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

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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 $POC = 7.4\ PON^{0.89}$.

1. Introduction

The Arctic Ocean make up around 3% of the total area of the world oceans, with over 50% of the total area comprising relatively shallow continental shelves that encompass the Artic 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 disproportionally important in the global carbon (C) cycle with up to 14% of the global CO_2 uptake (Bates and Mathis, 2009). Most temperate and high-latitude shelves act as net sinks of atmospheric CO_2 (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 CO_2 sinks (Vaquer-Sunyer et al., 2010). Whether the oceanic CO_2 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).

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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., 2013). 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 CO_2 and C-sequestration (assuming higher C:N in the material exported below the winter mixed layer), and thus increase the drawdown of atmospheric CO_2 (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 corresponds 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 pCO_2 (Bellerby et al., 2008). Autotrophs generally do 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 lead 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 emphasised (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 programmes (see overview in Table 1). Only observations shallower than 200 m in 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 (BAt), Arctic Barents Sea (BAr), 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 μmol 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.

Table 1
Overview of research programmes included in study.

Programme	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)