Faculty of Science and Technology

Vertical nitrate fluxes in the Arctic Ocean

—

Achim Randelhoff

A dissertation for the degree of Philosophiae Doctor – December 2016

Cover photo by Birgit Nesheim

Vertical Nitrate Fluxes in the Arctic Ocean

Achim Randelhoff

December 2016, Tromsø, Norway

SUPERVISION

DR. ARILD SUNDFJORD
Norwegian Polar Institute

PROF. MARIT REIGSTAD
Department of Arctic and Marine Biology, University of Tromsø

PROF. ILKER FER
Geophysical Institute, University of Bergen, and
Bjerknes Centre for Climate Research

PROF. ODD ERIK GARCIA
Department of Physics and Technology, University of Tromsø

Ipsa quoque adsiduo labuntur tempora motu,
non secus ac flumen. Neque enim consistere flumen
nec levis hora potest, sed ut unda inpellitur unda
urgeturque eadem veniens urgetque priorem,
tempora sic fugiunt pariter pariterque sequuntur
et nova semper; nam quod fuit ante, relictum est,
fitque, quod haud fuerat, momentaque cuncta novantur.

—P. OVIDII NASONIS Metamorphoseon Liber XV

SUMMARY

Upward mixing of remineralized nutrients is essential for photosynthesis in the upper ocean. Weak vertical mixing, which restricts nutrient supply, and sea ice, which leads to low light levels, conspire to severely inhibit marine primary productivity in the Arctic Ocean. However, little has been known about their relative contributions. No large-scale quantitative estimates of the vertical nutrient supply had previously been presented, which has impeded an understanding of its role in shaping the ecology and carbon cycle of the Arctic Ocean.

In order to estimate the vertical flux of nitrate into the surface layer in contrasting hydrographic and dynamic regimes, profiles of turbulent microstructure and nitrate concentrations were measured as part of a number of cruises and ice camps in the area extending from eastern Fram Strait into the Nansen Basin. These have been supplemented with obervations of the seasonal nutrient cycle at a mooring in the same area, and a reanalysis of available data on nitrate concentrations and turbulent mixing in other parts of the central Arctic Ocean.

Hydrography was found to be the biggest driver of variability in nitrate fluxes. Strong stratification, wherever encountered, restricted nitrate supply, often in concert with concurrently weak turbulent mixing, both in the seasonal nitracline (0.3–0.7 mmol N m^{-2} d) and the deep basin (0.01–0.2 mmol N m^{-2} d). Thus deep winter mixing supplies the bulk of the nitrate pool on the relatively productive shelves (e.g. 2.5 mmol N m^{-2} d in the inflow of Atlantic Water during winter), but in the strongly stratified Canadian Basin, fluxes are low year-round (on the order of 0.01 mmol N m^{-2} d) and place a tight limit on new production. Only the weakly stratified Atlantic derived water in the Nansen Basin close to Fram Strait seems to have a certain potential to support future increases in new production under a seasonal ice cover.

LIST OF PAPERS

I Randelhoff, A. and J. D. Guthrie (2016), Regional patterns in current and future export production in the central Arctic Ocean quantified from nitrate fluxes, *Geophysical Research Letters*, *43*, 8600–8608, doi:10.1002/2016gl070252.

II Randelhoff, A., A. Sundfjord, and M. Reigstad (2015), Seasonal variability and fluxes of nitrate in the surface waters over the Arctic shelf slope, *Geophysical Research Letters*, *42*, 3442–3449, doi:10.1002/2015gl063655.

III Randelhoff, A., I. Fer, and A. Sundfjord, Turbulent upper-ocean mixing affected by meltwater layers during Arctic summer, *revised manuscript submitted to Journal of Physical Oceanography*.

IV Randelhoff, A., I. Fer, A. Sundfjord, J.-É. Tremblay, and M. Reigstad (2016), Vertical fluxes of nitrate in the seasonal nitracline of the Atlantic sector of the Arctic Ocean, *Journal of Geophysical Research: Oceans*, *121*, 5282–5295, doi:10.1002/2016JC011779.

CONTENTS

1

Introduction and Background

1.1 Vertical fluxes and primary production

The growth of marine phytoplankton is confined to the uppermost layer of the ocean called the euphotic zone. Organic matter has a tendency to sink and thus exports essential nutrients to depth. This flux is called export production. In this way, the world ocean is partitioned into a photic, nutrient poor surface layer and the aphotic, nutrient rich deeper layers. Without any further exchange processes between these two pools, nutrients would be quickly buried in the sea floor and not support photosynthesis. An upward flux of nutrients is therefore crucial for maintaining primary production in the ocean (Margalef, 1978). The new production is limited by the net community production, i.e. the net increase in primary producer's biomass that can then be exported (see text box below).

Especially in the oligotrophic ocean, the vertical supply of inorganic nutrients constrains new production. Lewis et al. (1986) showed that the upward flux of nitrate matched its uptake by primary producers. Christian et al. (1997) found that the slower remineralization of carbon with depth matched the stoichiometry of carbon, nitrogen and phosphorus in the upward fluxes. The export of particulate matter thereby helps removing carbon from the surface layer and thus the atmosphere. Upward mixing of deeper water and its nutrients provides the lever on this process dubbed the biological pump, which represents the oceanic buffering capacity of atmospheric levels of carbon dioxide. The present and future of the nutrient supply to the photic zone in the world ocean has also received considerable attention regarding the future of marine ecosystems, since changes in the nutrient loading will have the ability to drive marked changes in the marine community structure (e.g. Li et al., 2009; Peter and Sommer, 2013; Sommer et al., 2016).

The upward flux can be both advective (like coastal upwelling or Ekman

The many measures of primary production

Net primary production (NPP) is all assimilation of inorganic nutrients into organic matter, adjusted only for autotrophic respiration, that is, respiration by the primary producers themselves. The production that is based on allochthonous nutrients (i.e., nutrients not formed locally; in practice taken to be nitrate) is termed "new production" (NP), while the remainder is "regenerated production", generally taken to result from uptake of ammonium (Dugdale and Goering, 1967). In this framework, only new production can contribute to vertical export of nutrients when the budget is balanced over several years. The net community production (NCP) is the primary production adjusted for all respiration, both by autotrophs and heterotrophs. NCP is then the upper limit of export production (Eppley and Peterson, 1979).

pumping) or diffusive (like turbulent mixing). In the absence of conditions consistently favourable for upwelling (such as coastal upwelling zones, subpolar gyres, and cyclonic eddies), turbulent (diapycnal) diffusion accounts for most of this upward transport. Importantly, strong stratification reduces the vertical mixing coefficient (Section 2.3), which in the Arctic Ocean (AO) restricts the nitrate flux into the photic zone.

1.2 Hydrographic setting

The Arctic Ocean's hydrography is dominated by the input of three distinct water masses: Warm, Atlantic Water through Fram Strait and the Barents Sea, relatively fresh Pacific Water through Bering Strait and river freshwater runoff, mainly through the Siberian and (to a smaller extent) the Canadian shelf (e.g. Dickson et al., 2007; Woodgate, 2013). The relatively weakly stratified Atlantic-derived water spreads along the eastern margins of the deep basin, while strongly stratified Pacific derived water masses spread into the western parts of the deep basin (e.g. Rudels et al., 2004, 2015). Thus deep winter mixed layers prevail in the East, and strong perennial stratification in the West (Fig. 1.1). On top of that comes the seasonal progression of sea ice melt derived freshwater input into the upper ocean, which is presented in Section 1.3. The seasonal pycnocline forms only in the summer months and does not significantly influence the overall shape of the nitrate gradient across the deeper, perennial pycnocline that is evident for the Nansen and Amundsen Basin profiles in Fig. 1.1.

As we will see in Section 3, the distinction between seasonal and perennial stratification gives rise to two distinct types of nitraclines, seasonal and perennial. A discussion of the implications of the hydrography for vertical and lateral gradients of nutrient concentrations can be found in Section 3.

1.3 The seasonal cycle

Due to the seasonal cycle of sunlight, photosynthesis at high latitudes is concentrated around a few summer months. Accordingly, concentrations of both phytoplankton and nutrients in the upper ocean vary mainly with seasons. In the spring, the nutrient pool is rapidly depleted, often aided by an explosive spring bloom. Throughout summer, nutrient concentrations remain low and the ecosystem switches to a recycling state, relying on regenerated nutrients (e.g., ammonium, NH_4^+). In fall, primary production ceases again, and the mixed layer nutrient pool is replenished to the concentrations it had at the end of the previous winter.

The abundance of nutrients in this pool is an important factor in spring blooms, but exactly what is responsible for the timing of the spring bloom, remains controversial (see e.g. Behrenfeld and Boss, 2014). A recurring theme are however intensities and depths of mixing, often related to the restratification of the water column (e.g. Sverdrup, 1953; Huisman et al., 1999). In the Arctic Ocean, phytoplankton blooms are often associated with retreat of the ice cover (Perrette et al., 2011). As ice melt implies both an increase in the amount of photosynthetically available radiation and an increasingly stable stratification, it is not straightforward to distinguish between light or mixing as triggering mechanisms in the field.

1.4 Approach and objectives

Dissolved inorganic nitrogen is, in most instances, the limiting nutrient in the Arctic Ocean (Tremblay and Gagnon, 2009, and references therein), so nitrogen is usually used as the base "currency" of biogeochemical models of the Arctic Ocean (see e.g. POPOVA et al., 2012; SLAGSTAD et al., 2015). In addition, availability of high-quality optical nitrate sensors (JOHNSON and COLETTI, 2002, and subsequent publications by this group) makes it possible to autonomously record high-resolution nitrate concentration data without the need for wet chemistry. This allowed us to measure nitrate concentration and gradients at a much greater vertical, lateral and temporal resolution than could be afforded by traditional bottle samples. The quantification of vertical nitrate fluxes can serve as a means to study the effects of turbulence and hydrography on primary production because organic matter is often found to follow a fixed stoichiometry, the so-called "Redfield ratio" (see the seminal paper by REDFIELD et al., 1963). While the importance of the vertical nitrate flux for Arctic marine ecology and nutrient cycling is frequently stressed, it has largely remained unquantified so far (TREMBLAY et al., 2015, but see BOURGAULT et al. (2011) for an exception).

The main objective of this dissertation is precisely to fill that gap, that is to quantify the vertical turbulent nitrate supply to the photic zone, both on a seasonally stratified inflow shelf (the Barents Sea shelf slope area) and in the perennially stratified deep Arctic Ocean. The hydrography and mixing in the seasonally stratified upper Arctic Ocean will be of particular importance to understand the physical environment in which marine primary producers grow. Along the way, I describe both large-scale patterns and the seasonal distribution of NO_3^- concentrations around the Barents Sea shelf slope, and place these in a pan-Arctic context.

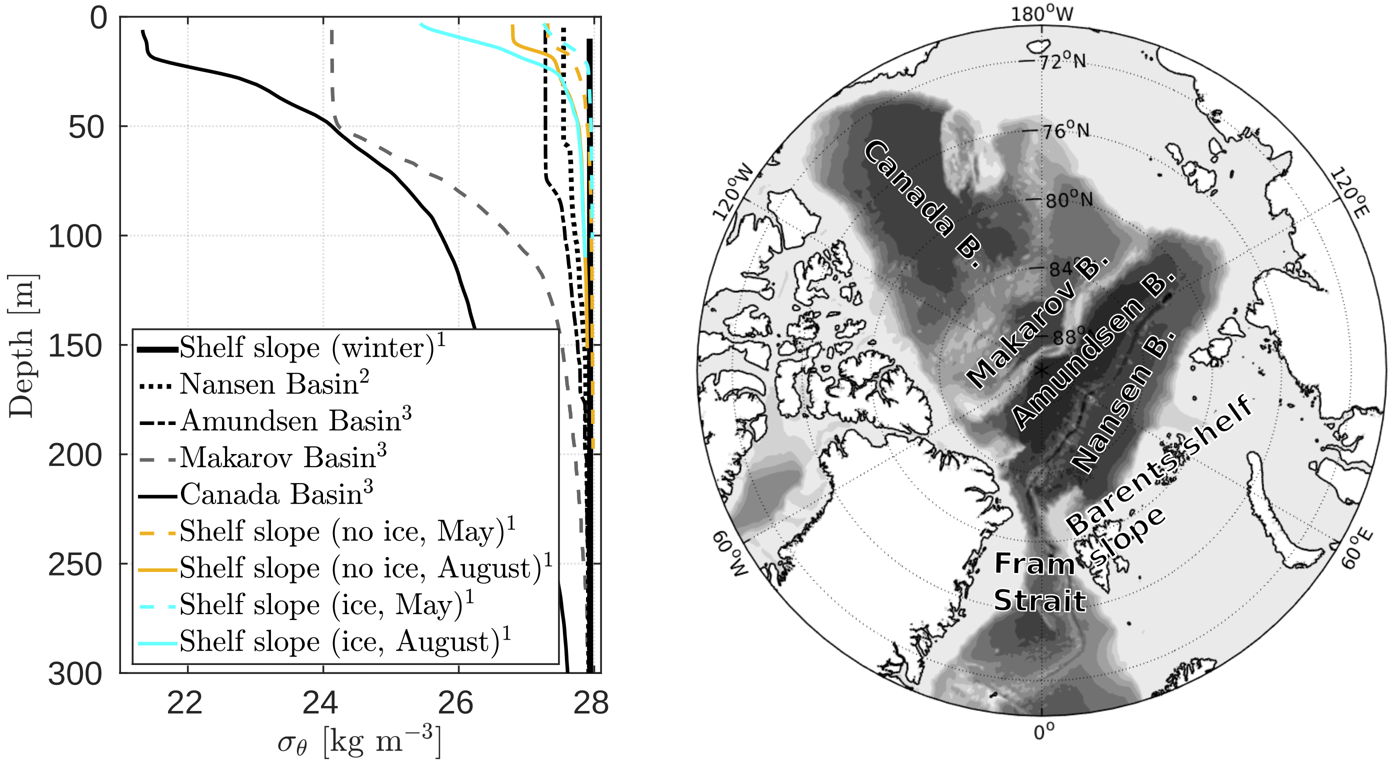

Figure 1.1: Representative profiles of potential density (σ_θ) across the Arctic Ocean in different seasons. All black and grey lines represent winter profiles; orange and cyan signify the seasonal evolution in the shelf break area. [1]Fram Strait area (Carbonbridge), [2]N-ICE2015 (`https://data.npolar.no/dataset/92262a9c-e6a4-59b5-9929-81c0429d7de6`), [3]`https://arcticdata.io/catalog/#view/doi:10.18739/A2HK6Z`

2

METHODS

2.1 THE WHAT AND HOW OF TURBULENT NITRATE FLUXES

To my knowledge, the direct measurement of turbulent nitrate fluxes has so far not been attempted because sampling frequency and instrument accuracy of currently available sensors are not sufficient to measure small-scale turbulent fluctuations in nitrate concentrations. A convenient method for ship-based campaigns is the combination of vertical profiles of velocity microstructure and nitrate concentrations ($\mathcal{N}$). This method relies heavily on parameterizing the vertical eddy diffusivity K_ρ (the proportionality constant between flux and mean-field gradient of a quantity, units of $\mathrm{m}^2\ \mathrm{s}^{-1}$) from the dissipation of turbulent kinetic energy ϵ ($\mathrm{W\ kg}^{-1} \equiv \mathrm{m}^2\ \mathrm{s}^{-3}$) and mean-field stratification, using an empiric formula (see Section 2.3). Then, combining K_ρ with the vertical gradient of nitrate concentration ($\mu\mathrm{M\ m}^{-1}$), the vertical turbulent nitrate flux is

$$\mathrm{F}_{\mathcal{N}} = K_\rho \frac{\partial \mathcal{N}}{\partial z} \tag{2.1}$$

in units of mmol N m^{-2} d. As mentioned previously, we can convert between carbon and nitrogen units by assuming a constant fixed ratio between the constituting elements of organic matter. Although the Redfield ratio (see Section 1.4) seems to depend on type of the organic matter and environmental conditions (e.g. STERNER et al., 2008; TAMELANDER et al., 2013; FRIGSTAD et al., 2014), such disputes concern relatively small corrections to the C:N ratios published in the literature, certainly smaller than the uncertainties in the estimation of turbulent fluxes. Giving the nitrate flux in units of g C $\mathrm{m}^{-2}\ \mathrm{yr}^{-1}$ (1 g C $\mathrm{m}^{-2}\ \mathrm{yr}^{-1} \approx 0.035$ mmol N m^{-2} d), our studies **I**, **II** and **IV** put the vertical nitrate flux into the context of other estimates of primary production.

2.2 FIELD WORK AND DATA SETS

Data for this thesis were collected during a total of five different campaigns associated with three different projects: Carbonbridge, N-ICE2015 and

TransSIZ (Table 2.1 and Fig. 2.1). All of them had a strong component focused on various aspects of the biogeochemical regime of physical-biological interactions in the Atlantic Arctic.

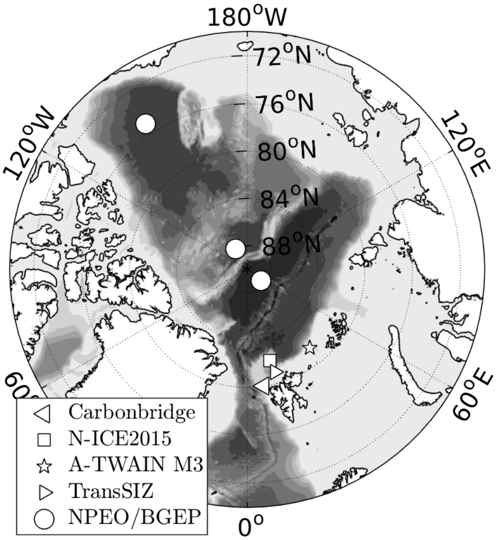

Figure 2.1: Overview map indicating areas where individual projects where conducted. Details about seasonal and regional coverage of campaigns other than NPEO/BGEP (North Pole Environmental Observatory, Beaufort Gyre Exploration Project) are presented in Table 2.1. The latter indicate only a reanalysis of existing data collected by projects the author is not affiliated with.

For the Carbonbridge project, data were collected on three different cruises in January, May and August 2014, covering the Marginal Ice Zone in Fram Strait and the shelf slope area north of Svalbard with a combination of cross-shelf slope transects and 24-hour process stations. The field measurements conducted for the N-ICE2015 project were distributed over successive ice camps in the period January till June 2015 in the pack ice north of Svalbard. From the TransSIZ campaign, only a single transect of NO_3^- concentration profiles was used to supplement the discussion of large-scale patterns in NO_3^- distribution (**IV**).

2.3 TURBULENT MICROSTRUCTURE

Microstructure shear, conductivity and temperature were measured using a loosely tethered microstructure profiler MSS-90L (IWS Wassermesstechnik, Germany) with two airfoil shear probes, falling freely at a constant rate between 0.55 and 0.85 m s^{-1}. Using the small-scale shear, one can infer

Table 2.1: Data sets collected for this thesis.

Campaign/Data set	Season[1]	Area[2]	Ice	Vessel
Carbonbridge (2014)				R/V Helmer Hanssen
January	Winter	Shelf, shelf slope	Open water	
May	Spring	Shelf, shelf slope	MIZ[3,4]	
August	Summer	Shelf, shelf slope	MIZ[3,4]	
N-ICE (2015)				R/V Lance
January – March	Winter	Basin	Pack ice	
April – mid-May	Winter	Plateau	Pack ice	
mid-May – June	Spring	Plateau & shelf slope	Pack ice&MIZ[3]	
TransSIZ	Winter, spring	Shelf, shelf slope, plateau	Pack ice	R/V Polarstern
A-TWAIN M3[5]	1 entire year	shelf slope (800 m isobath)		mooring

[1] Winter: No ice melt, spring: ice melt started within the last weeks, summer: ice melt started several months ago, severe nutrient depletion in the upper layers

[2] Nansen Basin, Yermak Plateau, shelf and shelf slope of the northern Barents Sea

[3] Marginal Ice Zone.

[4] also included open water stations

[5] selected mooring on the Barents sea shelf slope

the vertical eddy diffusivity, K_ρ, used in calculation of nutrient fluxes. The microstructure sampling was usually made in sets of at least three consecutive repeat profiles at any given station.

MSS data were processed following Fer (2006) for all data sets included in **I-IV**. Briefly, assuming local small-scale isotropy (Yamazaki and Osborn, 1990), dissipation of turbulent kinetic energy was estimated from the measured microscale shear as

$$\epsilon = 7.5\nu\langle(\partial_z u')^2\rangle, \tag{2.2}$$

where ν is the molecular viscosity of sea water and $\partial_z u'$ the turbulent shear. Combining turbulent microstructure with stratification, the eddy diffusivity of mass is estimated as

$$K_\rho = \Gamma\frac{\epsilon}{N^2} \tag{2.3}$$

following Osborn (1980), where $N^2 = -\frac{g}{\rho}\frac{\partial\rho}{\partial z}$ defines the buoyancy frequency N using gravitational acceleration g and water density ρ. The magnitude of the factor Γ and its dependence on other parameters is the subject of current research (e.g. Salehipour et al., 2016), but the work presented in this thesis employs the canonical value of 0.2 put forward by Osborn (1980), which represents the upper bound of an average over long spatial and temporal scales. Drawing on the Reynolds analogy for fully turbulent flows, it is then generally assumed that this eddy diffusivity is the same for all scalar tracers such as mass, heat, and dissolved salts like nitrate.

2.4 Sensor-based nitrate measurements

Vertical profile of nitrate concentrations ($\mathcal{N}$) were measured using the ISUS V3 (In-Situ Ultraviolet Spectrophotometer; Satlantic). The ISUS was used in various configurations based on campaign and setting. When deployed from one of the large vessels, it was mounted on the shipboard SBE911+ (Sea-Bird Electronics, USA) CTD (conductivity-temperature-depth) rosette system logging the analog output voltage of the unpumped ISUS. During the N-ICE2015 drift, the ISUS was deployed from a tent through a hole in the ice. Again, it was used in an unpumped configuration, mounted on a frame together with an SBE19+ system that was programmed to sample the analog output voltage of the ISUS. On the mooring array described in **II**, the ISUS was mounted 1 m below an SBE16plusV2 instrument (SeaCAT). The simultaneous acquisition of temperature and salinity data is crucial to all deployments in order to subtract seawater absorption from the absorption spectra following SAKAMOTO et al. (2009). A detailed account of ISUS and CTD data processing and quality screening is given in the Appendix of **IV**.

3

Findings

3.1 Patterns across the Arctic Ocean

In the Atlantic sector, a striking pattern in the lateral distribution of nitrate is the contrast between the shelves and the deeper basins. While the central Arctic Ocean is perennially stratified and thus has a perennial nitracline (**I**, **IV**), the upper shelf slope and the Barents shelf themselves are seasonally stratified (**IV**), with no or very weak stratification during the winter (Loeng, 1991). In fact, replenishment and complete vertical homogenization of the surface nitrate pool in the Atlantic inflow already happens by early winter around November/December (**II**). This means that in the shelf slope area around Svalbard, the annual NCP is supported mostly by the vertical homogenization during fall and winter, likely aided by increased wind mixing in fall and thermal convection in the weakly temperature-stratified Atlantic Water (**II**).

Across the central Arctic Ocean, there are large-scale patterns in hydrography and turbulent mixing. Going from the Yermak Plateau via the Nansen, Amundsen and Makarov to the Canada Basin, stratification strengthens and dissipation decreases. Accordingly, also $F_{\mathcal{N}}$ decreases from the eastern ($F_{\mathcal{N}}$ equivalent to as much as 7.0 g C m^{-2} yr^{-1} close to the Yermak Plateau) to the western ($\approx$ 0.5 g C m^{-2} yr^{-1}, an order of magnitude less than what Lewis et al. (1986) inferred for the oligotrophic North Atlantic) regions of the central Arctic Ocean. We calculated the Redfield-equivalent of the area-weighted average turbulent vertical nitrate supply to be in the range 1–2 g C m^{-2} yr^{-1} (**I**). Factoring in a range of other processes like horizontal advection, winter convection, and nitrogen fixation, we estimate the overall new production in the central Arctic Ocean that is exported across the nitracline to be in the range 1.5–3.0 g C m^{-2} yr^{-1}. The magnitude of these export fluxes is still extremely small relative to other areas of the world ocean (e.g. Honjo et al., 2008). Our estimates suggest that $F_{\mathcal{N}}$ is more important than previous comparisons of vertical (diffusive) with the lateral (advective) fluxes had suggested for the central Arctic Ocean

(ANDERSON et al., 2003). More importantly, our methodology makes it possible to not only estimate the present-day $\mathsf{F}_{\mathcal{N}}$, but also the maximum fluxes that a given stratification and mixing scenario could support, all other factors permitting. These maximum fluxes correspond to a scenario where enhanced light input, seasonal (summertime) mixing and the export efficiency act to make all nitrate in the Polar Mixed Layer accessible to export production. This provides a quantitative handle on the issue of nutrient vs. light limitation. Using our formalism, we concluded that the Amundsen and Canadian Basins are nutrient-limited, and only close to the Atlantic inflow around the Yermak Plateau and the shelf break is light currently a limiting factor for new production.

3.2 SEASONAL STRATIFICATION AND UPPER-OCEAN MIXING

Summertime upper-ocean hydrography in the seasonal ice zone is dominated by the formation of freshwater layers deriving from sea ice melt (**III**). In general, directly wind driven dissipation is restricted to the uppermost parts of such meltwater layers, below which dissipation scales with buoyancy frequency in a manner consistent with the dissipation of narrow-band internal waves, possibly near-inertial. Thus, effectively, the nitracline is decoupled from the enhanced mixing of the surface layer throughout later parts of the melt season. Based on hydrographic considerations, we expect these mechanisms to extend to other areas of the Arctic that are only seasonally stratified.

Across the data sets considered in this thesis, it was found that upper ocean nitrate drawdown was strongly linked to the onset of stratification (**IV**, Fig. 5). This was demonstrated clearly as we encountered a pre-bloom situation in the core of the inflowing Atlantic Water in Fram Strait in May, while freshwater-induced stratification further west was directly coupled to waters where nitrate had been consumed. Nitrate fluxes through the summertime nitracline in the Atlantic sector were found to depend primarily on the presence of ice cover, where fluxes under sea ice were measured to be half as large as in open water (**IV**). However, the reason is not reduced dissipation in ice covered conditions due to suppression of surface waves, Langmuir circulation etc, but rather that stratification is enhanced under sea ice due to continued input of meltwater (**III**). Although stratification in the Marginal Ice Zone in late summer is generally stronger than in spring when melt has just started, this difference is hardly noticeable in the nitrate fluxes. The reason is that as the season progresses, the nitracline migrates downward to below the pycnocline (**IV**), which itself remains shallow due to continued ice melt (**III**).

3.3 CONCEPTUAL FRAMEWORK

Because the turbulent nitrate flux depends on the magnitude of the gradient in NO_3^- concentrations, the seasonality of the nutrient concentrations is also reflected in the seasonality of the turbulent nutrient fluxes. However, due to the vertical structure in both mixing and nitrate gradients, one has to pay attention to the vertical level at which fluxes are computed in order to interpret them correctly.

The deep nitraclines of the central Arctic Ocean are removed from the direct influence of (potentially ice mediated) wind forcing, and thus the associated nitrate fluxes act with a similar magnitude year-round (Fig. 3.1 C, bottom). This maintains the interannually steady concentration of nitrate in the Polar Mixed Layer. A slight seasonality in fluxes could potentially stem from seasonally varying input of near-inertial energy due to changing ice concentrations (RAINVILLE and WOODGATE, 2009), or deep winter mixing reaching the perennial pycnocline (POLYAKOV et al., 2013).

Embedded in the upper layers are seasonal processes: The depth-integrated drawdown of nitrate is concentrated around the spring bloom (Fig. 3.1 C, top). The drawdown that happens during the summer is in theory constrained by the vertical flux through the nitracline (Fig. 3.1 C, second from top). First with fall and winter mixing, $F_{\mathcal{N}}$ becomes large enough to replenish the surface layer's nitrate pool. At the lowermost extent of the seasonal nitracline, fluxes only become noticeable in fall, and stand for the complete homogenization of the upper ocean (Fig. 3.1 C, third from top). What all four curves in Fig. 3.1 C have in common is that their annual integrals are equal to each other and to the end-of-season nitrate drawdown (e.g. CODISPOTI et al., 2013).

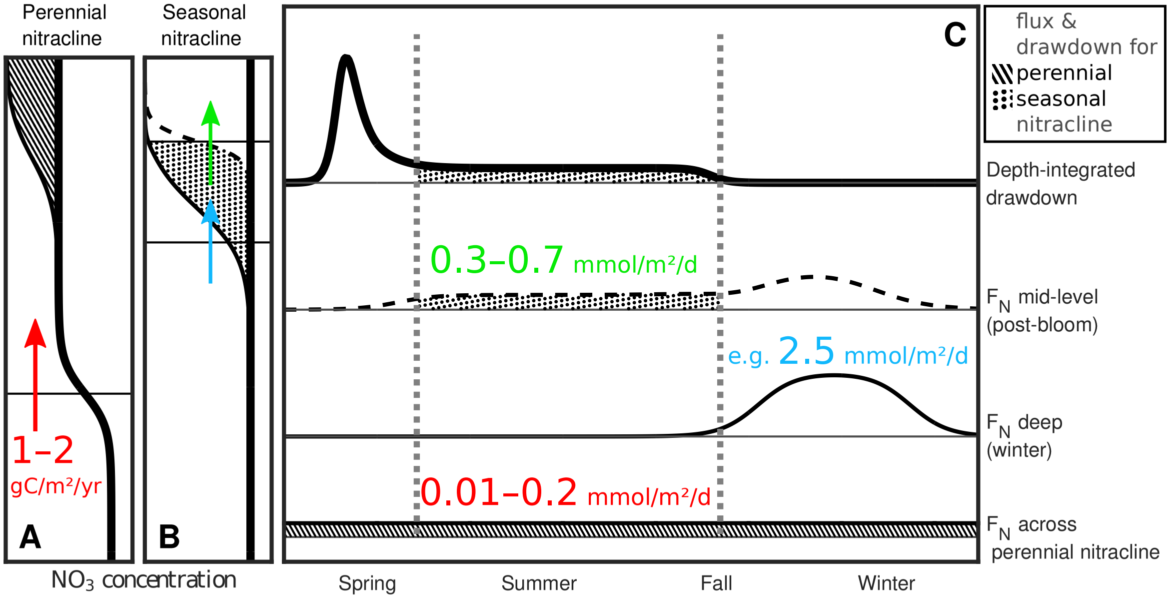

Figure 3.1: Conceptual framework for nitrate fluxes. A,B: Schematic vertical profiles of nitrate concentration. A: Scenario with perennial stratification, thick and thin lines represent winter and summer concentrations, respectively. Number is the Redfield-equivalent nitrate flux averaged across the deep Arctic Ocean (**I**). B: Scenario of seasonal nitrate drawdown. Thick, dashed and thin lines are winter, post-bloom and end-of-summer profiles, respectively. C: Annual cycles of upward nitrate fluxes evaluated at various depths. From top to bottom: Depth-integrated nitrate drawdown (≡consumption), $F_{\mathcal{N}}$ through the seasonal nitracline (green), $F_{\mathcal{N}}$ at the base of the seasonal nitracline (blue), and $F_{\mathcal{N}}$ through the perennial nitracline (red). Numbers indicate observed ranges of the individual fluxes estimated in papers **I**, **II** and **IV**. The shaded regions have equal areas for each of the different shadings.

4

PERSPECTIVES

4.1 VERTICAL NITRATE FLUXES AS A FRAMEWORK FOR STUDYING PRIMARY PRODUCTION

Traditionally, primary production is thought of as a composite process whose magnitude is set by a range of environmental parameters like nutrient loading, temperature, photosynthetically available radiation, and community structure, among other things (see e.g. VALIELA, 2015). This necessitates detailed and time-intensive measurements of e.g. nutrient uptake and primary production rates, all of which can vary greatly in time and space (e.g. MACKAS et al., 1985; ABBOTT, 1993). However, general circulation-biogeochemical coupled models fundamentally disagree about the future of Arctic marine primary production, largely due to different representations of vertical mixing processes (VANCOPPENOLLE et al., 2013). Constraining the vertical fluxes of nutrients and organic matter offers the chance to disentangle the imbalance between vertical supply of nutrients and primary production that leads to the large discrepancies in upper ocean nutrient inventories frequently observed in coupled biogeochemical models (POPOVA et al., 2012).

Instead of considering the host of biological processes that occur as a part of primary production in a food web, in this thesis I attempt to constrain the processes in the euphotic zone by the nutrient input through upward fluxes. These have to match the output at least approximately if a steady state is to be maintained. Since turbulent mixing is largely determined by physical processes, it is easier to estimate and more accessible to quantitative prediction at larger scales. This gives direct access to seasonal and annual integrals of nutrient fluxes and thus key terms of budgets in the nutrient cycle. The approach taken is therefore explicitly bottom-up. Neglecting top-down effects such as zooplankton grazing or viral mortality is only possible due to the focus on new production which enforces a strict nutrient budget perspective on all involved processes.

Hydrographic conditions vary widely across the Arctic Ocean, both in the annual mean and the seasonal cycle. Vertical homogenization in winter, wherever occurring, means that NCP has access to the entire nutrient reservoir in the water column, and thus even though summertime meltwater induced stratification might be strong and limit nutrient fluxes, annual integrals of $F_{\mathcal{N}}$ are large. It is not the case that the vertical turbulent nutrient supply to the photic zone in the Arctic Ocean is low because of strong stratification as such, as is commonly claimed in the literature. As we showed, $F_{\mathcal{N}}$ in the central Arctic is low primarily because of little mixing, not because of strong stratification (relative to other regions[1]). This is a crucial distinction as stratification and mixing are two distinct, albeit overlapping issues. However, the strong stratification is presumably at least co-responsible for creating such a quiescent environment (e.g. LINCOLN et al., 2016).

Low nitrate concentrations were associated with low uptakes rates (**IV**), estimated by bottle incubations using the N-15 isotope. The incubation results agree qualitatively with the expectation that strong stratification reduces nutrient supply. However, the uptake of nitrate (into the pool of particulate organic nitrogen) was more than one order of magnitude smaller than the nitrate flux supplied. We put forward several possible explanations in paper **IV**, but the one I in hindsight consider most plausible is that after the spring bloom, most (on the order of 90%) of the new production contributed to the build-up of the large pool of dissolved organic nitrogen that was observed in August (Lena Seuthe, pers. comm. 2016). Such a large shunt of nitrogen into the microbial loop would indicate that most new production that occurs during the summer months would not be exported, but instead respired later. This might however not have huge implications for the annually integrated export since $F_{\mathcal{N}}$ was small compared to the annual nitrate drawdown.

In this context it is worth stressing that the seasonal NCP (the maximum of which can be estimated e.g. from the end-of-season nutrient drawdown, see e.g. CODISPOTI et al., 2013) is not necessarily the same as the export

---

[1] In fact, many regions of the world ocean exhibit similar, if not lower, ratios between nitrate and density gradients across the nitracline, see e.g. σ_θ-$\mathcal{N}$ plots by OMAND and MAHADEVAN (2015); cf. the methodology employed in **I**.

production (EP). The discrepancy is then accounted for by (e.g., dissolved) organic matter that is not exported, but instead remineralized in the upper ocean during the following winter. Ideally, this wintertime respiration should be included in estimates of annual NCP, but observations are few and far between (e.g., Tremblay et al. (2008) speculated that the $\mathcal{N}$ increase they observed during winter was due to nitrification).

Similarly, NPP is usually larger than NCP due to reliance on regenerated nutrients throughout the summer. Importantly, in the framework of Arctic carbon cycling, the instrumental definition of new production (NP) as equal to NCP would often preclude a meaningful discussion of the associated export. It is therefore more precise to define NP=EP, and acknowledge that the NCP based on nutrient profiles measured in late summer is only an upper bound for EP. A linear extrapolation from trends or patterns in EP to NPP or even NCP is not advisable as community respiration is governed by many additional factors. Both the NPP:EP and NPP:NCP ratios are subject to the complicated interplay between nutrient loading, turbulence intensity, temperature, salinity, mortality, grazing, and heterotrophic respiration, that sets the community structure of marine ecosystems.

4.2 The future of Arctic marine primary production

The work presented in this thesis demonstrates a clear need to distinguish between annual NCP on one side and (summertime) daily NCP and NPP on the other side. As the open-water period lengthens, it has been observed that NPP increases (Arrigo and van Dijken, 2015), but the implications for EP are not immediately clear. Similarly, enhanced daily NCP during the summer might not necessarily be a significant fraction of annual NCP (**IV**). Predictions of Arctic marine primary production therefore have to be carefully defined both with respect to their temporal scope and the involved nutrient pools.

This thesis also indicates that the potential for increased new production is very limited. The recent Arctic-wide increases in primary production noted above are therefore likely attributable to enhanced recycling of nutrients. The fall blooms recently observed by Ardyna et al. (2014), however, might well be due to entrainment of new nutrients as stratification deepens when the ice cover is gone (**III**).

While climate related changes in the strength of stratification alone have the potential to drive marked changes in regional $F_{\mathcal{N}}$ (**I**), a major uncertainty is the future of the internal wave field in the Arctic Ocean. Recent findings suggest that the absence of sea ice enables near-inertial energy input (RAINVILLE and WOODGATE, 2009; DOSSER and RAINVILLE, 2016), but other observations suggest that most of this energy is dissipated in the strongly stratified surface (LINCOLN et al., 2016). The hydrographical contrasts across the Arctic Ocean and seasonal stratification likely also affect the input and redistribution of near-inertial energy. In the relatively weakly stratified Eurasian Basin, the near-inertial energy might penetrate deeper, but uncertainties arise from the unknown future of the shallow meltwater layers that cover much of the seasonal ice zone in summer.

4.3 OUTLOOK

The vast and shallow Arctic shelves are a large uncertainty in the projections of future Arctic marine ecosystems and nutrient cycling. This is partially because they are relatively unexplored, but not the least due to their complicated biogeochemistry dominated by extreme amounts of riverine freshwater and terrestrial carbon (e.g. SEMILETOV et al., 2012). An interesting question is whether vertical nitrate fluxes can provide a suitable framework for assessing new production also on the shallow shelves. One condition would be crucial: That the consumption of nitrate is restricted to an “upper” layer situated above a “lower” nutrient-rich pool throughout summer, i.e. that both mixing depth and euphotic zone are restricted to a distinct surface layer. This is not a given since the shallow topography could potentially make the entire water column available to mixing and light input.

As we demonstrated in paper **III**, it is primarily the sea ice melt that sets the structure of meltwater layers. These in turn affect both wind driven mixing and potentially deeper mixing due to downward radiation of near-inertial energy, and thus nutrient supply to the photic zone. Strong upper-ocean stratification sets the strength of the coupling between a variety of surface-dependent processes and the winter mixed layer on a seasonal basis, which itself is coupled to the ocean underneath via a perennial pycnocline on interannual time scales. However, future sea ice melt rates (in units of sea ice volume per area per time) have received relatively little attention as opposed to trends in sea ice extent and concentration. As the seasonal ice zone expands, I anticipate that melt rates and surface freshwater layers become increasingly important in predicting future Arctic Ocean climate.

Thanks

… go first and foremost to my supervisors Arild, Marit, Ilker and Odd Erik. Arild and Marit, you struck a wonderful balance between giving me the liberty to pursue my interests and reining me in when I was threatening to wander off. Thank you, Ilker, for a pleasant and productive (if rainy) stay in Bergen in 2015, and for pushing me just a tiny bit further whenever I was starting to be satisfied with some result. Arild, thanks for the trust you put in me when you let me take your precious instruments to just about anywhere — I'll claim it was luck I managed to bring back home as much as I did, and blame the rest on fate. I also wish to thank my other two co-authors Jean-Éric Tremblay and John D. Guthrie for joining me in my efforts. Philipp Assmy has on many occasions helped me with my dabblings in biology, both as an external evaluator and through inspiring discussions.

Vladimir Ivanov, Igor Polyakov and Andrey Pnyushkov showed me great hospitality during my stay at the International Arctic Research Center at the University of Alaska Fairbanks. Thanks also to Mikael Sejr for giving me the opportunity to join the MarineBasis program in Daneborg — it did not end up being part of my thesis, but the experience taught me a lot.

Many other people have contributed to this thesis in one way or another: My fellow Carbonbridge PhD students Maria and Marina — your long-time companionship has made all the cruises, workshops and conferences so much more enjoyable! My office mates Ingrid and Coralie — thanks for bearing with my stupid questions about biology and other things. The HavCryo section at NPI has been a stimulating scientific home ever since I first moved to Tromsø and started doing polar oceanography. Many of the participants on all the cruises I've been on have made the countless weeks and months at sea and in the ice much more bearable. Thanks go also to the crews and skippers of R/Vs Helmer Hanssen, Lance and Polarstern as well as the technicians — your patience with all my special requests is greatly appreciated. Marius, your enthusiasm for fixing stuff is wonderful.

Last but not least, thanks to all the friends, here and in the rest of the

world, who have made Tromsø such a nice place to live in, travel from and return to. My family down south — thanks for all the support, and apologies for living such a long way from home.

My position was financed through the Norwegian Research Council project “Carbonbridge: Bridging marine productivity regimes: How Atlantic advection affects productivity, carbon cycling and export in a melting Arctic Ocean”.

Bibliography

Abbott, M. R. (1993), *Patch Dynamics*, chap. Phytoplankton Patchiness: Ecological Implications and Observation Methods, pp. 37–49, Springer.

Anderson, L. G., E. P. Jones, and J. H. Swift (2003), Export production in the central Arctic Ocean evaluated from phosphate deficits, *Journal of Geophysical Research*, *108*(C6), doi:10.1029/2001jc001057.

Ardyna, M., M. Babin, M. Gosselin, E. Devred, L. Rainville, and J.-E. Tremblay (2014), Recent Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms, *Geophysical Research Letters*, *41*(17), 62076212, doi:10.1002/2014gl061047.

Arrigo, K. R., and G. L. van Dijken (2015), Continued increases in Arctic Ocean primary production, *Progress in Oceanography*, *136*, 60–70, doi: 10.1016/j.pocean.2015.05.002, Synthesis of Arctic Research (SOAR).

Behrenfeld, M. J., and E. S. Boss (2014), Resurrecting the ecological underpinnings of ocean plankton blooms, *Annu. Rev. Marine. Sci.*, *6*(1), 167194, doi:10.1146/annurev-marine-052913-021325.

Bourgault, D., C. Hamel, F. Cyr, J.-E. Tremblay, P. S. Galbraith, D. Dumont, and Y. Gratton (2011), Turbulent nitrate fluxes in the Amundsen Gulf during ice-covered conditions, *Geophysical Research Letters*, *38*(15), doi: 10.1029/2011GL047936.

Christian, J. R., M. R. Lewis, and D. M. Karl (1997), Vertical fluxes of carbon, nitrogen, and phosphorus in the North Pacific Subtropical Gyre near Hawaii, *Journal of Geophysical Research: Oceans*, *102*(C7), 15,667–15,677, doi:10.1029/97JC00369.

Codispoti, L., V. Kelly, A. Thessen, P. Matrai, S. Suttles, V. Hill, M. Steele, and B. Light (2013), Synthesis of primary production in the Arctic Ocean: III. Nitrate and phosphate based estimates of net community production, *Progress in Oceanography*, *110*, 126–150, doi:10.1016/j.pocean.2012.11.006.

Dickson, R., B. Rudels, S. Dye, M. Karcher, J. Meincke, and I. Yashayaev (2007), Current estimates of freshwater flux through Arctic and subarctic seas, *Progress in Oceanography*, *73*(3–4), 210–230, doi:10.1016/j.pocean.2006.12.003.

Dosser, H. V., and L. Rainville (2016), Dynamics of the changing near-inertial internal wave field in the Arctic Ocean, *Journal of Physical Oceanography*, *46*(2), 395415, doi:10.1175/jpo-d-15-0056.1.

Dugdale, R. C., and J. J. Goering (1967), Uptake of new and regenerated forms of nitrogen in primary productivity, *Limnology and Oceanography*, *12*(2), 196–206, doi:10.4319/lo.1967.12.2.0196.

Eppley, R., and B. Peterson (1979), The flux of particulate organic matter to the deep ocean and its relation to planktonic new production, *Nature*, *282*, 677–680.

Fer, I. (2006), Scaling turbulent dissipation in an Arctic fjord, *Deep Sea Research Part II: Topical Studies in Oceanography*, *53*, 77 – 95, doi:10.1016/j.dsr2.2006.01.003, IAPSO/SCOR Conference on Ocean Mixing.

Frigstad, H., T. Andersen, R. G. Bellerby, A. Silyakova, and D. O. Hessen (2014), Variation in the seston C:N ratio of the Arctic Ocean and pan-Arctic shelves, *Journal of Marine Systems*, *129*, 214–223, doi:10.1016/j.jmarsys.2013.06.004.

Honjo, S., S. J. Manganini, R. A. Krishfield, and R. Francois (2008), Particulate organic carbon fluxes to the ocean interior and factors controlling the biological pump: A synthesis of global sediment trap programs since 1983, *Progress in Oceanography*, *76*(3), 217285, doi:10.1016/j.pocean.2007.11.003.

Huisman, J., P. van Oostveen, and F. J. Weissing (1999), Critical depth and critical turbulence: Two different mechanisms for the development of phytoplankton blooms, *Limnology and Oceanography*, *44*(7), 1781–1787, doi:10.4319/lo.1999.44.7.1781.

Johnson, K. S., and L. J. Coletti (2002), In situ ultraviolet spectrophotometry for high resolution and long-term monitoring of nitrate, bromide and bisulfide in the ocean, *Deep Sea Research Part I: Oceanographic Research Papers*, *49*(7), 1291–1305, doi:10.1016/s0967-0637(02)00020-1.

Lewis, M. R., D. Hebert, W. G. Harrison, T. Platt, and N. S. Oakey (1986), Vertical nitrate fluxes in the oligotrophic ocean, *Science*, *234*(4778), 870873, doi:10.1126/science.234.4778.870.

Li, W. K. W., F. A. McLaughlin, C. Lovejoy, and E. C. Carmack (2009), Smallest algae thrive as the Arctic Ocean freshens, *Science*, *326*(5952), 539539, doi:10.1126/science.1179798.

Lincoln, B. J., T. P. Rippeth, Y.-D. Lenn, M. L. Timmermans, W. J. Williams, and S. Bacon (2016), Wind-driven mixing at intermediate depths in an ice-free Arctic Ocean, *Geophysical Research Letters*, *43*(18), 9749–9756, doi:10.1002/2016GL070454, 2016GL070454.

Loeng, H. (1991), Features of the physical oceanographic conditions of the Barents Sea, *Polar Research*, *10*(1), 5–18, doi:10.1111/j.1751-8369.1991.tb00630.x.

Mackas, D. L., K. L. Denman, and M. R. Abbott (1985), Plankton patchiness: biology in the physical vernacular, *Bulletin of Marine Science*, *37*(2), 652–674.

Margalef, R. (1978), Life-forms of phytoplankton as survival alternatives in an unstable environment, *Oceanologica acta*, *1*(4), 493–509.

Omand, M. M., and A. Mahadevan (2015), The shape of the oceanic nitracline, *Biogeosciences*, *12*(11), 3273–3287, doi:10.5194/bg-12-3273-2015.

Osborn, T. R. (1980), Estimates of the local rate of vertical diffusion from dissipation measurements, *J. Phys. Oceanogr.*, *10*(1), 83–89, doi:10.1175/1520-0485(1980)010⟨0083:EOTLRO⟩2.0.CO;2.

Perrette, M., A. Yool, G. D. Quartly, and E. E. Popova (2011), Near-ubiquity of ice-edge blooms in the Arctic, *Biogeosciences*, *8*(2), 515–524, doi:10.5194/bg-8-515-2011.

Peter, K. H., and U. Sommer (2013), Phytoplankton cell size reduction in response to warming mediated by nutrient limitation, *PLoS ONE*, *8*(9), e71,528, doi:10.1371/journal.pone.0071528.

Polyakov, I. V., A. V. Pnyushkov, R. Rember, L. Padman, E. C. Carmack, and J. M. Jackson (2013), Winter convection transports Atlantic water heat to the surface layer in the eastern Arctic Ocean, *Journal of Physical Oceanography*, *43*(10), 2142–2155, doi:10.1175/jpo-d-12-0169.1.

Popova, E. E., A. Yool, A. C. Coward, F. Dupont, C. Deal, S. Elliott, E. Hunke, M. Jin, M. Steele, and J. Zhang (2012), What controls primary production in the Arctic Ocean? Results from an intercomparison of five general circulation models with biogeochemistry, *Journal of Geophysical Research*, *117*, doi:10.1029/2011jc007112.

Rainville, L., and R. A. Woodgate (2009), Observations of internal wave generation in the seasonally ice-free Arctic, *Geophysical Research Letters*, *36*(23), doi:10.1029/2009GL041291, l23604.

Redfield, A. C., B. H. Ketchum, and F. A. Richards (1963), The influence of organisms on the composition of sea-water, in *The Sea*, edited by M. Hill, pp. 26–77, Academic Press.

Rudels, B., E. P. Jones, U. Schauer, and P. Eriksson (2004), Atlantic sources of the arctic ocean surface and halocline waters, *Polar Research*, *23*(2), 181–208, doi:10.1111/j.1751-8369.2004.tb00007.x.

Rudels, B., M. Korhonen, U. Schauer, S. Pisarev, B. Rabe, and A. Wisotzki (2015), Circulation and transformation of Atlantic water in the Eurasian Basin and the contribution of the Fram Strait inflow branch to the Arctic Ocean heat budget, *Progress in Oceanography*, *132*, 128–152, doi:10.1016/j.pocean.2014.04.003.

Sakamoto, C. M., K. S. Johnson, and L. J. Coletti (2009), Improved algorithm for the computation of nitrate concentrations in seawater using an in situ ultraviolet spectrophotometer, *Limnology and Oceanography: Methods*, *7*, 132–143.

Salehipour, H., W. R. Peltier, C. B. Whalen, and J. A. MacKinnon (2016), A new characterization of the turbulent diapycnal diffusivities of mass and momentum in the ocean, *Geophysical Research Letters*, *43*(7), 3370–3379, doi:10.1002/2016gl068184.

Semiletov, I. P., N. E. Shakhova, V. I. Sergienko, I. I. Pipko, and O. V. Dudarev (2012), On carbon transport and fate in the East Siberian Arctic land–shelf–atmosphere system, *Environmental Research Letters*, *7*(1), 015,201.

Slagstad, D., P. F. J. Wassmann, and I. Ellingsen (2015), Physical constrains and productivity in the future arctic ocean, *Frontiers in Marine Science*, *2*, doi:10.3389/fmars.2015.00085.

Sommer, U., K. H. Peter, S. Genitsaris, and M. Moustaka-Gouni (2016), Do marine phytoplankton follow Bergmanns rule sensu lato?, *Biological Reviews*, doi:10.1111/brv.12266.

Sterner, R. W., T. Andersen, J. J. Elser, D. O. Hessen, J. M. Hood, E. McCauley, and J. Urabe (2008), Scale-dependent carbon:nitrogen:phosphorus seston stoichiometry in marine and freshwaters, *Limnology and Oceanography*, *53*(3), 1169–1180, doi:10.4319/lo.2008.53.3.1169.

Sverdrup, H. (1953), On conditions for the vernal blooming of phytoplankton, *ICES Journal of Marine Science*, *18*(3), 287–295.

Tamelander, T., M. Reigstad, K. Olli, D. Slagstad, and P. Wassmann (2013), New production regulates export stoichiometry in the ocean, *PLoS ONE*, *8*(1), e54,027, doi:10.1371/journal.pone.0054027.

Tremblay, J.-E., and J. Gagnon (2009), *Influence of Climate Change on the Changing Arctic and Sub-Arctic Conditions*, chap. The effects of irradiance and nutrient supply on the productivity of Arctic waters: A perspective on climate change, pp. 73–89, Springer.

Tremblay, J.-E., K. Simpson, J. Martin, L. Miller, Y. Gratton, D. Barber, and N. M. Price (2008), Vertical stability and the annual dynamics of nutrients and chlorophyll fluorescence in the coastal, southeast Beaufort Sea, *Journal of Geophysical Research*, *113*(C7), doi:10.1029/2007jc004547.

Tremblay, J.-E., L. G. Anderson, P. Matrai, P. Coupel, S. Bélanger, C. Michel, and M. Reigstad (2015), Global and regional drivers of nutrient supply, primary production and CO2 drawdown in the changing Arctic Ocean, *Progress in Oceanography*, *139*, 171–196, doi:10.1016/j.pocean.2015.08.009.

Valiela, I. (2015), *Marine ecological processes*, 3rd ed., Springer-Verlag New York.

Vancoppenolle, M., L. Bopp, G. Madec, J. Dunne, T. Ilyina, P. R. Halloran, and N. Steiner (2013), Future Arctic Ocean primary productivity from CMIP5 simulations: Uncertain outcome, but consistent mechanisms, *Global Biogeochemical Cycles*, *27*(3), 605–619, doi:10.1002/gbc.20055.

Woodgate, R. (2013), Arctic ocean circulation: Going around at the top of the world, *Nature Education Knowledge*, *4*(8), 8.

Yamazaki, H., and T. Osborn (1990), Dissipation estimates for stratified turbulence, *Journal of Geophysical Research: Oceans*, *95*(C6), 9739–9744, doi:10.1029/JC095iC06p09739.