Water masses, shelf influences and depth distributions of arctic microbial species

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Abstract

Small organisms in the ocean include not only phytoplankton and bacteria, but diverse bacterial grazers and archaea. Local and global climate processes have a direct effect on the vertical stratification and circulation patterns in shelf and off shelf marine waters, which strongly influences the timing and magnitude annual phytoplankton production. Using molecular biology techniques we are now able to identify species and ecotypes of not only phytoplankton but the entire community of microorganisms and it is becoming practical to match community composition with biomass, oceanic processes and biogeochemical pathways.We show from our recent work in Arctic Seas that microbial communities change, not only with depth, but with region and that microbial species mostly track their water mass of origin. For example below the photic zone some watermasses are richer in bacterivores while others are dominated by likely parasites suggesting different fates for fixed carbon passing through these depths. We suggest that most changes in microbial community composition can be linked to the complex oceanic current patterns and advective processes. These microbial species changes may well determine the reproductive success of larger organisms and carrying capacity of an ecosystem since many marine fish and invertebrates have multiple free living life stages dependent on particular food types.

 Keywords: Phytoplankton, Archaea, Microbial communities, Pelagic-benthic coupling, Advection, Nitrogen

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Introduction:

Diversity and biogeochemical processes- Biological Oceanography texts are still largely devoted to the visible and apart from phytoplankton which are characteristic of the euphotic zone; other microbes are usually dealt with as part of the 'microbial food web', in contrast to alternative to 'classic food chains'. The upper euphotic zone is well studied since it is within this zone that biological activity (photosynthesis and respiration) is most evident and measurable (Del Giorgio and Duarte 2002). Surface and near surface phytoplankton are also amenable to global synopsis because chlorophyll (Chl *a*) concentrations can be estimated by satellite. Chl *a* values may then be converted to productively estimates and even used to detect particular species groups by use of empirically derived algorithms (Bouman et al. 2003). Such synoptic studies have highlighted the importance of fronts and upwelling (Sokolov and Rintoul 2007) and inter-annual variability of the onset and intensity of phytoplankton blooms (Stramska 2005). While the proximal reason for this variability is upwelling and advective input of inorganic nutrients, the physical and biological factors that control the source of inorganic nutrients from remineralized organic material to the photic zone has received relatively little attention. Under non-bloom conditions the upper water column is dominated by the microbial food web, with heterotrophic bacteria, viruses and bacterial grazers recycling carbon and other nutrients; limiting the amount of organic material sinking to depth (Anderson and Ducklow 2001). This view of microbes emphasizing euphotic zone consortia diverts thinking away from the diverse roles of other heterotrophic and chemotrophic microbes below the surface where nutrient remineralization and much of global biogeochemical cycling occurs.

Historically, microbial communities were treated as 'black boxes', but recent molecular environmental surveys have found that all three domains of life, Archaea, Bacteria and Eukaryota, form distinct communities with vertical distributions in the ocean. These distributions suggest differences in ecological capacity (Not et al. 2007a; Rodriguez et al. 2005) and novel energy pathways (Berg et al. 2007; Delong et al. 2006). The implications for community function and linkages between domains of life has received little attention to date (Galand et al. 2008a; Strom 2008) and there have been few, if any studies of community interactions across vertical zones. Studies of biogeochemically important processes are also rare but have identified regions where particular remineralization activity occurs such as silica dissolution (Bidle et al. 2003) and nitrification (Ward et al. 2007). The vertical structure of oceanic water columns is largely determined by physical oceanic processes (Carmack 2007), which in turn are correlated with the nutrient supply to the euphotic zone (Stramska 2005). Nutrient supply rate has been linked to phytoplankton species

composition (Archer 1995; Lovejoy et al. 2002). Other studies have noted that watermasses may transport communities across depth zones (Hamilton et al. 2008; Teira et al. 2006) suggesting that the changing current patterns driven by global climate systems could influence nutrient flux rates to the upper euphotic zone and global primary production in unexpected ways.

Methods

Samples were collected onboard CCGS Amundsen August 2005 as a part of the project Marine Microbial Biodiversity of the Arctic Seas (MMBOAS) in the North Water, between Greenland and Ellesmere Island. For a complete description of all sites and depths sampled see Hamilton et al. (2008). Samples were collected using a CTD rosette system equipped with 12 L Niskin bottles and a Sea Bird SBE-911 CTD.

Environmental DNA was collected by sequentially filtering 6 L of seawater through a 50-µm nylon mesh and a 3-µm polycarbonate filter to remove the majority of zooplankton, micro- and nanoplankton, then through a 0.2 µm Sterivex (Millipore) to collect the picoplankton (0.2-3 µm) size fraction. 18S rRNA gene libraries were constructed as in Lovejoy et al. (2006), but using Taq polymerase (NE Biolabs) and a BIORAD thermocycler. The clone inserts were verified by amplification with the vectors' M13 primers, positive inserts were identified on 1% agarose gel. Thirty positive clones were randomly chosen to be sequenced with 528f primer at Service de séquençage et génotypage du Centre Hospitalier de l'Université Laval (CHUL) with ABI 3730xl system. Sequences were manually checked and edited using Chromas software version 2.3 (Technelsium) and submitted to NCBI BLAST (Altschul et al. 1990). Sequences with their closest GenBank match under 97% were checked for chimeras by reblasting multiple fractions of the questionable sequence.

Results

Three libraries were constructed from two stations but represented three separate water masses described previously (Galand et al. submitted; Hamilton et al. 2008). As with many environmental clone libraries we also amplified metazoan sequences. For Station 21 these sequences matched the gelatinous zooplankton *Oikopleura*. In contrast we recovered Ctenophore sequences from the bottom of the Arctic Halocline (ABH). Overall, samples were not very diverse and an uncultivated presumed photosynthetic group, referred to as either picobiliphytes (Not et al. 2007b) or biliphytes (Cuvelier et

al. 2008) was common in all samples (Figure 1), but was the clear dominant in the Upper Arctic Water Sample (UAW) where a specific clade of Euarchaeota was common (Table 1). We recovered presumed bacterivorous marine stramenopiles (MAST) in the wintertime convection water (WCW), where a second type of Euarchaeota was previously identified (Galand et al submitted). In contrast, for ABH waters where Crenarchaeota (MGI) were the dominant archaea clade (Table 1), dinoflagellates and protist parasites (Alveolate groups One and Two) were recovered.

Discussion

Using molecular biology techniques we are now able to identify species and ecotypes of not only phytoplankton but the entire community of microorganisms. It is becoming practical to match community composition with biomass, oceanic processes and biogeochemical pathways. (Hamilton et al. 2008. Galand et al submitted). The North water is one of the most productive regions in the Arctic, but with persistently low surface nitrogen concentrations following early seasonal stratification (Mei et al. 2005). Tremblay et al. (2002a) attributed this phenomenon to episodic nutrient inputs linked to the complex hydrography of the region. Relatively rapid and shallow nitrification would be consistent with this suggestion and would require less frequent and lower mixing energy to be effective.

Nitrogen- Nitrogen is the major limiting macro nutrient for most oceanic and near shore marine systems (Boyd 2002; Harrison et al. 1996). Ammonia (NH_3) and nitrate (NO_3) are the two most common inorganic nitrogen species in the ocean. Most single celled organisms can take up ammonia in seawater, and it can be directly assimilated into cellular proteins. Nitrate uptake requires an active uptake system and organisms that are able to use it have a considerable advantage in regions where it is abundant but energy is required to reduce it inside the cell. (Armbrust et al. 2004). In the absence of other limiting nutrients, nitrate is quickly taken up in the upper euphotic zone where light energy is abundant, and for example, in the north Atlantic, spring diatom blooms quickly deplete standing nitrate stocks (Dugdale 1967). Diatoms are particularly adept at coordinating photosynthesis and nitrate metabolism and this may be one of the reasons they dominate photosynthetic production in much of the surface ocean (Allen et al. 2006). These episodic blooms are a response to episodic nutrient input; however sustained diatom production fuelled by nitrate requires sustained nitrate input (Lovejoy et al. 2002; Rixen et al. 2005; Tremblay et al. 2002b).

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Nitrogen is not only a nutrient source, required in abundance by living cells, but because of its multiple oxidation states is a useful terminal electron acceptor, transformations that are catalyzed by microorganisms. The basic transformations of nitrogen by living organisms are well studied in the lab and the biochemical pathways were thought to be understood (Zehr & Ward 2002). However environmental genomic and metagenomics surveys have resulted in the discovery of new pathways and organisms involved in nitrogen transformations (Church et al. 2005; Delong et al. 2006; Francis et al. 2007; Klotz and Stein 2008; Mincer et al. 2007; Zehr et al. 2007).

Sources of NH₃- Zooplankton and protists graze on photosynthetic organisms to obtain energy from fixed carbon and excrete excess nitrogen as ammonia (Dolan 1997). In addition viral lysis may lead to release of dissolved organic material and ammonia (Suttle 2005). This ammonia may then be recycled as ammonia and used by small photosynthetic phytoplankton (Cole 1999) resulting in a microbial food web. Alternatively it may be oxidized, releasing nitrite and nitrate into the surrounding waters (Clark et al. 2008; Klotz and Stein 2008). Nitrification rates in the ocean are not routinely measured and evidence is often circumstantial and difficult to determine directly (Lomas and Lipschultz 2006). We suggest the fate of excreted ammonia may be inferred by examining the associated microbial community and expression of key genes in biochemical pathways involved.

Crenarchaeota- One of the early major revelations from environmental 16S rRNA gene surveys was that Archaea were common throughout the world ocean, (Delong 1998) with two major branches, Crenarchaeota and Euarchaeota, often dominating in at different depths down the water column (Massana et al. 1997; Varela et al. 2008). The 'role' of Archaea in these non-extreme well oxygenated waters was unknown but in now seems that the diverse groups have diverse metabolisms (Hallam et al. 2006; Herfort et al. 2007; Herndl et al. 2005; Ouverney and Fuhrman 2000). The recent discovery that the gene ammonia monooxygenase (*amoA*), which codes for the first step in nitrification of Ammonia to Nitrate, is apparently common in the Crenarchaeota (MGI) (Francis et al. 2005) has proven to be a major incentive to re-examine the role and spatial distribution of nitrification in the ocean and other environments (Clark et al. 2008; Francis et al. 2005; Herfort et al. 2007; Mincer et al. 2007; Wuchter et al. 2006). A consensus has began to emerge that MGI and the archaeal *amoA* gene are common in the mesopelagic and deep waters (Varela et al. 2008) and in the euphotic zone in the Arctic and Antarctic (Church et al. 2003; Galand et al. 2008b; Galand et al. 2006). The existence of chemoautotrophic archaea fixing inorganic carbon exploiting ammonia as an energy source in the upper water column(Delong et al. 2006) adds complexity to global carbon flux

models based on the new versus regenerated production paradigm (Dugdale 1967) and carbon export models need to be re-examined (Clark et al. 2008).

Single celled eukaryota

Since the seminal publication by (Woese et al. 1990), describing the three domains of life based on differences in the gene coding for ribosomal RNA, there is an emerging consensus is that there are 5 to 8 major sub-domains (ca. the level of phyla and super phyla) among eukaryotes (Adl et al. 2005; Baldauf 2003). The biological oceanographers' two functional groups, phytoplankton and microzooplankton, are distributed among nearly all of these sub-domains (Vaulot et al. 2008). Similar to surveys targeting bacteria and archaea, environmental 18S rRNA gene surveys targeting Eukaryota have also revealed that there are novel organisms in the sea representing all taxonomic levels from cryptic new species (Montresor et al. 2003) to new phyla (Not et al. 2007b; Shalchian-Tabrizi et al. 2006). Several of the novel groups found in the first published surveys (Lopez-Garcia et al. 2001; Moon-Van Der Staay et al. 2001) had no known function. Among these, two groups of marine alveolates distantly related to dinoflagellates have since been found to have affinities with known parasites previously classified within the marine dinoflagellate order Syndiniales (Groisillier et al. 2006; Harada et al. 2007; Skovgaard et al. 2005). Alveolate Group II (AG Two) groups with *Amoebophyra* a parasite of dinoflagellates and other parasites such as *Syndinium* that infect crustacean zooplankton, while Alveolate Group I (AG One) is a distinct clade parasitic or symbiotic with a variety of organisms (Dolven et al. 2007; Harada et al. 2007). These 18S rRNA gene surveys also unveiled several novel clades of Heterokonta, or marine stramenopiles (MASTs) which are likely responsible for the majority of bacterivory in the upper ocean (Massana et al. 2004). More recent genomic surveys have revealed that diverse eukaryotic plankton are abundant even in deep water and have distinct vertical distributions (Countway et al. 2007; Not et al. 2007a). Using finer sampling scales, we find distinct communities in different watermasses independent of depth in the Arctic (Figure 1, Table 1).

Sharing the same space-The archaeal communities were different in the three samples (Galand et al. submitted), with MG1 Archaea as well as high *amoA* gene copy numbers in the ABH. This community would be adapted to rapid nitrification (RN) fuelled by ammonia released via dinoflagellate grazing of, for example, sinking diatoms; the ammonia would be converted to nitrate by Crenarchaeota and other organisms, and diffuse upwards to the photosynthetic community. Other marine regions are likely to contain RN communities; these would be predicted to occur in areas with

advective currents within or just below the photic zone such as zones of upwelling, which are often marked by prolonged high productivity and vertical complexity along a horizontal gradient. Earlier studies suggested that nitrification could be responsible for high rates of dark carbon fixation along such zones, for example Viner (1990) found that nitrification likely accounted for 8 to over 70% of total carbon fixation off the coast of New Zealand. We would hypothesize that these are also zones with RN protist and archaeal communities.

The balance between export and recycled production has not only been applied to predicting carbon flux to the deep ocean but is a useful concept for estimating energy available to pelagic fish versus benthic invertebrates and fish. Climate has a direct effect on the oceanic vertical stratification and circulation patterns, which strongly influences the timing and magnitude annual phytoplankton production and the distributions of larger organisms (Greene and Pershing 2007) and for example local production patterns may influence the distribution of species assemblages of bottom fish (Jorgensen et al. 2005). Poor recruitment of fish stocks has been linked to current changes, and phytoplankton species differences. In terms of life histories, global circulation is further implicated in advective transport of plankton and is a powerful mechanism for transporting and isolating populations with planktonic life stages including economically important pelagic species such as halibut (Knutsen et al. 2007). The success of these populations depends on coincidence of early life stages arriving in zones of high productivity (Hinckley et al. 2001), where we would predict RN zones.

While this work is extremely preliminary it suggests that microbial communities persist within water masses and differences in hydrography could determine whether a region is dominated over time by a microbial food web or by prolonged production by diatoms. We suggest that most changes in microbial community composition can be linked to the complex oceanic current patterns and advective processes.

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Water Mass	STN	Depth	Archaeal group	Eukaryote Community
ABH	11	62	MG1	Dinoflagellate-Ctenophore
UAW	21	90	IIa2	Biliphyte-Ciliate
WCW	21	180	IIa1	MAST-biliphyte-Oikopleura

Table 1: Stations (STN) Comparison of eukaryotic community with Archaeal community described for the same samples in Galand et al submitted. Arctic bottom halocline (ABH); Upper Arctic Water (UAW): and Wintertime convection waters (WCW).   Marine group I (MGI). Euarchaota groups are sub clusters of MGIIa (Galand et al. submitted).
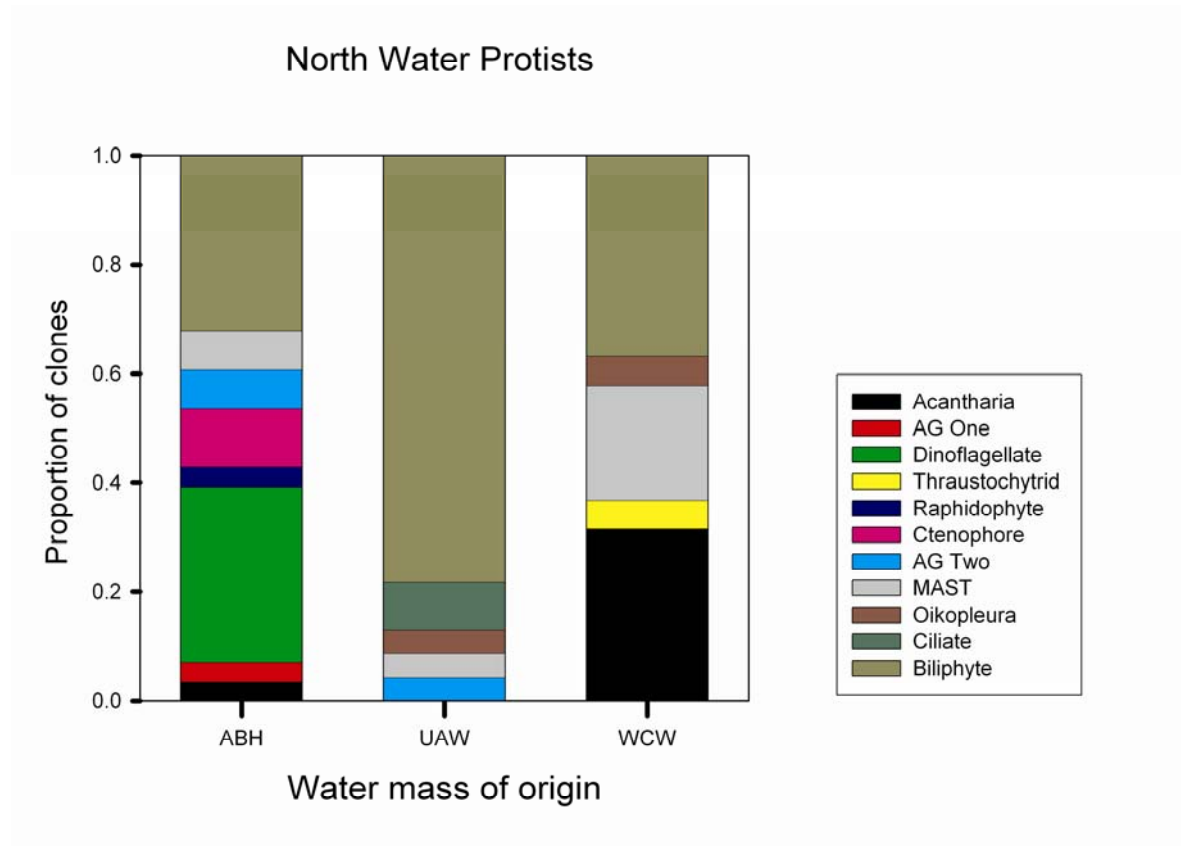
Figure 1: Proportion of different major clades of eukaryotes in different water masses in the North Water. ABH- Arctic bottom halocline, UAW- Upper Arctic Water, WCW- wintertime convection water. Abbreviations used for eukaryote groups are described in the text.