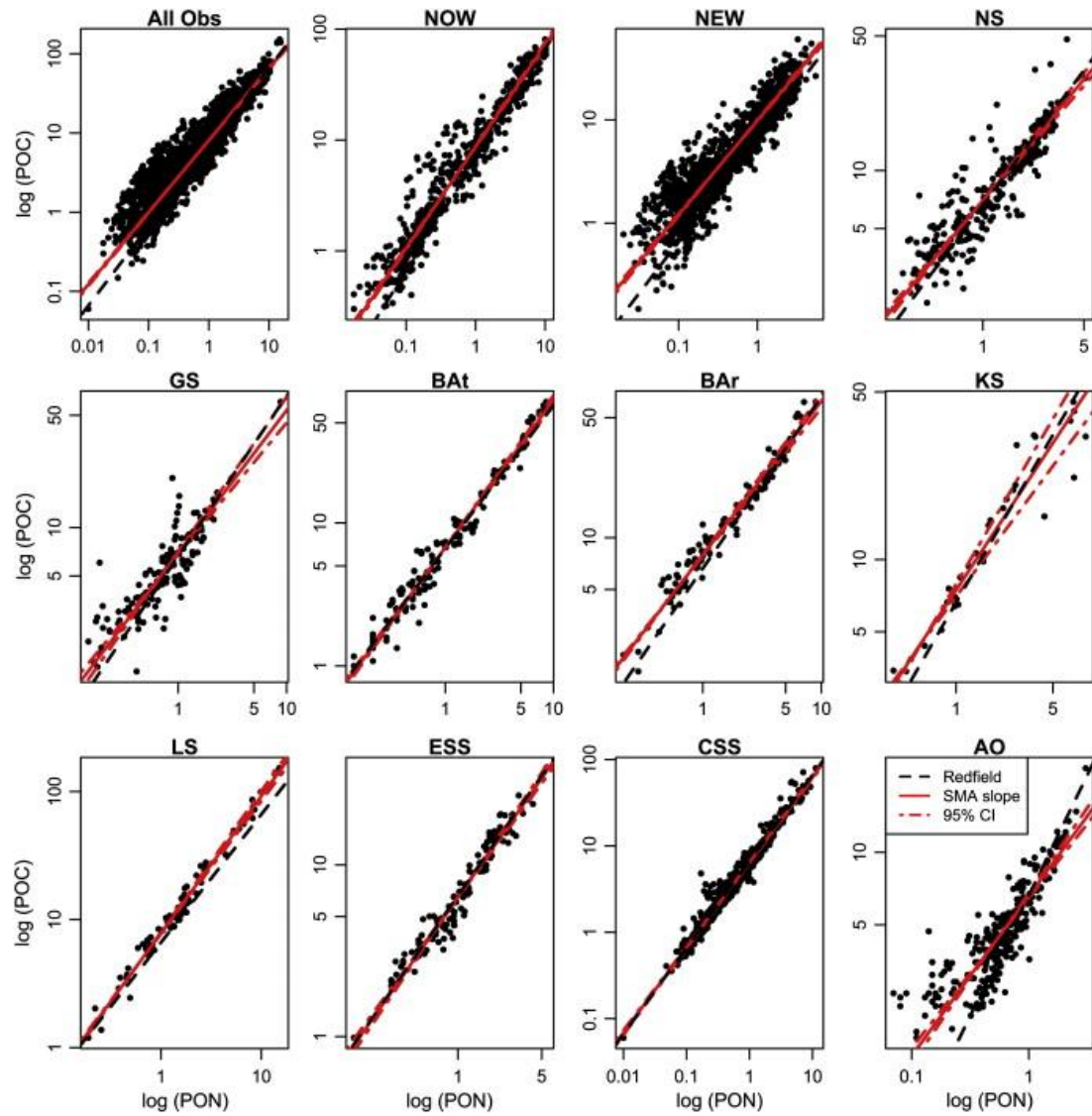


Figure 7. Slopes from SMA regression (Fig. 6) with 95% CI. All regions had slopes significantly different from 1, except the Atlantic Barents (BA_t) and East Siberian Seas (ESS).

