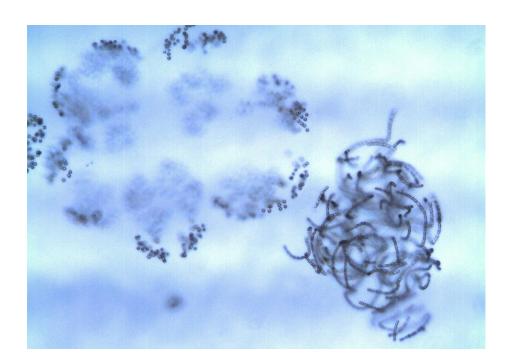
UNIVERSITY OF TROMSØ UIT

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Aspects of phytoplankton spring blooms in northern coastal/shelf areas: Diatoms vs. *Phaeocystis pouchetii* (Hariot, Lagerheim)



Gunilla Kristina Eriksen

BIO-3950 Master`s thesis in Biology November 2010



Acknowledgements

First of all I wish to thank my supervisor, Hans Christian Eilertsen, which has been a source of inspiration throughout my entire study period here at Faculty for Bioscience Fishery and Economy (BFE). His guidance as well as enthusiasm has been of great support during this Master project. I also wish to thank my talented fellow student and college Richard Andre Ingebrigtsen for great times, inbetween working "hanging out in the Planktonlab" discussing phytoplankton issues. I am also greatfull to Rahman Mankettikkara, Maria Degerlund and Siv Huseby for their help during my Master project, MATLAB is actually fun when knowing how to use it. The greatest of thanks to Bjarne Landfald and Tan Thi Nguyen for their patience in theaching me molecular methods for DNA extraction, unexperienced as I was. I would also like to thank the crew on R/V Jan Mayen. In addition I wish to thank my colleges and fellow students at BFE for being good company and inspiration. I also wish to thank all my friends for their patience with me since I have been a bit preoccupied lately. Finally I would like to thank my family for the continued support during my education and to you Arne-Magnus for always being there both on good and bad days and in so making the bad days good.

Contents

Abstract	1
1. Introduction	3
2. Materials and methods	9
2.1 Area description	9
2.2 The Barents Sea and East Finnmark	9
2.3 The Vestfjord archipelago	12
2.4 Physical oceanography and meteorology	14
2.5 Calculations and modeling	15
2.6 Species abundance and composition	16
2.7 Taxonomic identification of Phaeocystis spp. (Class Prymnesiophyceae)	16
2.8 Phaeocystis vs. diatom abundance	18
2.9 Principal Component Analysis (PCA)	19
3. Results	21
3.1 Environmental variables, Barents Sea, May in 2006, 2007 and 2009	21
3.2 Environmental variables, East Finnmark, May in 2009	26
3.3 Environmental variables, Vestfjord archipelago, April in 2006, 2007 and 2009	28
3.4 Identification of Phaeocystis spp., molecular approach	34
3.5 P. pouchetii vs. diatom dominance in the Barents Sea 2006	35
3.6 P. pouchetii vs. diatom dominance in the Barents Sea 2007	37
3.7 P. pouchetii vs. diatom dominance in the Barents Sea 2009	39
3.8 P. pouchetii vs. diatom dominance in East Finnmark 2009	41
3.9 P. pouchetii vs. diatom dominance in the Vestfjord archipelago 2006	44
3.10 P. pouchetii vs. diatom dominance in the Vestfjord archipelago 2007	46
3.11 P. pouchetii vs. diatom dominance in the Vestfjord archipelago 2009	49
3.12 Principal component analysis, Barents Sea and East Finnmark	52
3.13 Principal component analysis, Vestfjord archipelago	56

4. Discussion	62
5. Conclusions	75
6. Further research	76
7. References	78
Appendix A	86
Appendix B	90
Appendix C	94

Abstract

During the present study the relative abundance variations between *Phaeocystis pouchetii* (Hariot, Lagerheim) and diatoms were investigated. Both biological and environmental factors related to P. pouchetii and diatoms were studied in order to reveal possible inherent orderliness connected to their relative abundance variations in time and space. The areas sampled were the Barents Sea (May 2006, 2007 and 2009), the Vestfjord archipelago (April 2006, 2007 and 2009) and East Finnmark (May 2009). In order to get a vertical and horizontal overview of their dominance distribution, a ratio denoting their relative dominances was generated. I investigated three depths (0m, 10m and 50m) and the relative dominance of P. pouchetii and diatoms at each depth were plotted against latitude and longitude in the areas sampled. Their presence and distribution were interpreted based on correlations to cooccurring species and environmental variables. The vertical distribution showed a trend for P. pouchetii to dominate at 10m and diatoms at 0m in all three areas sampled. P. pouchetii seemed to be more abundant in the southern Barents Sea and East Finnmark relative to Vestfjord archipelago. Diatoms on the other hand seemed to be more abundant in the northern Barents Sea, especially at the ice edge and in Vestfjord archipelago relative to East Finnmark. P. poucetii was observed most dominant in 2009 in all three main areas sampled, while diatoms dominanted in 2006 in the Barents Sea and the Vestfjord archipelago. In the Barents Sea and East Finnmark, P. pouchetii was positively correlated to late spring bloom diatom species as well as environmental variables which also indicated a later appearance of P. pouchetii in the spring bloom. In the Vestfjord archipelago P. pouchetii was positively correlated to both early and late spring bloom species indicating P. pouchetii to be present throughout the spring bloom season. The environmental variables that P. poucehtii was positively correlated to however indicated a somewhat later appearance of *P. pouchetii*. Total diatom stock ("Tot. D") was correlated to species reported to have peak abundance earlier than the species P. pouchetii was positively correlated to in the Barents Sea and in East Finnmark. In Vestfjord archipelago "Tot. D" was positively correlated to both early and late spring bloom species, indicating the main species to stay abundant throughout the bloom season, as was also indicated for *P. pouchetii*. However, according to the physical parameters the main species constituting "Tot. D" generally seemed to be more abundant in the early spring bloom compared to P. pouchetii in both the Barents Sea, East Finnmark and Vestfjord archipelago. The vertical and horizontal distribution of P. pouchetii and diatoms in time and space is probably connected to both interspesific competition but also to life history strategies. *P. pouchetii* is probably better adapted to less turbulence than diatoms and it does not require silicate, thus avoiding competition with diatoms when silicate concentrations are low late in the spring bloom season. The life history strategies for *P. pouchetii* is however difficult to outline since their entire life cycle is not yet resolved. Most of the diatoms common during a spring bloom are spore producers. Whereas diatom spores requires deep mixing and irradiance to germinate, *P. pouchetii* resting stage (if any) is still not conclusively detected and its functioning can thus not be resolved. The bentic-pelagic dynamics is most likely important clues in the distribution of phytoplankton in time and space. As to the taxonomic identity of *P. pouchetii* genetic analyses performed indicated that it could also belong to both *Phaeocystis cordata* and *Phaeocystis antarctica*. However, examined from a morphological point of view the *Phaeocystis* cell-material collected from the Barents Sea in 2007 and 2009 were identified as *Phaeocystis pouchetii*.

Key words: spring bloom, phytoplankton dominance, *Phaeocystis pouchetii*, diatoms, Barents Sea, East Finnmark, Vestfjorden

1. Introduction

What is a phytoplankton bloom? As Smayda (1997) pointed out, a bloom is not simply a biomass issue. It also has regional, seasonal and species-specific aspects.

The most striking feature in the annual cycle of phytoplankton in the northern coastal and shelf areas, the north Norwegian coast and the Barents Sea, is the spring bloom. The spring bloom is relatively fixed in time, starting at the earliest late March, often lasting into May with peak abundances in April (Degerlund & Eilertsen 2009). Exceptions though exists, for example in Porsangerfjord where the spring bloom continues into the summer (Hegseth et al. 1995, Eilertsen & Frantzen 2007) or in Vestfjord where peaks in shallow areas may be observed in March (Degerlund & Eilertsen 2009). This annual increase in phytoplankton biomass is important in that it feeds the entire marine system during the spring when it is breeding season for northern marine organisms, e.g. newly hatched fish schools (matchmismatch, Cushing (1990). Thus the assessment of the timing and mechanisms regulating the spring bloom is important in order to understand variations in e.g. fisheries being crucially important along the coast of northern Norway and in the Barents Sea. This was originally historically the first motivation for studying the northern spring bloom. Vestfjord, an area that serves as the main spawning ground for north east atlantic cod, was the first area in northern Norway where extensive phytoplankton studies were performed (Føyn 1929, Gran 1930, Braarud et al. 1958, Braarud & Nygaard 1980, Huseby 2002). Several other extensive studies have later taken place in north Norwegian fjords, e.g. Skjomen (Schei 1974, Eilertsen 1983), Balsfjord (Gaarder 1938, Eilertsen et al. 1981b, Eilertsen & Taasen 1984, Lutter 1989, Sandberg 1996), Malangen (Gaarder 1938, Throndsen & Heimdal 1976, Hegseth et al. 1995, Sandberg 1996), Ullsfjord (Heimdal 1974) and Altafjord and Porsangerfjord (Hegseth et al. 1995, Eilertsen & Frantzen 2007). In the Barents Sea the phytoplankton studies ranges over more than a century (Cleve 1883, 1899, Gran 1902, Gran 1904, Braarud 1935, Smayda 1958, Heimdal 1983, Eilertsen et al. 1989, Heimdal 1989, Hegseth 1992, Hegseth 1997, Wassmann et al. 1999). Characteristic of these are though that they cover only limited periods of time, i.e. they do not discuss annual variations. Only three Norwegian sources covers larger periods of the year (Eilertsen et al. 1989, Evensen 1994, Degerlund & Eilertsen 2009). There also exists several Russian publications that, peculiarly enough, seldom are cited. However, the extensive monograph by Kuznetsov (1992) is one to take note of.

Another aspect of phytoplankton blooms are harmful algae blooms, influencing ecosystems and causing economically losses to the fish- and shellfish industry. This has though not been so much in focus in the north, probably due to seldom occurrences, but it is a fact that e.g. *Phaeocystis pouchetii* may act toxic (Hansen et al. 2004). The understanding of the dynamic mechanisms regulating biomass, species succession and assemblages of phytoplankton blooms are also crucially important for an understanding of biological events at higher trophic levels.

The area northwards from the Polar Circle is unique in that large seasonal fluctuations in environmental conditions influence phytoplankton biomass changes. Much effort has been put into research on physical-biological regulatory mechanisms since the last period of the 19th century (Cushing 1978) when researchers hypothesized that variability in physical parameters influenced marine life (Sars 1879). The most common explanatory mechanism associated with the bloom onset is the Sverdrup paradigm (1953), assuming that nutrients are not limiting and stating that a mixed depth has to be equal to or shallower than a critical depth. However, the spring bloom in northern areas often starts in unstratified water masses, i.e. prior to a measurable density stratification of the water column (Gaarder 1938, Heimdal 1974, Schei 1974, Eilertsen et al. 1981b, Eilertsen & Taasen 1984, Skofteland 1985, Hansen & Eilertsen 1995, Eilertsen & Frantzen 2007), contrary to what is observed in more southern areas. This delayed northern stratification is a result of less effective solar heating and surface salinities being higher due to less runoff compared to southern Norway. Northern Norway has a smaller drainage basin in addition to later ice melting, with a peak in runoff in June, due to the characteristic light regime (Eilertsen et al. 1981a). In the winter twilight period the sun is below the horizon from 27 November to 15 January and during summer the sun is above the horizon from the 20 May to 22 July in the Tromsø area (69°N). In this intervening time the daily incident irradiation increases rapidly with increasing day number and latitude. During 90 days at 70°N the day-length increases from 8.3 to 24 h with a mean increase in day-length of 0.081 h day⁻¹. At 80°N the day-length increases from 2.5 to 24 h in only 45 days which results in a mean increase in day-length of 0.48 h day⁻¹. Another factor also weakening the stratification of the water column early in the spring is the prolonged period with winter overturning of the water masses (Sælen 1950, Svendsen & Thompson 1978, Eilertsen et al. 1981a). Measurements from a 23 years period show a positive heat flux (cooling of the sea) from September to April and a negative heat flux during May-August for the northern coastal

areas (Eilertsen & Skarðhamar 2006). This is however true for coastal areas north of Tromsø, i.e. areas hypothesised to be much less influenced by seaborne telecommunication mechanisms than southern temperate areas (Eilertsen & Skarðhamar 2006). The northernmost coastal areas that are significantly influenced by seaborne telecommunication mechanisms are according to Eilertsen and Skarðhamar (2006) Vestfjord. The Vestfjorden basin traps and slows down the north flowing Norwegian Coastal Current (NCC), which both influences the atmospheric and ocean climate in that particular area. The Barents Sea is also to a greater extent influenced by seaborne telecommunication mechanisms by warm and salty Atlantic Water (AW) flowing through the Barents Sea Opening (BSO).

The succession of species during a bloom is most often explained by changing physical, as well as chemical and biological conditions during spring (Margalef 1958, Smayda 1980). Nevertheless, when phytoplankton start to appear in the water masses in early spring, they most often show a characteristic pattern. Typically small species appear in early spring, followed by larger ones (Gaarder 1938, Schei 1974, Eilertsen et al. 1981b). This is in accordance with Margalef's (1958) succession scheme which consists of three defined succession steps. Starting out with small-celled diatoms there is a shift to a mixed community of bigger diatom cells followed by a third step dominated by dinoflagellates (Margalef 1958). However, the sampling along the north Norwegian coast and in the Barents Sea has often been sporadic both in time and space. Attempts to monitor the species succession are therefore difficult. However, there are fewer drawbacks with such data when investigating species assemblages and key species. Several attempts have been made to define species assemblages connected to spring blooms, by assemblages meaning typical associations of species connected to specific geographical areas (Cleve 1896, Gran 1900, Gran 1902, Jørgensen 1905, Gran 1927, Gaarder 1938, Sakshaug 1972, Heimdal 1974, Braarud & Nygaard 1980, von Quillfeldt 2000, Degerlund & Eilertsen 2009).

An inherent property of the northern phytoplankton works cited above is also that they most often show that *P. pouchetii* may be abundant and that its amount relative to diatoms may vary. *P. pouchetii* is also considered one of the main species in the Arctic spring bloom in terms of both cell numbers and biomass (Lagerheim 1896, Eilertsen et al. 1989, Degerlund & Eilertsen 2009). The literature connected to *P. pouchetii* is extensive due to its great ecological and economical impact, and a focus on all aspects of *P. pouchetii* biology is beyond the scope of the present text. A extended collection of some "central" *P. pouchetii*

literature is though compiled in Appendix C. Peculiarly enough, few of the formerly suggested species assemblages mention *P. pouchetii*, although it is a commonly occurring species during the spring bloom in temperate and polar areas. However, the latest species assemblage suggested for the north Norwegian coast and the Barents Sea (68-80°N) by Degerlund and Eilertsen (2009) consists of *P. pouchetii* and several diatoms like *Fragilariopsis oceanica*, *Chaetoceros socialis*, *Chaetoceros furcellatus*, *Chaetoceros compressus*, *Chaetoceros debilis*, *Skeletonema costatum*, *Thalassiosira* spp. and *Bacterosira bathyomphala*.

In addition to being taxonomically different, i.e. P. pouchetii belongs to Class Prymnesiophyceae and the diatoms belong to Class Bacillariophyceae. They thus exhibit different physiological and ecological characteristics (e.g. nutritive value) which in turn may have great ecological impacts. Worth taking note of is also that P. pouchetii only is (assumedly) one species whereas the "diatoms" consists of 164 genera and 1365—1783 species which was said to be underestimated by Sournia in 1991 and increasing with approximately 320 per year (Sournia et al. 1991). However, this is an estimate of the diatom species in the world and not in temperate and cold water areas where the number is much lower but though relatively high. Despite this, P. pouchetii is a very successful species both concerning biomass and abundance in comparison to the total bulk of diatoms during the spring bloom. Characteristic for P. pouchetii is the formation of gelatinous colonies, consisting of a variety of polysaccharides (van Rijssel et al. 2000). This has been considered being the main reason for the success of this species (Lancelot & Rousseau 1994, Hamm 2000, Veldhuis et al. 2005). Maximum colony size reported by Jahnke and Baumann (1987) for P. pouchetii is 1,5-2 mm in diametre. In addition high doubling rates (faster than 1 division per day) has been reported for colonial cells of P. pouchetii (Eilertsen 1989, Veldhuis et al. 2005, Verity et al. 2007). Its massive potential for rapid increase in biomass makes colony-forming Phaeocystis spp. one of a few phytoplankton taxa with significant biogeochemical impact on a global scale. P. pouchetii plays a key role as an intermediary in the transfer of carbon as well as sulphur between ocean and atmosphere and vice versa. However, unlike diatoms they carry no stable frustules/cell wall (needs no silicon) and is therefore not as easily traced in the carbon cycle as diatoms i.e. sediment records. The lack of a "heavy and protective" frustule might also be the reason for the reported higher vertical flux attenuation efficiency for P. pouchetii than for diatoms. The overall contribution of P. pouchetii to vertical carbon export has been reported to be small (Reigstad & Wassmann

2007). Studies show that at the end of the spring bloom *P. pouchetii* colonies sink out of the euphotic zone. However, due to autolysis, leakage, rapid microbal degradation and zooplankton grazing marine snow disintegrates in the upper part of the euphotic zone (Wassmann et al. 1990). In addition *P. pouchetii* and diatoms as mentioned differ in their metabolic behavior. Fernández (1992) found an active protein metabolism during a diatom bloom whereas a carbohydrate-dominated metabolism in a *Phaeocystis* spp. outburst. In addition does fatty acids (EPA and DHA), which are essential for the growth of multicellular animals, probably only occur in trace amounts in *Phaeocystis*, whereas they are common in many other phytoplankton species (Nichols et al. 1991). This will have great effect on the trophic structure assuming the classical food web to dominate during a diatom bloom and the microbial loop to dominate during a *P. pouchetii* boom. Also supporting this is several authors reporting zooplankton to favor diatoms over *P. pouchetii* due to nutritional value, size and/or toxicity (Verity & Smayda 1989, Estep et al. 1990, Weisse et al. 1994, Haberman et al. 2003). However, the nutritional value of *P. pouchetii* is highly debated and is not straight forward, but probably depend on several factors.

Few of the dominating diatom species of the northern spring bloom are reported to be toxic. This is however not the case for P. pouchetii which has been shown to act toxic towards marine organisms. Different effects like reduced appetite and weight loss in Atlantic salmon and cod larvae (Eilertsen & Raa 1995), lethal effect on cod larvae (Aanesen et al. 1998), toxic and anaesthetic properties in Blowflies (Calliphora vomitoria) (Stabell et al. 1999), avoidance of *P. pouchetii* blooms by herring (Savage 1932) and copepode avoiding grazing upon healthy (young) colonies of P. pouchetii (Estep et al. 1990), have probably been caused by a toxin produced by P. pouchetii. The toxic compound polyunsaturated aldehyde (PUA) 2-trans-4trans-decadienal (DD), known to inhibit mitotic cell division in several different cell types, identified in P. pouchetii by Hansen et al. (2004) was first identified in the diatoms Skeletonema costatum, Pseudo-nitzschia delicatissima and Thalassiosira rotula (Hansen & Eilertsen 2007). These diatom species are also occasionally present in northern spring blooms, but at minor amounts and therefore probably have little biogeochemical effect on the ecosystem in question. The exception may be S. costatum which has been reported occasionally being one of the main species making up the bulk of the biomass along the north Norwegian coast, especially early in spring bloom season (Gaarder 1938, Eilertsen et al. 1981b, Hegseth et al. 1995). The allelopathic function of the PUA is still connected to

uncertainty. It is assumedly released by diatoms and *P. pouchetii* as a response to mechanical stress, possibly triggered by grazing activity (Pohnert 2000, Wolfe 2000, Pohnert 2002). However, any adverse effects on co-occurring phytoplankton species during "normal" bloom progress may be difficult to pinpoint (Hansen & Eilertsen 2007). In addition to being toxic, *P. pouchetii* has been regarded a nuisance species. The gelatinous polysaccharide matrix of the colonies can cause clogging of fishing nets and accumulation of fetid foam on beaches (Lancelot 1995). There is no doubt that the inter-specific differences between the two taxa are great. Therefore the relative abundance variation between these taxa will have great impact on the ecosystem in question both from a biological, economical and environmental point of view.

The relative abundance variation between *P. pouchetii* and diatoms is in fact a main and important characteristic of the northern spring blooms (Eilertsen et al. 1989b (Svalbard); Heimdal 1974 (Ullsfjord); Pedersen et al. 1989 (Trondjord); Eilertsen et al. 1981b (Balsfjord); Føyn. 1929 (Lofoten); Schei 1979 (Skjomen); Sakshaug 1972 (Trondheim). The aim of this study is therefore to look into the characteristics of these variations interannually, and also seek for what causes changes in the ratios between *P. pouchetii* and diatoms.

2. Materials and methods

2.1 Area description

The data used in this study was collected during the cruises to the Barents Sea in May 2006, 2007 and 2009, Vestfjord (Vestfjord archipelago) in April the same years and East Finnmark in May 2009 (Table 1, Fig. 1, 2, 3 and Appendix C). In May 2009, data was collected both in the Barents Sea and East Finnmark. I myself participated on five of these cruises, i.e. in 2007 in the Barents Sea, 2009 in the Barents Sea and East Finnmark and in 2006, 2007 and 2009 in the Vestfjord archipelago. The locations sampled in the Barents Sea varied between years due to different focus of the projects. The cruise to the Barents Sea in 2006 was part of an EU project (MARISCO), and the 2007 and 2009 cruises were part of a RCN bioprospecting project (MabCent). In the Vestfjord archipelago the four locations Vestfjorden, Henningsværstraumen, Austnesfjord and Tysfjord were sampled all three years. The cruises to Vestfiord the archipelago were part of Marine **Ecology** (http://www0.nfh.uit.no/phaeocystis/mar/) led by Professor Hans Christian Eilertsen. See Appendix B for further details on sampling locations and periods for the different cruises.

Table 1: Overview of sampling periods, maximum and minimum latitude (°N) and longitude (°E) and number of stations sampled during each cruise (positions are decimal degrees).

Location	Year	Latitude (°N)	Longitude (°E)	Sampling	No. stations
		(min-max)	(min-max)	periods	
Barents Sea	2006	76.56-81.77	09.34-33.34	10-15 May	24
Barents Sea	2007	73.87-78.69	10.26-33.94	10-18 May	17
Barents Sea	2009	72.85-77.99	09.03-31.27	15-25 May	24
East Finnmark	2009	69.68-71.69	25.18-31.00	26-30 May	12
Vestfjord archipelago	2006	67.56-68.35	13.27-16.48	01-07 Apr.	20
Vestfjord archipelago	2007	67.82-68.35	13.65-16.48	12-18 Apr.	19
Vestfjord archipelago	2009	67.56-68.35	13.28-16.47	15-19 Apr.	12

2.2 The Barents Sea and East Finnmark

The Barents Sea is an open arcto-boreal shelf sea, bordering the Norwegian Sea in the west and the Arctic Ocean in the north. The eastern border is Novaja Zemlya and the southern border is the Norwegian and Russian coast. The average depth is 230m and the sea covers approximately 1.4 million km² (Ottersen & Chr 2001). The shallowest shelf areas are located around Svalbard and south from Hopen to Bjørnøya (Spitsbergenbanken). The bathymetry plays a crucial role in the circulation pattern in the Barents Sea, especially the trough between

Bear Island and Fugløya. In this section, named the Barents Sea Opening (BSO), the Atlantic water (AW) bifurcates into the North Cape Current (NCC) flowing eastward into the Barents Sea through BSO and the West Spitsbergen Current (WSC) flowing northwards along West Svalbard into the Fram Strait (Hopkins 1991). In the northern part of the BSO there is an outflow of Barents Polar Water (BPW). The inflow is varying over time and is profoundly influencing the temperature of the Barents Sea (Loeng 1991, Ingvaldsen et al. 2004). North of the AW the Polar Front separates this water mass from BPW. All in all it can be said that the climate in the Barents Sea is variable, and this variation is closely linked to both the characteristics of the inflowing water-masses and to the prevailing atmospheric conditions, again being linked to e.g. NAO (Furevik 2001).

The ice conditions in the Barents Sea in May 2006 made it possible to conduct sampling much further north than during 2007 and 2009 (Fig. 1). This was exploited well and the sampling area was located north and east of Svalbard (Fig. 1). The cruise period was from 10 to 15.05.06. The cruise started north of Svalbard at 80.13°N - 9.58°E. North of Svalbard, at 81.73°N - 15.80°E, six stations were sampled during a 24 hour sampling programme (diurnal station). Further a new diurnal sampling programme including six stations was set up east of Svalbard at 80.90°N - 30.00°E. The last station sampled was the southernmost station (76.56°N - 27.40°E), located west of Hopen. The 2007 sampling in the Barents Sea was conducted during the period 10 to 18.05.07. The sampling started north of Bjørnøya at 75.51°N - 20.02°E (Fig. 1). Further the cruise went into the ice at the east side of Svalbard as far north as 78.08°N - 33.90°E. Three stations south of Bjørnøya were sampled, with the southernmost location situated at 73.87°N - 18.63°E. The last stations to be sampled were on the western side of Svalbard where the northernmost point in 2007 was sampled, i.e. at 78.69°N - 10.26°E. The 2009 sampling took place in the waters around southern Svalbard plus the area between Svalbard and the Norwegian mainland where sampling also was conducted around Bjørnøya and along the eastern coast of Finnmark (Fig. 1 and 2). The cruise period was from 15 to 30.05.09. The first station sampled was at the northernmost position, 77.99°N - 9.03°E, i.e. outside Isfjorden on the western side of Svalbard. Further the cruise went into the waters around Bjørnøya and then to the eastern side of Svalbard where sampling was conducted as far north as the ice condition allowed, i.e. at 77.72°N. When leaving the ice edge a transect was made towards Honningsvåg at the northern tip of the Norwegian mainland. Along the coast of East Finnmark the first sampling was conducted in Varangerfjord and thereafer in Porsangerfjord. Varangerfjord is the most water-rich fjord in Norway. However, in a strict sense it is a false fjord as it does not have a sill. The circulation in Varangerfjord is structurally different from other fjord areas due to its wide entrance, maybe comparable to Porsangerfjord, and is mainly driven by wind and Coriolis force (Pedersen et al. 2009), see Table 2. Porsangerfjord is the largest fjord in Northern Norway and the third largest fjord in Norway, and because of its size the water circulation is here also mainly driven by wind and the Coriolis force (Svendsen 1991). The sill in the inner part of Porsangerfjord, situated 30 m from the fjord head, prevents basin water from having free exchange with the open sea. However, the outer part of Porsangerfjord has free exchange with the open sea (Table 2). The innermost Porsangerfjord is considere true Arctic.

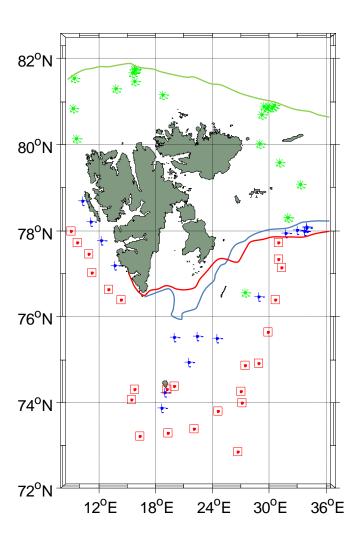


Figure 1: Map of the Barents Sea showing sampled stations in 2006, 2007 and 2009, green (∗) is 2006, blue (+) is 2007 and red (□) is 2009. The location of the ice edge is shown in same color as the station color for each year.

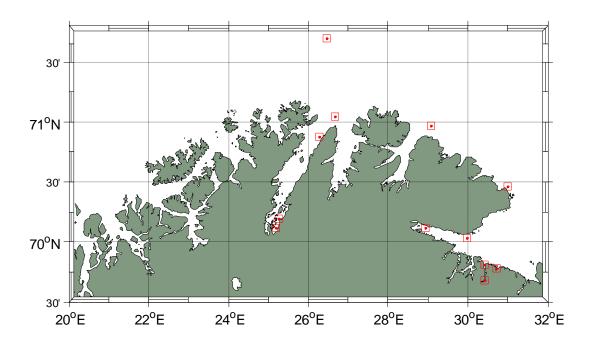


Figure 2: Map of East Finnmark showing sampled stations in 2009.

2.3 The Vestfjord archipelago

The southernmost studied location was the Vestfjord archipelago with its adjacent fjords located in Nordland. Three fjords in the Vestfjord archipelago were selected for further investigation in the present study: Vestfjorden, Austnesfjord and Tysfjord, in addition to the sound Henningsværstraumen (Table 2, Fig. 3 and Appendix C). Vestfjorden lies between the mainland of Norway and the Lofoten Island archipelago (67-69°N - 11-19°E). It is an atypical fjord due to its size, even though it has a deep sill. The sill is located between Bodø and Røst and is at 227m depth. From a dynamical point of view Vestfjorden is rather a coastal embayment, being wider and deeper than most other fjords (Mitchelson-Jacob & Sundby 2001). The characteristic topography of the Vestfjord archipelago captures an inner branch of the Norwegian Coastal Current (NCC). The NCC originates from the warm and salty Atlantic Water (AW) and mixes with fresh water run-off from the Norwegian coast (Sætre & Mork 1981). The North Norwegian coastal areas are all to some degree under influence of the northward flowing NCC. The NCC turns into Vestfjord archipelago on the south-east side and flows out on the north-west side (Furnes & Sundby 1981). Austnesfjord which is situated on the western side of Vestfjord archipelago has quite similar water structure as Vestfjorden due to the absence of a sill (Furnes & Sundby 1981). This is not the case for Tysfjord, the second deepest fjord in Norway, which is located on the eastern side of Vestfjord archipelago. Tysfjord has three sills, and the innermost is 60 m, influencing the inflow of dense and warm NCC into the fjord. The sound Henningsværstraumen is relatively shallow, no deeper than maximum 130m, causing strong currents due to the tides.

All three years a transect in Vestfjorden consisting of four to five stations were sampled, i.e. the two fjords Austnesfjord and Tysfjord in addition to the sound Henningsværstraumen. In 2006 the sampling started in the innermost part of Vestfjorden. At first a transect including five stations was made throughout Vestfjorden. Then the western side of Vestfjord archipelago was sampled where a diurnal station including four stations in Henningsværstraumen and a diurnal station including five stations in Austnesfjord were set up. At last a transect consisting of five stations was made throughout Tysfjord, located on the east side of Vestfjord archipelago. The sampling period was from 1 to 7.04.06 (Fig. 3). The 2007 cruise to the Vestfjord archipelago followed the same sampling route as in 2006, except that Austnesfjord was visited before Henningsværstraumen. The cruise was from 12 to 18.04.07. In Vestfjorden a transect consisting of four stations were sampled. As much as 12 of the stations sampled were part of a diurnal sampling programme. The first diurnal station included six stations and was located in Austnesfjord. The second diurnal station also included six stations and was located in Henningsværstraumen. In Tysford three stations were sampled (Fig. 3). In 2009 the cruise period was from 15 to 19.04. The sampling started in the innermost part of Vestfjorden, and a transect including five stations was made throughout Vestfjorden. Then the western side of Vestfjord archipelago was sampled, at first three stations in Henningsværstraumen and secondly two stations in Austnesfjord. In Tysfjord, on the east side of Vestfjord archipelago, two stations were sampled (Fig. 3).

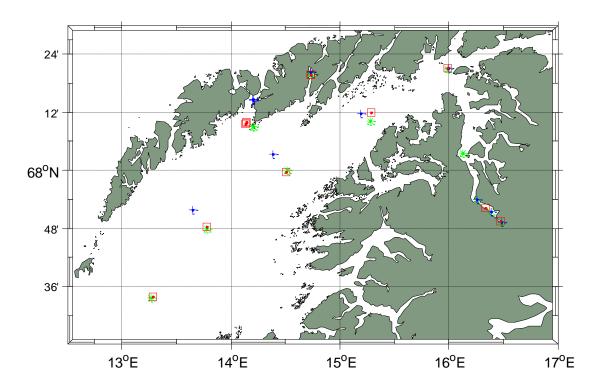


Figure 3: Map of the Vestfjord archipelago showing sampled stations in 2006, 2007 and 2009, green (∗) is 2006, blue (+) is 2007 and red (□) is 2009.

Table 2: Overview of fjord systems investigated showing depth of sill(s) (m), length (km), max. depth (m) and max. width (km).

Fjord	Depth of sill(s) (m)	Length (km)	Max. depth (m)	Max. width (km)
Vestfjorden	227	180	>400	70 (at the sill)
Tysfjord	205 (Outer)	62	897	14
	303 (Middle)			
	60 (Inner)			
Austnesfjord	No sill	12	120	4
Porsangerfjord	60	100	310	20
	(30km from fjord head	l)		
Varangerfjord	No sill	90	420	70

2.4 Physical oceanography and meteorology

The vessel FF/Jan Mayen (184 ft) was used during the cruises to the Barents Sea and the Vestfjord archipelago. During these cruises vertical profiling of temperature, salinity, density (σ t) and in vivo fluroescence (FL) were sampled at all stations applying a CTD (Sea-Bird SBE 9) with an attached Seapoint in vivo FL sensor. The degree of stability was computed as the density difference from surface (0m) to 10m depth. Metrological data, wind speed (ms⁻¹), wind direction (°), sea and air temperature (°C), humidity (0-1) and air pressure (mbar), were obtained as means of registrations during station time from the automated meteorological station onboard the vessel while cloud cover (scale 0-9; 1= clear, 9=snowy or fog) and

visibility (km) was observed manually. Missing data were replaced by data values from the previous nearby station.

2.5 Calculations and modeling

Surface heat flux (Q_t) was computed as $Q_t = Q_h + Q_e + Q_b + Q_s$, where Q_h is sensible heat, Q_e latent heat, Q_b long-wave radiation (black-body radiation) and Q_s is short wave radiation (Gill 1982). Sensible heat was calculated according to the formula Q_h =- C_h ρ C_p V_{10} $(T_{air}$ - $T_{sea})$ where C_h is heat flux coefficient (1.1 x 10^{-3} for neutral stratification), ρ is air density (1 Kg m⁻¹ 3), C_{p} is heat capacity (air) at constant pressure (1004 J Kg^{-1} K^{-1}), V_{10} is wind in ms^{-1} 10m above sea surface and T is temperature (°C) (Brown 1990). Air temperature measurements were missing for the Barents Sea 2007 dataset, so the constant value of -5.1 was used in the model (as subjectively judged from earlier records). Wind in ms⁻¹ was also missing for the Barents Sea 2007 dataset, so the constant value of 8.7 (judged as a typical mean for area) was used in the model. Latent heat was calculated according to formula Q_e= ρ L_v C_e V₁₀ (q_{air}-q_{sea}) where L_v is latent heat of evaporation (2.5 x 10^6 J Kg^{-1}), $C_e = C_h$ and q denotes specific humidity at 10m altitude and at the sea surface (0m) (Smith et al. 1983). The $q_{air}\!/q_{sea}\!\!=\!\!\epsilon\ell$ $_{air/sea}/(p_h-(1$ - $\epsilon)$ e $_{air/sea})$ where ϵ =0.622 is the ratio between molecular weight of water vapour and dry air. Further is e $_{air/sea}$ = r611.0 x $10^{(7.5T~air/sea+275.15-35.86))}$ where r is the relative humidity of the air, 0-1, and ph is mean air pressure in the northern hemisphere (101400 Pa). Humidity data was missing for the Barents Sea 2007 and Vestfjord archipelago 2009 dataset, so the constant value of 0.7 was used for the Barents Sea and 0.6 for Vestfjord archipelago in the model. The net long wave radiation was computed as $Q_b = \varepsilon_g \delta (f_{air}(273.15 + T_{air})^4 - T_{air})^4$ (273.15+ T_{sea})⁴) (Henderson-Sellers 1986). Further ϵ_g is long-wave emissivity for sea (0.97), δ is the Stefan Boltzmann's constant (5.67 x 10^{-8} J s⁻¹ K⁴ m⁻²), f_{air} is explained by the formula $(1 - 0.261 \text{ e}^{-7.77 \times 104 \text{ T} 2 \text{air}}) \text{ x } (1 + 0.275 \text{ } f_{\text{c}}) \text{ where } f_{\text{c}} \text{ is the relative proportion of cloud cover.}$ Cloud cover was missing for the Barents Sea 2007 dataset, so the constant value was set to 6 in the model. The basis for the short wave irradiance model was the algorithm in Frouin et al. (1989) (Eq. 1). Here the short-wave solar irradiance (Qs, PAR) for clear sky is computed in Wm⁻² after input of surface visibility, humidity and regression coefficients for maritime atmospheres and solar zenith angle. Visibility measurements were missing for the Barents Sea 2007 dataset, so the constant value of 97 was used in the model. The solar zenith angle was computed at given geographical position and time according to the equations in Iqbal (1983).

$$Q_{s} = I_{R} * \left(\frac{d}{d_{0}}\right)^{2} * \cos\theta \frac{\exp\left[-\left(a + \frac{b}{V}\right)/\cos\theta\right]}{1 - A\left(a' + \frac{b'}{V}\right)} * \exp\left[-a_{v}\left(\frac{U_{v}}{\cos\theta}\right)^{b_{v}}\right] * \exp\left[-a_{0}\left(\frac{U_{0}}{\cos\theta}\right)^{b_{0}}\right]$$

Equation 1

Where I_R is the monochromatic extraterrestrial irradiance integrated over 400-700nm (PAR), d/d_0 is the ratio of actual to mean Earth-Sun separation, a and b are regression coefficients representing different aerosol types, subscripts v and θ denotes water vapour and ozone, θ is albedo, θ is surface visibility (km) and θ is vertically integrated absorber amount (cm).

Both surface and sub-surface irradiance were modelled (Eilertsen & Holm-Hansen 2000). The basis for the surface irradiance (Is) model was integrated 24 hour PAR with cloud cover incident on surface in Wm^{-2} at date of measure. The basis for the sub-surface irradiance (Id) was the same as for surface irradiance except the integrated 24 hour PAR measurements was from the sampling depth calculated from the diffuse attenuation coefficient (k). The diffuse attenuation coefficient was modelled by Eilertsen and Holm-Hansen (2000) and based on analysis of their Chla and subsurface PAR data sets. For further information on modelling see e.g. Eilertsen and Wyatt (2000).

2.6 Species abundance and composition

Water samples for cell counts (cells 1⁻¹) were collected using 51 Niskin water bottles mounted on the CTD. Phytoplankton species were enumerated live in an inverted Leica microscope using a modified method of Utermöhl (1958) where a 2ml four-well Nunclon counting chambers were used. Cell counts were performed onboard the vessel with a minimum of 2 hours settling time. Phytoplankton species identification was mainly based on Tomas (1997).

2.7 Taxonomic identification of Phaeocystis spp. (Class Prymnesiophyceae)

Molecular methods are becoming increasingly common for taxonomic and ecological studies of phytoplankton. At the Planktonlab., Institute for Arctic Marine Biology (AMB), Faculty for Bioscience Fishery and Economy (BFE) resources that permit molecular methods were provided allowing me to use the polymerase chain reaction (PCR) based techniques to identify *Phaeocystis* spp. in this study. Two runs were preformed with material (*Phaeocystis* spp.) from different locations in the Barents Sea. The first *Phaeocystis* spp. material (ID 76.2) was collected on 18 May in 2007 in the Barents Sea (77.78°N – 12.29°E) where a single

colony was isolated and kept in culture at the Planteplanktonlab up till present. Harvesting of this culture was done by filtering approximately 100ml of dense culture onto 0.6µm polycarbonate filter (Millipore Corp.) supported by a pre-burnt GF/C filter (450°C in 8h). The sample was immediately frozen in liquid nitrogen and stored at -80°C. The second Phaeocystis spp. material (ID 89) was collected on 22 May in 2009 in the Barents Sea (75.64°N - 29.92°E) by filtration during a massive *Phaeocystis* spp. monoculture bloom where the pellet was immediately frozen in liquid nitrogen and stored at -80°C. The extraction of total DNA was performed using the spin column based DNeasy Blood and Tissue kit Quiagen where the manufactures instructions for total DNA from animal tissues were followed. In addition RNase A was used (4µl, 100mg/ml) to reduce the amount of free RNA, this was listed as optional in the manufactures instruction. Prior to PCR a 24µl master-mix containing 12.5µl reddyMix PCR mastermix (Thermo Scientific), 1.5µl MgCl₂, 1µl primer F (forward) (10pmol/µl), 1µl primer R (reverse) (10pmol/µl) was added to the template containing 10ng of DNA (10ng/10pmol/μl), further H₂O was added to a total volume of 25 (10pmol/μl). Primers used was an 18S rRNA gene-target PCR primer pair specific for the haptophyte genus Phaeocystis (PhaeoF-489 and PhaeoR-683) designed by Nejstgaard et al. (2008). The PCR reaction programme was set to a 3 min denaturing step at 94°C, followed by 35 cycles of (94°C for 45 s, 53°C for 90 s, 72°C for 90 s) and the last step was 7 min at 72°C. The reaction was run in an Applied Biosystems 2720 Thermal Cycler. Purification of the PCR product was done by salt precipitation, where the PCR product, 95% EtOH and 3M NaOAc, pH 5.2 were mixed according to ratio 10:20:1. Further the sample was vortexed and incubated on ice for 30 min, centrifuged on 13200 rpm for 25 min and the supernatant was discarded. The pellet was washed with 75% EtOH where 100µl was used per pellet and then centrifuged at 13200 rpm for 5 min. Then the supernatant was again discarded while the pellet was set to dry before it was dissolved in 20µl MilliQ water. Prior to sequencing PCR the DNA concentration had to be diluted to 5ng/µl. The DNA concentration was checked using the nano-drop method. The sequencing mix consisted of 1µl Big Dye v. 3.1 (Applied Biosystems, USA), 2.5µl Big Dye buffer (5x) and 1.6µl primer (2pmol/µl of each of the F and R primer), 2 µl template (5ng/µl) and H₂O adding up to a total volume of 20µl. The PCR sequencing followed the reaction of an initial denaturing step at 96°C for 5 min, further running 25 cycles of (96°C for 10 s, 50°C for 5 s) and at last 60°C for 4 min. The sequences were worked up at the DNA sequencing facility at the University hospital in Tromsø where an Applied Biosystems 3130x1 Genetic Analyzer was used. Further end-trimming of sequences were performed using 4 Peaks v. 1.7.2

(A. Griekspoor and Tom Groothuis, Netherlands). Finally the blast program (basic Local Alignment Search Tool), BLASTN v. 2.2.24 at the NCBI GenBank server (http://www.ncbi.nlm.nih.gov/blast/Blast.cgi) was used to search for uploaded sequences that matched my sequences.

2.8 Phaeocystis vs. diatom abundance

Surface maps with abundance indices were generated to illustrate and get an overview of the relative variation in *Phaeocystis pouchetii* and diatoms abundance in time and space at different depths. In the present project cell numbers were used as abundance indicators. It is obvious that if the biomass was computed as e.g. cell volume, C, N or similar, it would increase diatom abundance relative to P. pouchetii. Hence, the approach applied by me only reflects the relative changes in abundances and not in "actual" biomass. In order to operate with two variables to be plotted against each other, P. pouchetii solitary and colony cell counts were merged and the same was done for the diatom species registered at the specific locations. This resulted in the two variables, total *P. pouchetii* ("Pp") and total diatoms ("Tot. D"). The two variables were log-10-transformed (since blooms most often increase biomass exponentially) and total diatoms were thereafter subtracted from total P. pouchetii. This ratio, for simplicity refered to as "Phaeocystis dominance", was used as a measure of the two variables total P. pouchetii and total diatoms. A positive ratio denotes P. pouchetii dominance and a negative ratio diatom dominance i.e. "Tot. D"> 0 < Pp. This means that a negative "Phaeocystis dominance" value is equal to diatoms being more abundant than P. pouchetii. The "Phaeocystis dominance" was calculated for each station sampled and was plotted against latitude and longitude. Prior to analysis the TriScatteredInterp function in MATLAB (MATLAB 7.10.0 (R2010a), The MathWorks Inc., MA, 2010) was used to perform interpolation on the scattered dataset consisting of three matrices that resides in the 2D surface plot. The surface plots were generated using the *pcolor* function in MATLAB. The pcolor(X, Y, C), where X=longitude, Y=latitude and C="Phaeocystis dominance", draws a plot of the elements of C at the locations specified by X and Y. The color system used was set to shading flat where the constant color of each cell is the color associated with the corner having the smallest x-y coordinates. Hence, C (i, j) determines the color of the cell in the ith row and the *j*th column. Note that due to interpolation between sampling positions there will be an increasing uncertainty in the "Phaeocystis dominance" value the further one moves away from the sampling position.

2.9 Principal Component Analysis (PCA)

Principal Component Analysis (PCA) was used to reduce a large number of variables and summarize the original information to reveal typical patterns (correlations) between the variables. PCA was applied to P. pouchetii and the eight most dominating diatom species sampled at each main location during all three years, all depths are included. Since I only had data from eastern Finnmark from one year these data were pooled with the Barents Sea data in the PCA analyses. Hence, eight dominating diatom species were chosen for the Barents Sea and East Finnmark and eight for the Vestfjord archipleago when all data in all three years were considered. Total diatoms, ("Tot. D") was also included in the analysis, but as a supplementary variable whereas the nine phytoplankton species were ordinated as active variables. Active variables are used in the derivation of the principal components and the supplementary variables are projected onto the factor space computed from the active variables. Phytoplankton species are occasionally difficult to distinguish from one another in light microscope. This especially applies to Thalassiosira hyalina and Thalassiosira antarctica and Fragilariopsis oceanica can be confused with Fossula arctica or Fragilariopsis cylindrus (Quillfeldt 2001). However, I chose to use T. hyalina, T. antarctica and F. oceanica, though identification was based on light microscope merely, i.e. I considered this identification to be precise and appropriate for my purpose. Prior to analysis species abundance data were natural-log-transformed. Transformation such as log may improve linear relationships between variables (again exponential increase assumed), homogeneity of variances and to reduce the influence of outliers. This is according to Quinn and Keough (2009), especially the case if the unequal variances and outliers are a result of non-normality which often is to be found in phytoplankton datasets. In addition transformation will reduce the influence of variables with high values, e.g. species with very high abundances (Quinn & Keough 2009). Variables not transformed will have larger ranges and will be more represented in the data than others, in this case placing emphasis on phytoplankton group biomass rather than pattern. That is why scaling is so crucially in multivariate analysis. Correlation was used as the association matrix in PCA. It is important to have in mind that data from correlation research cannot be used to conclusively prove causality, but only to track relations/correlations among the variables (phytoplankton species). In other words concusions are based on "circumstantial evidence". In addition to variable "Tot. D", environmental variables were ordinated as supplementary variables. Prior to analysis the environmental data were normalized (Eq. 2).

$$N=(X-(X_{mean}))/X_{mean}$$

Equation 2

Where X is the specific environmental variable and X_{mean} is the specific mean environmental variable for the total Barents Sea and East Finnmark or Vestfjord archipelago dataset considering all three years. Environmental variables are more complex than species abundance variables concerning units of measurements, which often are different between environmental variables. In addition environmental variables naturally have different ranges (Cao et al. 1999). Another particularly important complexity pointed out by Cao (1999) is that the biology and ecotoxicology, in this case environmental factors, of different variables vary greatly. "Log transformation indiscriminately increases the importance of a low range across all variables, and thus distorts the responses of species to pollution" (Cao et al. 1999). Extreme environmental values which can have great effect on biology are "flatten out" by log transformation having the intention of reducing the effect of "outliers". Even if there is a greater statistical significant relationship between one environmental variable to a species abundance variable than another, the biological significance might be of another character (e.g. a surface sensible heat flux increase from 0-50W m⁻² might have no effect on species abundance compared to a pH increase of 0.1 from within the buffering capacity to slightly above the buffering capacity of the particular geographical area). Environmental data has thus been normalized allowing data on different scales to be compared, transforming them onto a common scale.

3. Results

Due to limited availability of resources and vessel-time, the areas sampled in the Barents Sea as mentioned varied somewhat between years. Therefore, only some of the areas can be directly compared for interannual characteristics. On the other hand, the area close to the ice edge can be interannually compared since it is a biotope determined by its environmental state (ice-low temperatures) rather than geographical position.

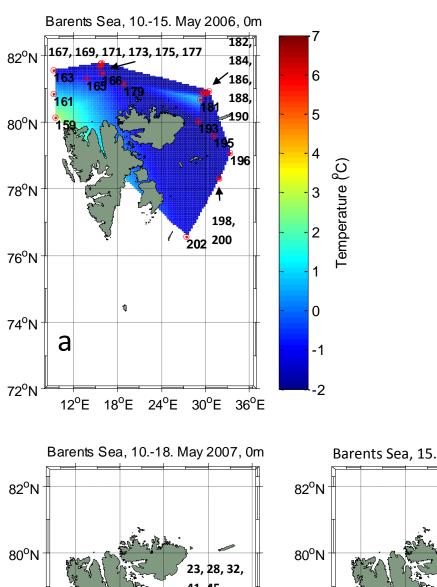
3.1 Environmental variables, Barents Sea, May in 2006, 2007 and 2009

The range of the surface (0m) sea temperature in the Barents Sea in May 2006 was from -1.85°C to 2.78°C (Fig. 4a). The highest 0m temperature was measured at station 159 located northwest of Svalbard. Station 159 differed clearly from the other sampled stations, having high temperatures both in surface (2.80°C) and deeper (50m), 3.54°C (Appendix A, Fig. 1A). The lowest 0m temperature was measured at station 193 located between Nordaustlandet and Kvitøya. The temperatures down to 50m were at all other stations between -1°C and -2°C (Appendix A, Fig. 1A). The only exceptions, in addition to station 159, were station 179 (located north of Nordaustlandet) having a 10m temperature of 0.96°C and station 181 (located north of Kvitøya) having a 0m temperature of 1.01°C (Appendix A, Fig. 1A).

In May 2007 the 0m sea temperature range was from -1.88°C to 5.89°C in the sampled area (Fig. 4b). The highest 0m temperature was measured south of Bjørnøya at station 67, i.e. at the southernmost station sampled. The lowest 0m temperature was at station 45 which was one out of six stations located in ice on the eastern side of Svalbard. The temperatures at 0m and 10m were comparable, except at station 5 located between Bjørnøya and Hopen where the temperature was 1.72°C at 0m and -1.72°C at 10m (Appendix A, Fig. 2A). At stations 2, 9, 19, 28, 32, 41, 45 and 57 located in the eastern part of the sampling area temperatures at 50m were comparable to the surface ones (0m and 10m). At stations 12 and 23, also located in the eastern part of the sampling area, and stations 103, 109 and 115 on the western side of Svalbard the 50m temperatures were higher than the surface ones. The opposite was measured at stations 60 and 67 located south of Bjørnøya, and at station 98 west of Svalbard where the 50m temperature was lower than the surface ones (Appendix A, Fig. 2A).

The 0m sea temperature range in May 2009 was from -1.72°C to 6.27°C (Fig. 4c). The highest surface temperatures were measured at stations 238 and 241 located northwest of Bjørnøya

(6.27°C). The lowest temperature at 0m was measured at station 251 which was located in the ice east of Svalbard. As for 2006 and 2007, there were no great differences between the temperatures at 0m and 10m at the stations (Appendix A, Fig. 3A). The greatest difference between 0m and 50m temperatures were at stations 248, 249 and 250, all located northeast and station 232 located northwest in the sampling area. All these stations had higher values at 50m than at 0m. (Appendix A, Fig. 3A). The 0m temperatures at the stations 248, 249, 250 and 232 were -0.46°C, -1.69°C, -1.63°C and 3.51°C while the 50m temperatures were 0.93°C, 0.96°C, -0.82°C and 4.58°C respectively. As much as 12 out of the 24 stations sampled had lower temperatures at 50m than at 0m. The mean decrease in temperature from 0m to 50m was 0.47°C. The station with the greatest decrease in temperature from 0m to 50m was station 244 located southeast in the sampling area with a 0m temperature of 5.44°C and a 50m temperature of 4.61°C. An overview of temperature characteristics for the years 2006, 2007 and 2009 is in Table 3.



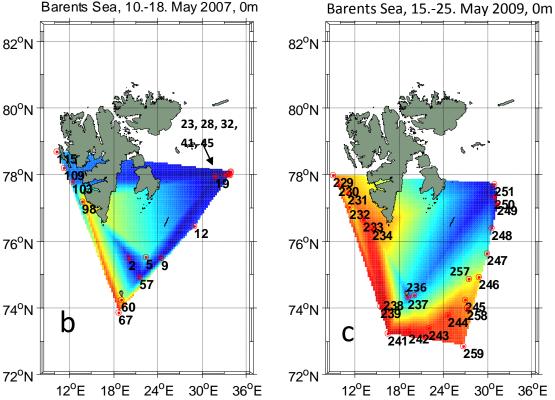


Figure 4: Sea surface temperatures (0m) in the Barents Sea, May 2006 (**a**), 2007, (**b**) and 2009 (**c**). Note missing 0m sea temperature data at station 245 in 2009 (station location is though shown). Sampling stations are marked with red circles. Bold black numbers are station numbers. Temperature scale color-bar is shown in **a**.

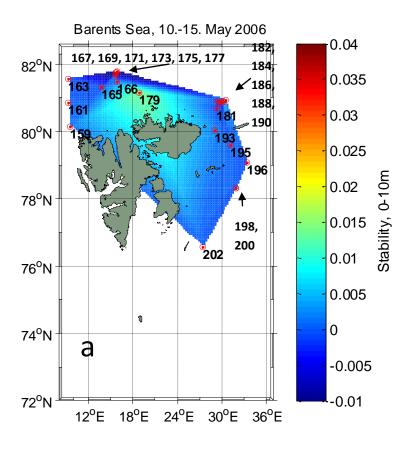
Table 3: Overview of sea temperature characteristics in the Barents Sea in May in 2006, 2007 and 2009 at 0m, 10m and 50m station depth. Maximum (Max. T°C) and minimum (Min. T°C) temperatures are shown as well as percent of stations (stations at specific year and station depth) with higher and lower temperatures than the mean for all stations and depths (=0.73°C). Note that stations with missing data are not included. Main areas with high and low temperatures are also mentioned.

Year	Depth	Max.	Stations	Main areas with high	Min.	Stations	Main areas with low
	(m)	T (°C)	>0.73°C	temperatures	$T(^{0}C)$	<0.73°C	temperatures
			(%)			(%)	
2006	0	2.78	8	Outside northwest Svalbard	-1.85	92	The rest of the sampled area was in general below 0°C
2006	10	2.80	8	Same trend as at 0m	-1.86	92	Same trend as at 0m
2006	50	3.54	8	Same trend as at 0m	-1.86	92	Same trend as at 0m
2007	0	5.89	18	North of Bjørnøya and at the southernmost station west of Svalbard	-1.88	82	At the ice edge east of Svalbard, the northernmost stations west of Svalbard and northeast of Bjørnøya
2007	10	5.88	18	Same trend as at 0m	-1.88	82	Same trend as at 0m
2007	50	5.29	37.5	Same trend as at 0m	-1.88	62.5	Same trend as at 0m
2009	0	6.27	74	West of Svalbard and south in the sampling area	-1.72	26	Just south of Bjørnøya and at the ice edge east of Svalbard
2009	10	6.27	75	Same trend as at 0m	-1.75	25	Same trend as at 0m
2009	50	6.31	87	Same trend as at 0m	-1.65	13	Same trend as at 0m

The variation in stability (computed as the density difference from 0m to 10m depth) in the sampled areas in the Barents Sea varied between years and areas. In 2006 the surface stabilities varied between -0.01 and 0.01 (Fig. 5a). The highest stability was at station 179, recall that station 179 had a temperature difference of 2.55°C between 0m and 10m. Station 169 had the lowest stability. Both stations were located north of Svalbard whereas station 169 was located in the ice.

The highest stability in 2007 was registered at station 60 just south of Bjørnøya, 0.004, while the lowest stability was at station 103 located on the western side of Svalbard, -0.004 (Fig. 5b).

In 2009 the highest stability was registered at the northernmost station, station 229 located west of Svalbard (0.58) and the lowest stability was at station 233 also west of Svalbard (-0.003) (Fig. 5c). An overview of surface stability for the years 2006, 2007 and 2009 is in Table 4.



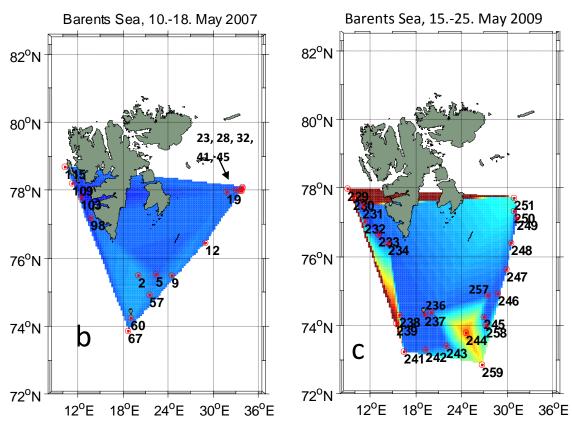


Figure 5: Stability ($\Delta \sigma t$ difference, the degree of stability was computed as the density difference from 0m to 10m depth) in the Barents Sea in May in 2006 (a), 2007 (b) and 2009 (c). Note missing stability data at station

245 in 2009 (station location is though shown). Sampling stations are marked with red circles. Bold black numbers are station numbers. Stability color-bar is shown in **a**.

Table 4: Overview of stability (density difference from 0m to 10m depth) in the Barents Sea in May in 2006, 2007 and 2009. Maximum (Max. stab.) and minimum (Min. stab.) stabilities are shown as well as percent of stations (stations at specific year and depth) with higher and lower stabilities than the mean for all the years (0.01). Note that stations with missing data are not included. Main areas with high and low stabilities are also shown.

Year	Max. stab.	Stations >0.01 (%)	Main areas with high stabilities	Min. stab.	Stations <0.01 (%)	Main areas with low stabilities
2006	0.014	4	Area between Nordaustlandet and the ice edge	-0.014	96	The stability was evenly low in the rest of the area
2007	0.004	0		-0.004	100	
2009	0.580	22	The northernmost areas west and east of Svalbard, west of Bjørnøya and southeast in the sampling area	-0.003	78	The stability was evenly low in the rest of the area

3.2 Environmental variables, East Finnmark, May in 2009

The 0m sea temperature range in East Finnmark was from 4.45°C to 6.15°C (Fig. 6). The highest temperature was observed northwest of Nordkapp at station 260, the outermost station. The temperatures decreased from the outermost stations to the inner part of the two main fjords sampled (Porsangerfjord and Varangerfjord). However, exceptions were stations 265 located in the outer part of Jarfjord and 264 located in the outer part of Kobbholmfjord which both had temperatures of ca. 5.5°C. Jarfjord and Kobbholmfjord are located in the outer part of Varangerfjord, more precise on the southern side. The lowest 0m temperatures were observed at stations 275 in the inner part of Porsangerfjord and 270 in the inner part of Varangerfjord, 4.45°C and 4.64°C respectively. The 0m and 10m temperatures were comparable between the sampled stations except from stations 264 and 267 in Varangerfjord where the temperatures at 0m were higher than at 10m, i.e. 0m temperatures were 5.49°C and 5.38°C and 10m temperatures were 4.11°C and 4.12°C respectively (Appendix A, Fig. 4A). In addition the 0m temperature (4.69°C) was lower than the 10m temperature (5.56°C) at station 272 located in Porsangerfjord. All 50m temperatures were lower than the surface ones. The temperature differences between 50m and 0m were however minimal at the outermost stations (160, 161, 162 and 163) where the mean decrease in temperature was 0.57°C from 0m to 50m. The greatest temperature difference between 50m and 0m were observed in Porsangerfjord at

stations 271, 272 and 275 where the mean temperature decreased with 5.09°C from 0m to 50m. The mean temperature for all depths was 4.38. All 0m temperatures were higher than the mean temperature and 75% of the 10m temperatures and 50% of the 50m temperatures were higher than the mean temperature.

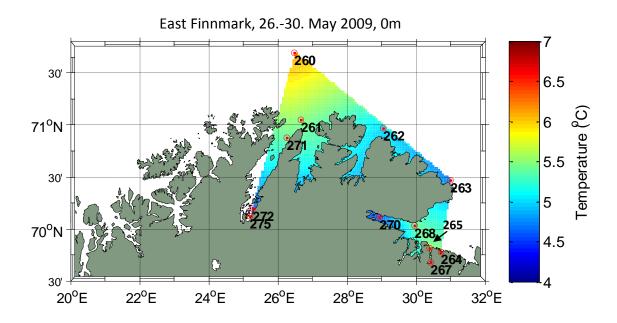


Figure 6: Sea surface temperatures (0m) in East Finnmark in May in 2009. Sampling stations are marked with red circles. Bold black numbers are station numbers.

In East Finnmark the highest stabilities were at stations 271 located in the outer part of Porsangerfjord and 267 in the inner part of Jarfjord, both with a stability of ca. 3.0 (Fig. 7). The lowest stabilities were at stations 264 in the outer part of Kobbholmfjord and 265 in the outer part of Jarfjord, both with stability -0.13. The mean stability (calculated as the density difference from 0m to 10m depth) for all stations was 0.68, whereas 25% of the stations had higher stabilities than this mean value.

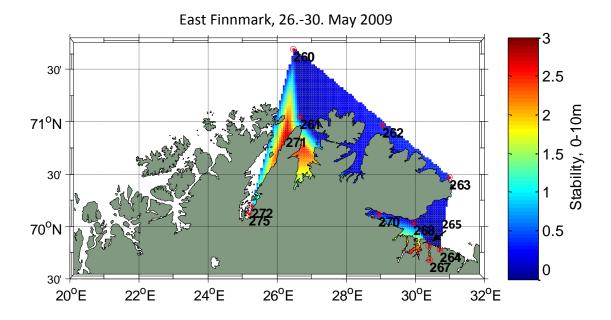


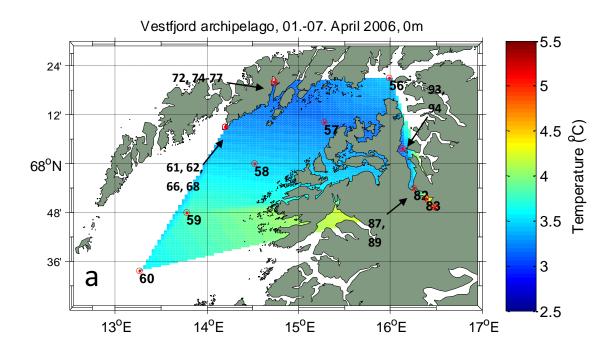
Figure 7: Stability ($\Delta \sigma t$, the degree of stability was computed as the density difference from 0m to 10m depth) in East Finnmark in May 2009. Sampling stations are marked with red circles. Bold black numbers are station numbers.

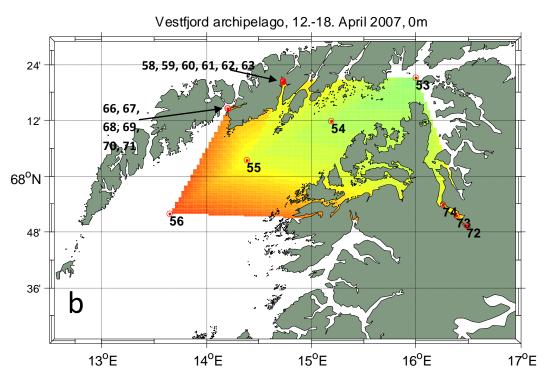
3.3 Environmental variables, Vestfjord archipelago, April in 2006, 2007 and 2009

The 0m sea temperature range in the Vestfjord archipelago in April 2006 was from 2.88°C to 4.47°C in the sampled area (Fig. 8a). The highest 0m temperature was measured at station 89, the innermost station in Tysfjord. The lowest 0m temperature was measured at station 76 located in Austnesfjord (Fig. 8a). A dirunal sampling station was set up both in Henningsværstraumen, four samplings, and in Austnesfjord including five samplings (Fig. 8a). The individual samplings at the diurnal stations are not shown on the surface color map in Figure 8a. This is since the stations were sampled in the same geographical area and consequently the mean of the stations are expressed in the plot at each location since the temperature ranges were minimal. The temperature difference between 0m and 10m was minimal, on average the temperatures decreased only with 0.042°C from 0m to 10m at all stations (Appendix A, Fig. 5A). The greatest difference between 0m and 10m temperature was at station 76 (the station with the lowest 0m temperature in the area sampled) where the temperature decreased with 0.29°C (Appendix A, Fig. 5A). The temperature difference between 0m and 50m could only be calculated at stations 82, 93 and 94 located in Tysfjord, since these stations were the only ones where both the 0m and 50m temperatures were measured. Here the temperature differences between 0m and 50m were great. On average the 50m temperatures, that varied between 0.06°C and 0.26°C were 3.19°C lower than the 0m temperatures, which again were between 3.24°C and 3.47°C (Appendix A, Fig. 5A).

In April 2007 the 0m sea temperatures varied between 4.03°C and 4.95°C in the sampled area (Fig. 8b). The highest and the lowest 0m temperatures were at stations 56 which was the outermost station in Vestfjorden and 53, the innermost station in Vestfjorden (Fig. 8b). Note that the 0m temperature at station 56 was missing and was replaced by the measured sea temperature at 5m. As in 2006, diurnal samplings were performed in Henningsværstraumen and in Austnesfjord. At both diurnal stations six samplings were made. Maximum and minimum 0m temperatures in Henningsværstraumen were 4.81°C and 4.69°C and in Austnesfjord 4.65°C and 4.39°C respectively. There were no great temperature differences between 0m and 10m in the area. However, exceptions were stations 72, 73 and 74 located in Tysfjord where temperatures were slightly lower at 10m than at 0m, i.e. the mean difference for all the three stations were 0.17°C (Appendix A, Fig. 6A). Station 53 had the highest difference in temperature between surface and 50m, i.e. 0.49°C (Appendix A, Fig. 6A).

In April 2009 the 0m sea temperature range was from 3.35°C to 5.30°C at the sampled stations. The highest temperature was at station 165, the innermost station in Tysfjord, and the lowest temperature was at station 161 located in Austnesfjord (Fig. 8c). The three stations in Henningsværstraumen and the two stations in Austnesfjord had mean temperatures of 3.51°C and 3.63°C respectively. The temperatures at 0m and 10m were comparable. Exceptions were stations 161 and 162 located in Austnesfjord where the 0m temperatures were 3.35°C and 3.90°C, while the 10m temperatures were 4.22°C and 4.18°C respectively (Appendix A, Fig. 7A). Another exception was station 149 located in the middle of the Vestfjorden transect, where the temperature at 0m (4.18°C) was higher than the temperature at 10m (3.89°C). In contrast to the other years, the 50m temperatures were higher than the surface temperatures at all stations where the 50m temperature was measured i.e. at stations 147, 148, 149, 151 and 153 constituting the Vestfjorden transect (Appendix A, Fig. 7A). The greatest difference between 0m (3.47°C) and 50m temperature (5.10°C) was at station 148, located in the inner part of the Vestfjorden transect. An overview of temperature characteristics for the years 2006, 2007 and 2009 is in Table 5.





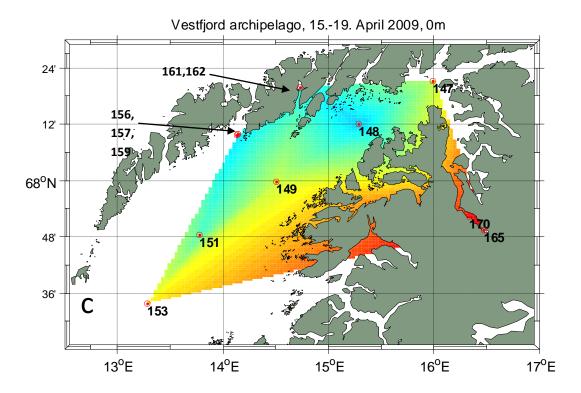


Figure 8: Sea surface temperatures (0m) in the Vestfjord archipelago in April in 2006 (a), 2007 (b) and 2009 (c). Note missing 0m sea temperature data at stations 58 and 87 in 2006 and at station 170 in 2009 (station location is though shown). Sea temperature at 0m is missing for station 56 in 2007, and was replaced by the 5m temperature. Sampling stations are marked with red circles. Bold black numbers are station numbers. Temperature scale color-bar is shown in **a**.

Table 5: Overview of temperature characteristics in the Vestfjord archipelago in April in 2006, 2007 and 2009. Maximum (Max. T°C) and minimum (Min. T°C) temperatures are shown as well as percent of stations (stations at specific year and depth) with higher and lower temperatures than the mean for all stations and depths (3.68°C). Note that stations with missing data are not included. Main areas with high and low temperatures are also shown.

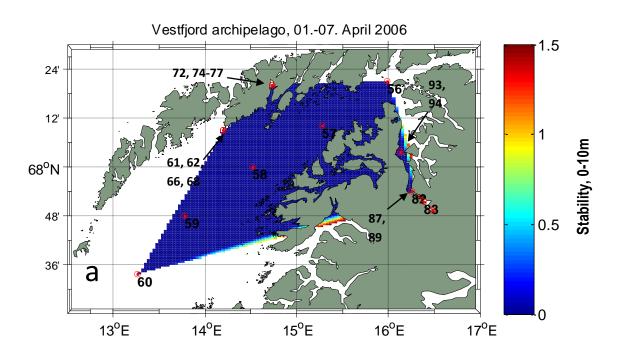
Year	Depth	Max.	Stations	Main areas with high	Min.	Stations	Main areas with low
	(m)	T (°C)	>3.68°C	temperatures	T (°C)	<3.68°C	temperatures
			(%)			(%)	
2006	0	4.47	17	The innermost part of	2.88	83	Austnesfjord and
				Tysfjord and the second			Henningsværstraumen
				outermost station in			
				Vestfjorden			
2006	10	4.20	19	Same trend as at 0m	3.04	81	Same trend as at 0m
2006	50	0.26	0		0.06	100	Tysfjord (only area sampled)
2007	0	4.95	100	Austnesfjord and outermost part of Vestfjorden	4.03	0	
2007	10	4.95	100	Same trend as at 0m	3.99	0	
2007	50	4.94	100	Same trend as at 0m, except the innermost part of Vestfjorden was the second warmest area	4.16	0	
2009	0	5.30	55	Tysfjord, Vestfjorden transect (except the second innermost station)	3.35	45	Henningsværstraumen and Austnesfjord
2009	10	5.30	67	Same trend as at 0m, in addition to one station in Austnesfjord	3.45	33	Same trend as at 0m
2009	50	5.10	100	Vestfjorden (only area sampled)	4.32	0	

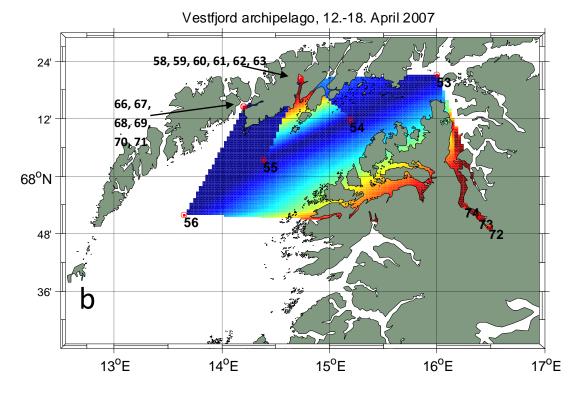
The surface stabilities (density difference between 0m and 10m depth) in the Vestfjord archipelago were relatively low in the Vestfjorden transect and in Henningsværstraumen compared to the two sampled fjords (Austnesfjord and Tysfjord) (Fig. 9a, b and c). In 2006 the highest stability was at station 83 located in Tysfjord (2.35) (Fig. 9a). The second highest stability was 0.08 at station 76 in Austnesfjord. The lowest stability was -0.001 outside Henningsværstraumen at station 66.

In 2007 the highest stabilities were in Tysfjord at stations 73, 72 and 74 (3.93, 3.07 and 1.90 respectively). High stability (1.92) was also observed at station 62 in Austnesfjord (Fig. 9b).

The lowest stability was at station 71 which was part of the diurnal sampling programme in Henningsværstraumen (-0.01).

In 2009 the highest stabilities were in Austnesfjord and Tysfjord (Fig. 9c). Stations 161 and 162 in Austnesfjord had stabilities 0.54 and 0.18 respectively, while station 165 in Tysfjord had 0.33. The lowest stability was just outside Henningsværstraumen at station 157 (-0.03). An overview of stability characteristics for the years 2006, 2007 and 2009 is in Table 6.





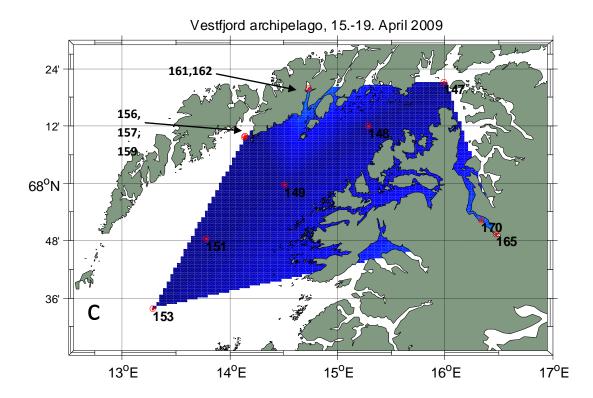


Figure 9: Stability (Δσt difference, the degree of stability was computed as the density difference from 0m to 10m depth) in the Vestfjord archipelago in April in 2006 (a), 2007 (b) and 2009 (c). Note missing stability data at stations 58, 87 89, 93 and 94 in 2006, station 68 in 2007 and station 170 in 2009 (station location is though shown). Sampling stations are marked with red circles. Bold black numbers are station numbers. Stability colorbar is shown in **a**.

Table 6: Overview of stability (density difference from 0m to 10m depth) characteristics in the Vestfjord archipelago in April in 2006, 2007 and 2009. Maximum (Max. stab.) and minimum (Min. stab.) stabilities are shown as well as percent of stations (stations at specific year and depth) with higher and lower stabilities than the average for all the years (0.01). Note that stations with missing data are not included. Main areas with high and low stabilities are also shown.

Year	Max. stab.	Stations >0.36	Main areas with high stabilities	Min. stab.	Stations <0.36	Main areas with low stabilities
		(%)			(%)	
2006	2.350	7	Tysfjord	-0.001	93	Generally low in the rest of the area
2007	3.930	29	Tysfjord and Austnesfjord	-0.010	71	Generally low in the rest of the area
2009	0.540	9	Austnesfjord	-0.030	91	Generally low in the rest of the area

3.4 Identification of Phaeocystis spp., molecular approach

The Blast search performed in GenBank showed that the four sequences i.e. the F and R sequence from *Phaeocystis* samples 76.2 (AMB culture collection) and 89 (environmental sample), were significantly similar to the sequences in GenBank which is shown in Table 7.

My sequences showed maximum identity to *Haptophyceae* sp., *Phaeocystis* sp., *Phaeocystis* pouchetii, *Phaeocystis cordata* and *Phaeocystis antarctica*.

Table 7: Sequences uploaded from NCBI GenBank producing significant alignments to own *Phaecystis* spp. sequences (sample ID 76.2 and 89) showing GenBank accession number, "type" description and maximum score and identity.

Accession	Description	Max. score	Max. ident.
EF432545.1	Haptophyceae sp. W5-1 18S ribosomal RNA gene,		
	partial sequence	235	100
EF432535.1	Haptophyceae sp. W6-4 clone A1 18S ribosomal		
	RNA gene, partial sequence	235	100
EF432520.1	Haptophyceae sp. 8 clone B1 18S ribosomal RNA		
	gene, partial sequence	235	100
EF432517.1	Haptophyceae sp. 8 clone A1 18S ribosomal RNA		
	gene, partial sequence	235	100
AM491023.1	Phaeocystis sp. PLY559 partial 18S rRNA gene,		
	strain PLY 559	235	100
AF182114.1	Phaeocystis pouchetii isolate P360 small subunit		
	ribosomal RNA, complete sequence	235	100
AF180940.1	Phaeocystis sp. PLY559 small subunit ribosomal		
	RNA gene, complete sequence	235	100
AJ278036.1	Phaeocystis pouchetii 18S rRNA gene, strain P361	235	100
AF163147.1	Phaeocystis cordata small subunit ribosomal RNA		
	gene, complete sequence	235	100
X77475.1	P.pouchetii (Hariot) Lagerheim 18S rRNA gene	235	100
X77481.1	P.antarctica Karsten SK23 18S rRNA gene	235	100
X77479.1	P.antarctica Karsten SK21 18S rRNA gene	235	100
X77478.1	P.antarctica Karsten SK20 18S rRNA gene	235	100
X77480.1	P.antarctica Karsten SK22 18S rRNA gene	235	100

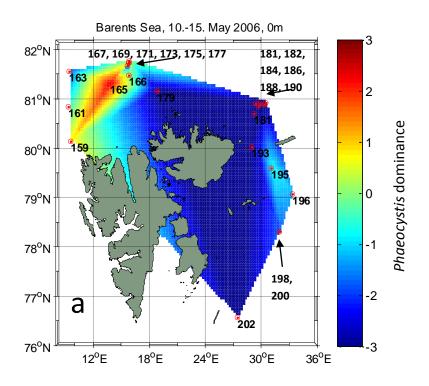
3.5 P. pouchetii vs. diatom dominance in the Barents Sea 2006

From the depth profile, three depths (0m, 10m and 50m) were chosen to illustrate the horizontal variation in dominance between *P. pouchetii* and diatoms ("*Phaeocystis* dominance", see Material and Methods) (Fig. 10). At 0m, a majority (i.e. at 16 out of 24 stations) of the stations were dominated by diatoms (Fig. 10a). The highest diatom dominance value (-3.24) was detected northeast of Svalbard at station 184. This station, situated at the ice edge, was one of six stations in a diurnal sampling programme. Due to ice drift the stations

were not sampled at the exact same location during the diurnal sampling programme. All the other stations in the diurnal sampling programme had diatom dominance as well, where average was -3.05 for the six stations. The second highest value of diatom dominance (-3.08) was at the southernmost station, i.e. station 202 (Fig. 10a). *P. pouchetii* dominated at five stations and all stations were located northwest in the sampling area, north of Svalbard (Fig. 10a). A peak in *P. pouchetii* dominance (2.35) was observed at station 165 (Fig. 10a). The four other stations with *P. pouchetii* dominance were 159, 161, 167 and 173 where the two last stations were part of the diurnal sampling programme north of Svalbard (Fig. 10a). Three stations were neither dominated by *P. pouchetii* or diatoms, i.e. they were "neutral" (having ~ equal abundance or not precent at all). Two of these stations, stations 169 and 175 were included in the diurnal sampling programme north of Svalbard. The third station (166) was located in the transition between *P. pouchetii* dominance and diatom dominance (Fig. 10a).

Much of the same trend in "*Phaeocystis* dominance" distribution was present at 10m (Fig. 10a and b). At 10m 17 stations were dominated by diatoms, six by *P. pouchetii* and one station was "neutral". The diatom dominance at 0m and 10m was geographically quite similar (Fig. 10a and b). Peak in diatom dominance (-3.29) was observed at station 184 and the second highest value (-3.22) was at station 202. The *P. pouchetii* dominance distribution was also quite similar at 0m and 10m (Fig. 10a and b). Peak in *P. pouchetii* dominance (2.71) was observed at station 159. Different from 0m, *P. pouchetii* dominance was observed at station 200, east of Kong Karls Land (Fig. 10b). This station had the eight highest value of diatom dominance at 0m.

At 50m the diurnal sampling programme north of Svalbard was not sampled, except station 171 which was dominated by diatoms. The diurnal sampling programme northeast of Svalbard and station 179 located north of Svalbard was also not sampled at 50m. From the 12 stations sampled, *P. pouchetii* and diatoms dominated at six stations each and the "*Phaeocystis* dominance" distribution was quite similar to 10m (Fig. 10b and c). The only great difference between 10m and 50m was the shift in dominance from diatoms to *P. pouchetii* at station 202. Recall though, at both 0m and 10m station 202 had the second highest value of diatom dominance. An overview of "*Phaeocystis* dominance" for the year 2006 is in Table 8.



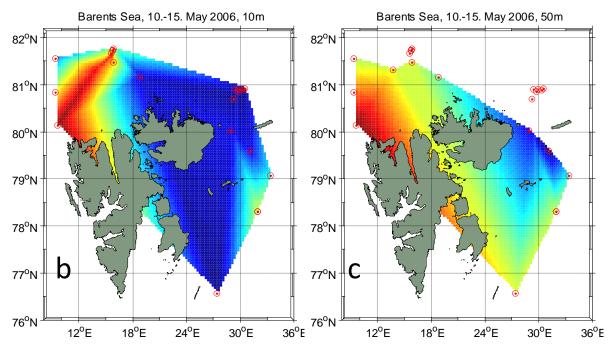


Figure 10: *Phaeocystis* dominance (negative value denotes diatom dominance) in the Barents Sea in May 2006 at 0m (a), 10m, (b) and 50m (c). Note, 50m is not sampled at station 179 (station location is though shown). Sampling stations are marked with red circles. Bold black numbers are station numbers. *Phaeocystis* dominance color-bar is shown (*P. pouchetii* > 0 < diatoms) in a.

3.6 P. pouchetii vs. diatom dominance in the Barents Sea 2007

At 0m *P. pouchetii* and diatoms dominated at eight stations each, leaving one station (station 45), situated in the ice east of Svalbard, where only flagellates were present. Peak dominance

of *P. pouchetii* (2.02) was observed at station 5 located south of Edgeøya (Fig. 11a). The five stations 9, 12, 19, 23 and 28 located on the east side in the sampling area, between station 5 and the ice edge, were also dominated by *P. pouchetii* (Fig. 11a). *P. pouchetii* dominance was also observed at the two northernmost stations, station 115 and 109, on the west side of Svalbard. However, the two other stations, station 103 and 98, in this area were dominated by diatoms (Fig. 11a). The highest diatom dominance was observed at stations 57 (-2.56) and 2 (-1.80), located just southwest of the *P.pouchetii* peak dominance station (station 5) (Fig. 11a). High diatom dominance (-2.12) was also observed at station 32 situated in the ice. In the ice a diurnal sampling programme was set up with five samplings at approximately the same location. Concerning time, the first two stations were dominated by *P. pouchetii*, the second two by diatoms and the last one was the station where both were absent.

At 10m as much as 13 stations were dominated by diatoms and four stations were dominated by *P. pouchetii*. The four stations dominated by *P. pouchetii* (stations 9, 12, 19 and 67) were all located on the east side in the sampled area (Fig. 11b). The highest *P. pouchetii* dominance (0.55) was observed at station 19 and the second highest (0.34) at station 12, both located northeast in the sampled area. The highest diatom dominance (-2.55) was observed at the northernmost station, station 115, and the second highest diatom dominance (-2.34) was observed at station 57 located northeast of Bjørnøya (Fig. 11b).

As for 10m, at 50m diatoms dominated at more stations than *P. pouchetii*. Of the 17 stations, nine stations were dominated by diatoms and five by *P. pouchetii*, the two stations (32 and 45) situated in the ice were "neutral", and no abundance data was sampled from station 5 (Fig. 11c). At station 32 it was an equal abundance of *P. pouchetii* and diatoms, while they were not present at all at station 45. As for 10m, at 50m *P. pouchetii* was dominating on the east side in the sampled area. In addition *P. pouchetii* dominated at the northernmost station (115) on the western side of Svalbard at 50m (Fig. 11c). Recall, at 10m this station (115) had the highest peak dominance of diatoms. The highest *P. pouchetii* dominance (1.80) was observed at station 41 and the second highest (0.52) at station 23, both included in the diurnal sampling programme situated in the ice east of Svalbard. The highest peak dominance of diatoms (-2.73) at 50m was observed at the ice edge at station 19 and the second highest (-2.26) at station 2 north of Bjørnøya (Fig. 11c). An overview of "*Phaeocystis* dominance" for the year 2007 is in Table 8.

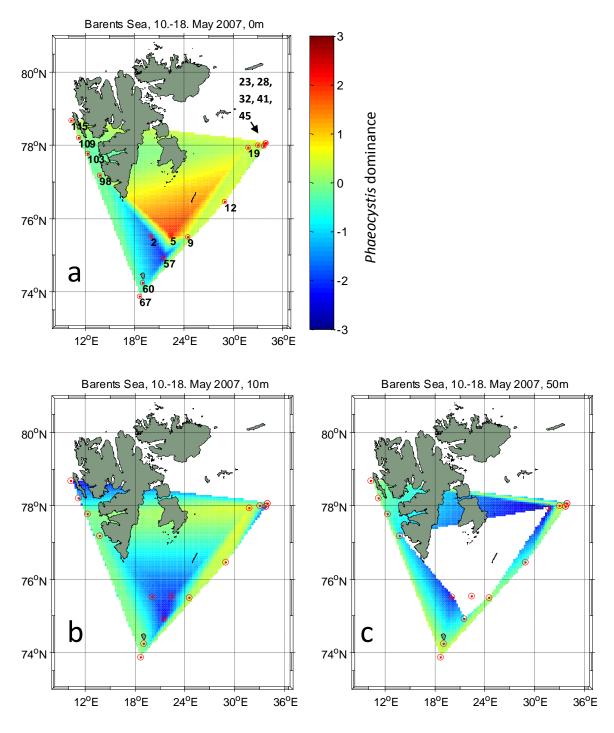


Figure 11: *Phaeocystis* dominance (negative value denotes diatom dominance) in the Barents Sea in May 2007 at 0m (**a**), 10m, (**b**) and 50m (**c**). Sampling stations are marked with red circles. Bold black numbers are station numbers. *Phaeocystis* dominance color-bar is shown (*P. pouchetii* > 0 < diatoms) in **a**.

3.7 P. pouchetii vs. diatom dominance in the Barents Sea 2009

Of the 24 stations sampled at 0m, 12 were dominated by diatoms and 11 by *P, pouchetii*. Station 245 located east of Bjørnøya was not sampled (Fig. 12a). The highest diatom dominance values were observed at stations 236 (-3.09) on the eastern side of Bjørnøya and

241 (-2.04) located southwest of Bjørnøya. The highest *P. pouchetii* dominance values were observed east of Bjørnøya at stations 257 (0.74) and 258 (0.56).

At 10m all 24 station were sampled, whereas 10 of these were dominated by diatoms and 14 by *P. pouchetii* (Fig. 12b). The area with the highest diatom dominance had shifted slightly to the east compared with the stations with the highest diatom dominance at 0m. The highest diatom dominances were now observed at stations 237 (-1.92) and 242 (-1.88). The area with the highest *P. pouchetii* dominance was also comparable from 0m to 10m. The highest *P. pouchetii* dominances at 10m were observed at stations 246 (3.41) and 245 (3.16), which were the nearby stations to the 0m stations 257 and 258, having the highest *P. pouchetii* dominance at 0m. High *P. pochetii* dominance (2.49) was also observed at station 234 located southwest of Sørkapp Land.

At 50m all stations, except station 237 south of Bjørnøya, were sampled (Fig. 12c). From the 23 sampled stations diatoms and *P. pouchetii* dominated on 10 stations each while stations 232 and 233 located west of Sørkapp Land and 239 southwest of Bjørnøya were "neutral". The area north of Bjørnøya had quite similar distribution in "*Phaeocystis* dominance" at 10m as at 50m (Fig. 12b and c). However, the second highest dominance of *P. pouchetii* (2.59) was now observed at station 234 west of Sørkapp Land. Recall, at 10m station 234 had the third highest dominance of *P. pouchetii*. The highest *P. pouchetii* dominance (2.92) was observed at station 245 which had the second highest *P. pouchetii* dominance at 10m. The highest diatom dominance (-2.27) was observed east of Bjørnøya at station 244, close to station 245 having the highest *P. pouchetii* dominance, while the second highest diatom dominance (-2.04) was east of Bjørnøya at station 238. An overview of "*Phaeocystis* dominance" for the year 2009 is in Table 8.

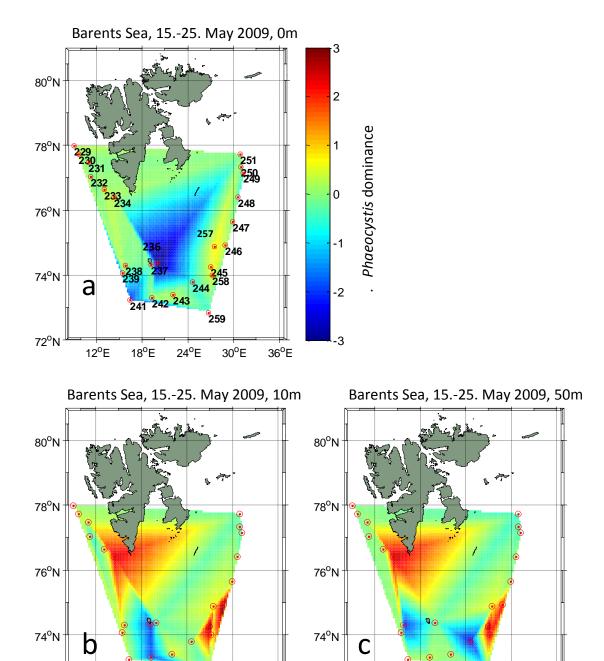


Figure 12: *Phaeocystis* dominance (negative value denotes diatom dominance) in the Barents Sea in May 2009 at 0m (a), 10m, (b) and 50m (c). Note missing data at station 245 at 0m and station 237 at 50m (station location is though shown). Sampling stations are marked with red circles. Bold black numbers are station numbers. *Phaeocystis* dominance color-bar is shown (*P. pouchetii* > 0 < diatoms) in **a**.

72⁰N

12°E

24°E

18°E

30°E

36°E

3.8 P. pouchetii vs. diatom dominance in East Finnmark 2009

30°E

36°E

72°N

12°E

18°E

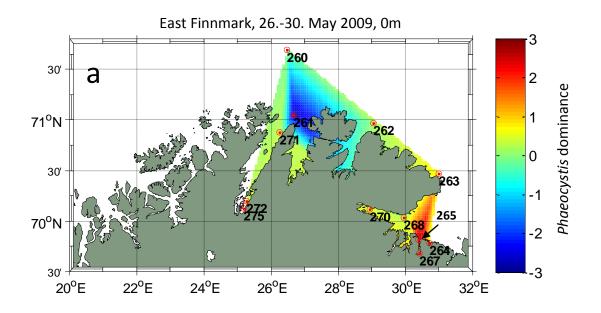
24°E

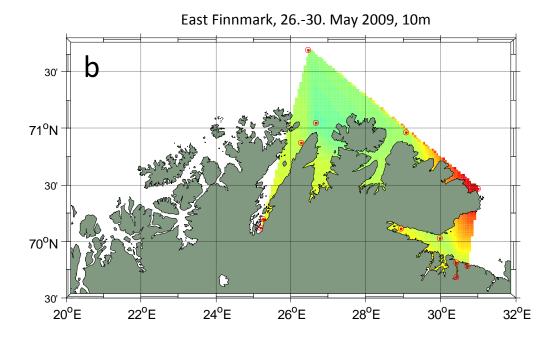
A total of 12 stations were sampled in East Finnmark. At 0m two stations were dominated by diatoms and 10 stations by *P. pouchetii* (Fig. 13a). The two stations dominated by diatoms

were 261 (-2.77) located just outside Porsangerfjord and the offshore station 260 (-0.14). The highest *P. pouchetii* dominances were observed in Jarfjord at stations 265 (2.73) and 267 (0.92). Station 263 just outside Vardø had the third highest *P. pouchetii* dominance (0.76).

At 10m it was station 263 that had the highest *P. pouchetii* dominance (2.81) while station 267 still (according to 0m) had the second highest *P. pouchetii* dominance (0.73) (Fig. 13b). Only one station was dominated by diatoms, station 261 just outside Porsangerfjord with a diatom dominance of -0.24.

At 50m three stations were dominated by diatoms and 9 by *P. pouchetii* (Fig. 13c). The highest diatom dominance (-2.49) was now observed at the offshore station 260. The second highest diatom dominance (-0.47) was observed outside Porsangerfjord at station 261, which was the station with the highest diatom dominances at 0m and 10m. Station 262 outside Vardø was also dominated by diatoms (-0.24). The highest *P. pouchetii* dominance (2.74) was observed in the innermost station (275) in Porsangerfjord while the second highest (1.01) was observed at station 263 which had the highest *P. pouchetii* dominance at 10m (Fig. 13b and c). An overview of "*Phaeocystis* dominance" for the year 2009 is in Table 8.





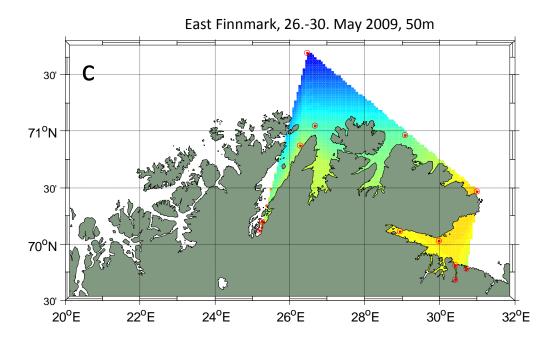


Figure 13: *Phaeocystis* dominance (negative value denotes diatom dominance) in East Finnmark in May 2009 at 0m (a), 10m, (b) and 50m (c). Sampling stations are marked with red circles. Bold black numbers are station numbers. *Phaeocystis* dominance color-bar is shown (*P. pouchetii* > 0 < diatoms) in **a**.

Table 8: Overview of *Phaeocystis* dominance characteristics in the Barents Sea in May in 2006, 2007 and 2009 and East Finnmark in May 2009 (*). Maximum *P. pouchetii* dominance (Max. Pp) and diatom dominance (Max. "Tot. D") are shown as well as percent of stations (stations at specific year and depth) dominated by *P. pouchetii* (Pp) and diatoms ("Tot. D"). Note stations with missing data are not included. Main areas dominated by *P. pouchetii* and diatoms are also shown.

Year	Depth	Max	Stations	Main areas dominated	Max.	Stations	Main areas dominated by
	(m)	. Pp	P. po	by P. pouchetii	"Tot.	"Tot.	diatoms
			(%)		D"	D" (%)	
2006	0	2.35	24	North of Svalbard	-3.24	76	Rest of the area
2006	10	2.71	26	Same trend as at 0m	-3.29	74	Same trend as at 0m
2006	50	2.63	50	Rest of the area	-3.30	50	Northeast of Svenskeøya
2007	0	2.02	50	Between Bjørnøya and the ice edge east of Svalbard	-2.56	50	Just northeast of Bjørnøya
2007	10	0.55	24	At the ice edge east of Svalbard	-2.55	76	Just northeast of Bjørnøya and the northernmost stations west of Svalbard
2007	50	1.80	36	Same trend as at 10m	-2.73	64	Same trend as at 10m
2009	0	0.74	48	West of Svalbard and east in the sampling area	-3.09	52	East of Bjørnøya and southeast in the sampling area
2009	10	3.41	58	Same trend as at 0m	-1.92	42	South of Bjørnøya
2009	50	2.92	50	Same trend as at 0m	-2.27	50	West and southeast of Bjørnøya
2009*	0	2.73	83	Jarfjord and outside Vardø	-2.77	17	Outside Porsangerfjord
2009*	10	2.81	92	Outside Vardø	-0.24	8	Same trend as at 0m
2009*	50	2.74	75	Same trend as at 0m	-2.49	25	Same trend as at 0m

^{*}East Finnmark

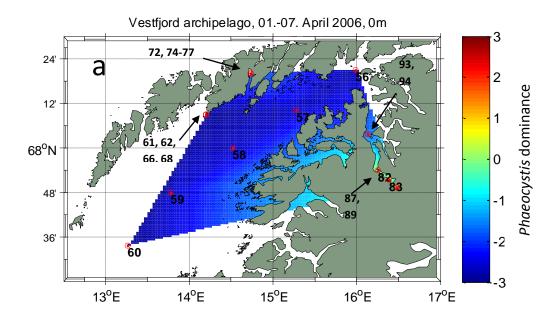
3.9 P. pouchetii vs. diatom dominance in the Vestfjord archipelago 2006

In the Vestfjord archipelago, 20 stations were sampled. However, at stations 58 in the Vestfjorden transect and 87 in the Tysfjord transect species abundance data from 0m was missing. Of the 18 stations sampled, only two stations (72 and 77, located in Austnesfjord) were dominated by *P. pouchetii*, with quotient values (see Material and Methods) of 0.52 and 0.24 respectively (Fig. 14a). These two stations were part of the diurnal sampling programme. Of the remaining 16 stations, station 82 located in Tysfjord was "neutral" (similar amounts of diatoms and P. pouchetii) while the rest of the stations were dominated by diatoms (Fig. 14a). As mentioned earlier, each individual sampling in the diurnal sampling programme does not

show in the surface color map since only the mean of the stations values are expressed in the plot. However, all stations in Henningsværstraumen were dominated by diatoms and the mean value for these four stations was -2.93. In Austnesfjord the mean value for the four stations in the diurnal sampling programme was -0.91. The three highest values of diatom dominance were at stations 62, 68 and 61 in the diurnal sampling programme in Henningsværstraumen, with values -3.03, -2.99 and -2.98 respectively (Fig. 14a).

At 10m diatoms were still dominating at most stations. Stations dominated by *P. pouchetii* had increased from two at 0m to five at 10m. As at 0m, station 82 was "neutral". The stations 87, 89, 93 and 94, all located in Tysfjord, were not sampled at 10m. The highest diatom dominance (-3.12) was observed at station 58 located in the middle of the Vestfjorden transect (Fig. 14b). The second highest value (-3.01) was observed at the innermost station in Vestfjorden. The next four highest diatom dominance values were all observed in the diurnal sampling programme in Henningsværstraumen, which had a mean value of -2.90. The diurnal sampling programme in Austnesfjord was also, according to the mean value -0.25, dominated by diatoms. However, four of the five stations, stations 77, 74, 72 and 76, were dominated by *P. pouchetii*, with values 0.54, 0.41, 0.35 and 0.17 respectively. The fifth station (75) was dominated by diatoms (-2.78). The last station dominated by *P. pouchetii* (0.22) at 10m was station 59.

The only stations sampled at 50m were stations 82, 87, 93 and 94 located in Tysfjord. All stations were dominated by diatoms. The diatom dominance value increased from the innermost part of the fjord and outwards. Stations 87 and 82 had values of -0.21 and -1.94 respectively. The two outermost stations 93 and 94 were sampled at the same geographical area only differing in time of sampling and had peak values of -2.59 and -2.20 respectively. An overview of *Phaeocystis* dominance for the year 2006 is in Table 9.



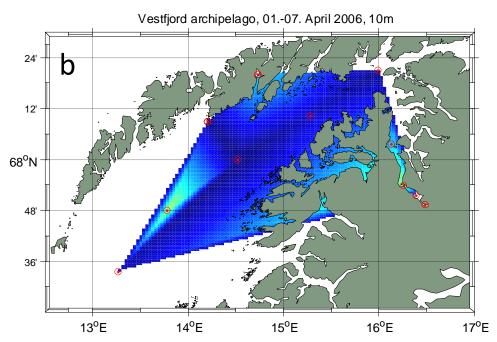


Figure 14: *Phaeocystis* dominance (negative value denotes diatom dominance) in the Vestfjord archipelago in April 2006 at 0m (a), 10m, (b). Note missing data at stations 58 and 87 at 0m and stations 87, 89, 93 and 94 at 10m (station location is though shown). Sampling stations are marked with red circles. Bold black numbers are station numbers. *Phaeocystis* dominance color-bar is shown (*P. pouchetii* > 0 < diatoms) in **a**.

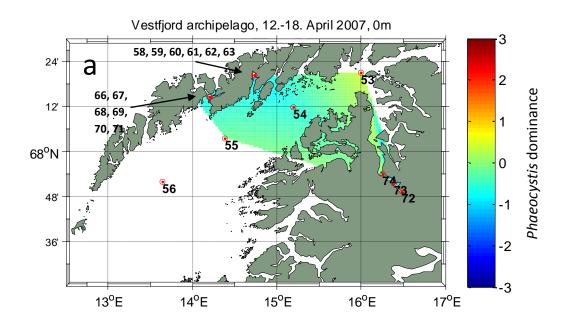
3.10 P. pouchetii vs. diatom dominance in the Vestfjord archipelago 2007

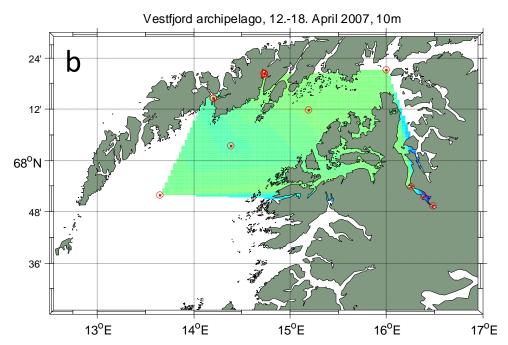
Of the 19 stations sampled, the majority, i.e. 13 stations, were dominated by diatoms while two were dominated by *P. pouchetii*. Stations 72 and 74 located in Tysfjord were "neutral". Stations 54 and 56 in the Vestfjorden transect were not sampled at 0m. The highest value of diatom dominance (-2.71) was observed at station 59 in Austnesfjord, station 73 in Tysfjord

had the second highest (-2.28) and station 68 in Henningsværstraumen the third highest (-1.06) (Fig. 15a). In Austnesfjord all six stations in the diurnal sampling programme were dominated by diatoms, and the mean value was -0.91. In Henningsværstraumen only one of the six stations in the diurnal sampling, station 66, was dominated by *P. pouchetii* (0.04). The mean value for the diurnal sampling in Henningsværstraumen was -0.32. The last station dominated by *P. pouchetii* (0.45) was the innermost station (53) in the Vestfjorden transect (Fig. 15a).

Diatoms still dominated at 10m for most of the stations. Of the 19 stations, at 10m, 12 stations were dominated by diatoms and five by *P. pouchetii*. Station 74 located in Tysfjord was "neutral" and station 68 in Henningsværstraumen was not sampled at 10m. The area with the highest diatom dominance at 10m was in Tysfjord at stations 72 and 73, -2.32 and -2.21 respectively (Fig. 15b). In the Vestfjorden transect all stations were also dominated by diatoms at 10m (Fig. 15b). It was only on the western side of Vestfjorden *P. pouchetii* dominance were observed. The highest *P. pouchetii* dominance (0.76) was observed at station 62 in Austnesfjord. Three of the six stations in the diurnal sampling programme in Austnesfjord were dominated by *P. pouchetii* and the average value for the six stations was 0.07. The second highest *P. pouchetii* dominance value (0.43) was observed at station 66 in Henningsværstraumen. In Henningsværstraumen two of the five stations in the diurnal sampling were dominated by *P. pouchetii* and the average dominance value for the five stations was -0.13.

The diurnal sampling programme in Austnesfjord and Henningsværstraumen were not sampled at 50m (Fig. 15c). From the seven stations sampled, five were dominated by diatoms and two by *P. pouchetii* at 50m. At stations dominated by diatoms the specific dominance values were even higher at 50m than at 0m and 10m (Fig. 15a, b and c). Station 55 located in Vestfjorden had the highest diatom dominance value (-2.36) in the sampled area at 50m. The three stations 73, 74 and 72 in Tysfjord were also dominated by diatoms, having the three highest values next to station 55, -2.25, -2.17 and -2.11 respectively. The two stations dominated by *P. pouchetii* were observed at the innermost (53) and outermost (56) stations in the Vestfjorden transect with a dominance value of 0.26 and 0.07 respectively (Fig. 15b). An overview of *Phaeocystis* dominance for the year 2007 is in Table 9.





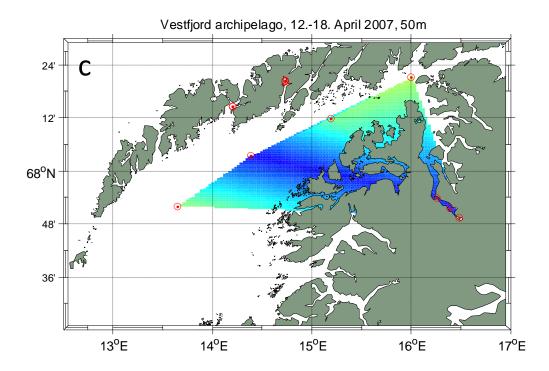


Figure 15: *Phaeocystis* dominance (negative value denotes diatom dominance) in the Vestfjord archipelago in April 2007 at 0m (**a**), 10m, (**b**) and 50m (**c**). Note missing data at stations 54 and 56 at 0m, station 68 at 10m and at all stations on the west side of Vestfjord archipelago at 50m (station location is though shown). Sampling stations are marked with red circles. Bold black numbers are station numbers. *Phaeocystis* dominance color-bar is shown (*P. pouchetii* > 0 < diatoms) in **a**.

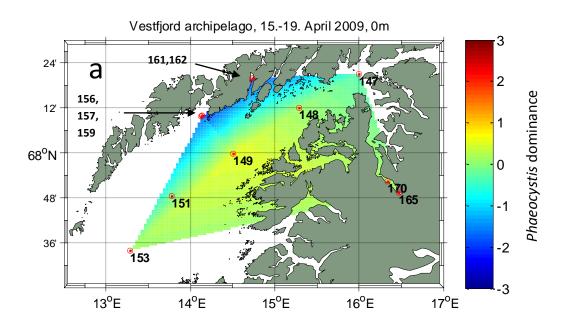
3.11 P. pouchetii vs. diatom dominance in the Vestfjord archipelago 2009

At 0m diatoms dominated at 7 stations, *P. pouchetii* at four (station 170 in Tysfjord was not sampled). The area with the highest diatom dominance at 0m was observed on the western side of Vestfjorden, where the highest value (-2.05) was at station 157 in Henningsværstraumen (Fig. 16a). All three stations (156, 157 and 159) sampled in Henningsværstraumen were dominated by diatoms with an average value of -1.86. The second highest diatom dominance (-2.0) was observed at station 162 in Austnesfjord. As in Henningsværstraumen, the two stations (161 and 162) in Austnesfjord were dominated by diatoms with an average value of -1.90. The highest *P. pouchetii* dominance (0.58), though relatively low, was observed at station 149 in the middle of the Vestfjorden transect and the second highest value (0.17) was at the innermost station in Tysfjord, station 165 (Fig. 16a).

At 10m *P. pouchetii* and diatoms dominated at six stations each. However, much of the same trend in *Phaeocystis* dominance distribution was observed at 10m as at 0m (Fig. 16a and b). The stations on the west side of Vestfjorden were dominated by diatoms while the east side was dominated by *P. pouchetii* at 10m. The greatest difference was that station 159 in

Henningsværstraumen had shifted in dominance from diatoms at 0m to *P. pouchetii* at 10m. In addition there was a shift in dominance at the two outermost stations of the Vestfjorden transect, where diatoms dominated at station 151 and *P. pouchetii* at station 153 at 0m while the opposite was observed at 10m (Fig. 16a and b). The highest diatom dominance values were still observed in Henningsværstraumen at stations 156 and 157, both with value -1.92, and in Austnesfjord at station 162 (-1.91). The two highest *P. pouchetii* dominance values (0.40 and 0.38) were observed in Tysfjord at the two stations 165 and 170 respectively.

At 50m the only stations sampled were the five stations in the Vestfjorden transect. The four outermost stations 148, 149, 151 and 153 were dominated by diatoms, -0.50, -0.06, -2.34 and -0.33 respectively and the innermost station 147 was dominated by *P. pouchetii* (0.17). An overview of *Phaeocystis* dominance for the year 2009 is in Table 9.



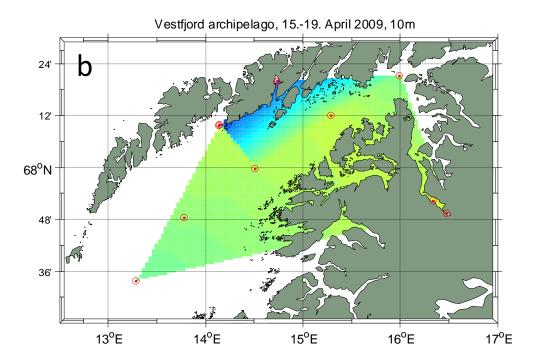


Figure 16: *Phaeocystis* dominance (variation in dominance between *P. pouchetii* and diatoms) in the Vestfjord archipelago in April 2009 at 0m (a), 10m, (b). Note missing data at station 170 at 0m (station location is however still shown). Sampling stations are marked with red circles. Bold black numbers are station numbers. *Phaeocystis* dominance color-bar is shown (*P. pouchetii* > 0 < diatoms) in **a**.

Table 9: Overview of *Phaeocystis* dominance in the Vestfjord archipelagio in April in 2006, 2007 and 2009. Maximum *P. pouchetii* dominance (Max. Pp) and diatom dominance (Max. "Tot. D") are shown as well as percent of stations (stations at specific year and depth) dominated by *P. pouchetii* (Pp) and diatoms ("Tot. D"). Note stations with missing data are not included. Main areas dominated by *P. pouchetii* and diatoms are also shown.

Year	Depth (m)	Max. Pp	Stations P. po (%)	Main areas dominated by P. pouchetii	Max. "Tot. D"	Stations "Tot. D" (%)	Main areas dominated by diatoms
2006	0	0.55	12	Austnesfjord	-3.03	88	Rest of the area, especially Henningsværstraumen
2006	10	0.54	33	Same trend as at 0m	-3.12	67	Same trend as at 0m
2006	50		0		-2.59	100	Tysfjord (only area sampled)
2007	0	0.45	13	Henningsværstraumen and innermost station in Vestfjorden	-2.71	87	Rest of the area, especially Austnesfjord
2007	10	0.76	29	Henningsværstraumen and especially Austnesfjord	-2.32	71	Rest of the area, especially Tysfjord
2007	50	0.26	29	Innermost and outermost station in Vestfjorden	-2.36	71	Rest of the area, especially Tysfjord and the second outermost station in Vestfjorden
2009	0	0.58	36	Tysfjord and the middle and the outermost area in Vestfjorden	-2.05	64	Austnesfjord and especially Henningsværstraumen
2009	10	0.40	50	Same trend as at 0m	-1.92	50	Same trend as at 0m
2009	50	0.17	20	Innermost station in Vestfjorden (Vestfjorden transect only area sampled)	-2.34	80	The rest of the stations in Vestfjorden (Vestfjorden transect only area sampled)

3.12 Principal component analysis, Barents Sea and East Finnmark

The PCA analysis for the Barents Sea and East Finnmark is based on all three sampled years in May in the Barents Sea (2006, 2007 and 2009) and May 2009 in East Finnmark, and all depths are included. Species represented in the PCA are the eight most dominating diatoms in addition to *P. pouchetii* and variable "Tot. D" (total diatoms registered at each sampling station). Number of diatom species registered in 2006 (n=79); 2007 (n=60); 2009 (n=52). For species included in the PCA analysis see Table 10. As Austin and Greig-Smith (1968) points at, the less abundant species contribute with very little information, and an efficient ordination can often be obtained from less than 25% of the total population. Nine principal components,

corresponding to the nine active species variables were generated. A listing of species, with the two highest loading of each species on the nine components, is given in Table 10. These loadings represent the correlation of the species with the component, indicating the degree to which changes in that species will affect individual scores for that component. Six of the species had their highest factor loadings contained in the two first principal components, which also were the only two principal components with an eigenvalue greater than 1 (Table 10). However, the three other species, Chaetoceros socialis, Thalassiosira nordenskioeldii and Chaetoceros debilis, had their second highest factor loading contained in the two first principal components constituting 49% of the variation within the species data, whereas PC1 explains 31.4% and PC2 explains 17.5% of the variance (Fig. 17, Table 10). The PCA analysis for the Barents Sea and East Finnmark is based on PC1 and PC2. PC1 separates P. pouchetii and C. debilis from all the other diatoms included in the analysis. PC2 separates Navicula pelagica and Thalassiosira hyalina from Fragilariopsis oceanica, Thalassiosira antarctica, T. nordenskioeldii, C. socialis and Chaetoceros compressus (Fig. 17). The supplementary variable "Tot. D" is contained in the last species grouping. In addition to the variable "Tot. D", all 11 environmental variables which were projected onto the factor space computed from the active variables, had their highest factor loadings contained in the two first principal components.

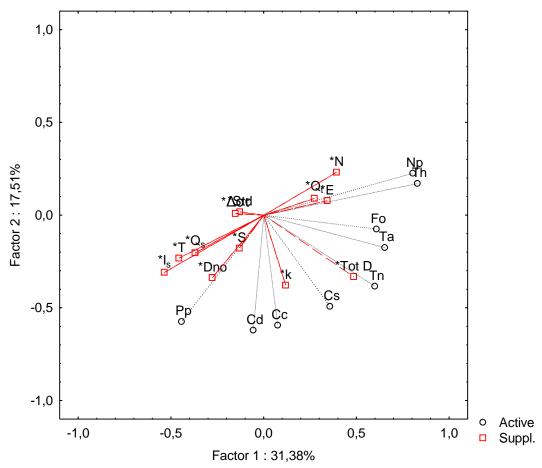


Figure 17: PCA scaling (ordination) plot of the Barents Sea (May 2006, 2007 and 2009) and East Finnmark (May 2009) data based on a correlation matrix of association between nine dominating phytoplankton species and variable "Tot. D" consisting of the sum of all diatoms (number of diatoms in 2006 n=79, 2007 n=60 and 2009 n=52, natural Log (Log_ε)-transformed species abundance, cell l⁻¹). Species acronyms: **Pp** *Phaeocystis pouchetii*, **Fo** *Fragilariopsis oceanica*, **Cs** *Chaetoceros socialis*, **Np** *Navicula pelagica*, **Tn** *Thalassiosira nordenskioeldii*, **Th** *Thalassiosira hyalina*, **Cd** *Chaetoceros debilis*, **Ta** *Thalassiosira antarctica*, **Cc** *Chaetoceros compressus*. Environmental acronyms: **Std** stations depth (m), **N** latitude (°), **E** longitude (°), **T** sea temperature (°C), **Dno** day number in year, **k** diffuse attenuation coefficient, **I**_s diurnal PAR incident on surface, **Q**_s short-wave radiation at surface, **Q**_t total surface heat flux, **S** salinity ‰ and Δσt stability (density difference from 0m to 10m depth). See Materials and Methods for further details on variables. All environmental variables are normalized except for stability which is standardized. Total number of cases in dataset (stations and corresponding stations depths sampled) n=377. Both environmental data and "Tot. D" are ordinated as supplementary variables (marked with *). Active variables are used in the derivation of the principal components and the supplementary variables are projected onto the factor space computed from the active variables.

P. pouchetii had its strongest positive correlation to diurnal PAR followed by day number in year, temperature, the diffuse attenuation coefficient, short-wave radiation incident on sea surface, stability, station depth and salinity (ranked from strongest to weakest correlation, Fig. 17). All the diatoms were also positively correlated to the diffuse attenuation coefficient. The three variables that P. pouchetii were negatively correlated to were latitude, total surface heat flux and longitude. The most significant correlation for diatoms, except C. debilis, were a

positive correlation to latitude (Fig. 17). This was also the case for longitude, except for that C. compressus was negatively correlated to this variable together with C. debilis. All diatoms except C. socialis were positively correlated to total surface heat flux. The only diatoms positively correlated to day number in year and salinity were the three Chaetoceros species. In addition C. debilis and C. compressus were positively correlated to temperature and shortwave radiation incident on sea surface. C. debilis and C. socialis were positively correlated to diurnal PAR. In the PCA plot (Fig. 17) the three Chaetoceros ordinated similarly. F. oceanica, T. nordenskioeldii and T. antarctica also had positive correlations to and ordinated similarly to the environmental variables latitude, longitude, diffuse attenuation coefficient and total surface heat flux. All species in the PCA analysis had strong positive correlation to the supplementary variable "Tot. D". The species with the highest similarity to P. pouchetii was C. debilis, C. compressus and C. socialis. C. debilis had the highest similarity to P. pouchetii i.e. they had six positive correlations to environmental variables in common while C. compressus and C. socialis had five and four environmental variables in common respectively. All the other diatoms had only one positive correlation to environmental variables in common with P. pouchetii which was the diffuse attenuation coefficient. In total P. pouchetii was positively correlated to eight environmental variables.

Table 10: Factor coordinates of the Barents Sea (May 2006, 2007 and 2009) and East Finnmark (May 2009) species data (active variables) and environmental data (supplementary variables). The two highest values are shown, highest absolute value is underlined, eigenvalues of correlation matrix and cumulative proportion of total variance explained by each vector of the principal components analysis of the active variables.

Species	Factor	Factor	Factor	Factor	Factor	Factor	Factor	Factor	Factor
Active var.	1	2	3	4	5	6	7	8	9
P. pouchetii	-0.44	<u>-0.57</u>							
F. oceanica	<u>0.61</u>					0.52			
C. socialis		-0.49	0.50						
N. pelagica	0.81							0.37	
T. nordenskioeldii	0.60						0.64		
T. hyalina	0.83							0.27	
C. debilis		-0.62		0.70					
T. antarctica	<u>0.65</u>				-0.63				
C. compressus		<u>-0.59</u>	-0.58						
Eigenvalue	2.82	1.58	0.97	0.83	0.70	0.65	0.63	0.51	0.31
Cumulative (%)	31.38	48.89	59.65	68.89	76.68	83.94	90.98	96.60	100
Station dept	<u>-0.13</u>						-0.12		
Latitude	0.39	0.23							
Longitude	<u>0.34</u>		0.22						
Sea temp.	<u>-0.46</u>	-0.23							
k*		<u>-0.38</u>	0.22						
I_s*	<u>-0.54</u>	-0.31							
Q_t^*	<u>0.27</u>		-0.22						
Q_s*	<u>-0.37</u>	-0.20							
Day no. in year	-0.28	<u>-0.34</u>							
Salinity	-0.13	<u>-0.18</u>							
$\Delta \sigma t^*$	<u>-0.15</u>							0.12	
Tot. Diatoms	0.49	-0.33							

^{*}Explanation to environmental variable acronyms; **k** diffuse attenuation coefficient, I_s diurnal PAR incident on surface, Q_t total heat flux, Q_s short-wave radiation at surface and $\Delta \sigma t$ stability (density difference from 0m to 10m depth). See Materials and Methods for further details on environmental variables.

3.13 Principal component analysis, Vestfjord archipelago

The Vestfjord archipelago data compromises all three years (2006, 2007 and 2009) in April and all depths were included. The eight most dominating diatoms and *P. pouchetii* were included in the PCA analysis as active variables. Species included in the PCA analysis can be seen in Table 11. The variable "Tot. D" compromises all diatoms registered at each sampling station and were included in the analysis as a supplementary variable, number of diatoms in 2006 (n=63); 2007 (n=26); 2009 (n=29). The first four, out of a total of nine principal components corresponding to the nine active species variables, had an eigenvalue greater than 1 (Table 11). Six of the species had their highest factor loadings contained in the two first principal components, *P. pouchetii, C. socialis, T. nordenskioeldii, Pseudo-nitzschia seriata, Bacterosira bathyomphala* and *Chaetoceros furcellatus*. *F. oceanica* had its highest factor

loadings contained in the fourth principal component and Skeletonema costatum and Chaetoceros decipiens in the fifth principal component (Table 11). However, S. costatum and C. decipiens had, unlike F. oceanica, their second highest factor loading contained in the two first principal components. The two first principal components constituted 43.30% of the variation within the species data (Table 11). PC1 explains 25.76% and PC2 explains 17.54% of the variance (Fig. 18). PC1 separates P. pouchetii, P. seriata, T. nordenskioeldii and C. furcellatus from the rest of the species included in the analysis (Fig. 18). F. oceanica was separated from S. costatum, C. decipiens, B. bathyomphala, C. socialis and the supplementary variable "Tot. D" by PC2 (Fig. 18). The environmental variables in Figure 18 (supplementary variables) were the same as used in the PCA analysis for the Barents Sea and East Finnmark. Nine of the eleven environmental variables had their highest factor loadings contained in the two first principal components: station depth, latitude, longitude, sea temperature, diurnal PAR, total surface heat flux, short-wave radiation incident on sea surface, day number in year and stability (Table 11). The diffuse attenuation coefficient and salinity had their highest factor loadings contained in the fourth principal component (Table 11). However, the diffuse attenuation coefficient had its second highest factor loading contained in the two first principal components.

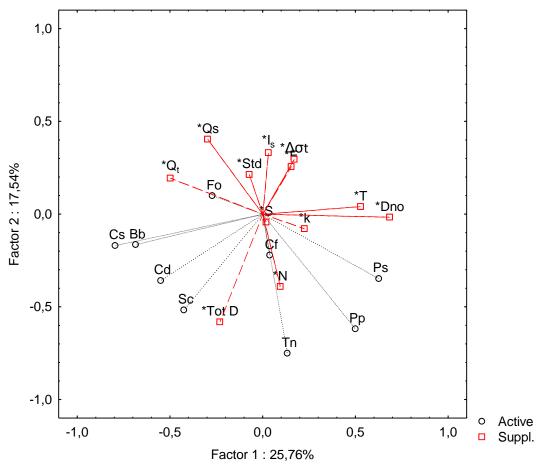


Figure 18: PCA scaling (ordination) plot of the Vestfjord archipelago (April 2006, 2007 and 2009) data based on a correlation matrix of association between nine dominating phytoplankton species and variable "Tot. D" consisting of the sum of all diatoms (number of diatoms in 2006 n=63, 2007 n=26 and 2009 n=29, natural Log (Log_ε)-transformed specie abundance, cell 1⁻¹). Species acronyms: **Pp** *Phaeocystis pouchetii*, **Sc** *Skeletonema costatum*, **Cs** *Chaetoceros socialis*, **Tn** *Thalassiosira nordenskioeldii*, **Ps** *Pseudo-nitzschia seriata*, **Fo** *Fragilariopsis oceanica*, **Bb** *Bacterosira bathyomphala*, **Cd** *Chaetoceros decipiens*, **Cf** *Chaetoceros furcellatus*. Environmental acronyms: **Std** stations depth (m), **N** latitude (°), **E** longitude (°), **T** sea temperature (°C), **Dno** day number in year, **k** diffuse attenuation coefficient, **I**_s diurnal PAR incident on surface, **Q**_s short-wave radiation at surface, **Q**_t total surface heat flux, **S** salinity ‰, Δσt stability (density difference from 0m to 10m depth). See Materials and Methods for further details on variables. All environmental variables are normalized except for stability which is standardized. Total number of cases in dataset (stations and corresponding stations depths sampled) n=269. Both environmental data and "Tot. D" are ordinated as supplementary variables (marked with *). Active variables are used in the derivation of the principal components and the supplementary variables are projected onto the factor space computed from the active variables.

The species group according to PCA analysis figure 18 consisting of *P. pouchetii*, *P. seriata*, *T. nordenskioeldii* and *C. furcellatus* was positively correlated to day number in year, latitude, sea temperature and diffuse attenuation coefficient (environmental variables is ranked from strongest to weakest correlation according to *P. pouchetii*), except *C. furcellatus* that was not positively correlated to temperature. In addition, *P. seriata* was positively correlated to longitude, salinity and stability while *C. furcellatus* correlated positively to diurnal PAR,

short-wave radiation incident on sea surface and salinity. The haptophycean P. pouchetii had its strongest negative correlation to total surface heat flux, short-wave radiation incident on sea surface and diurnal PAR. All other species, i.e. S. costatum, C. socialis, F. oceanica, B. bathyomphala and C. decipiens were positively correlated to total surface heat flux. F. oceanica alone was positively correlated to the diffuse attenuation coefficient, day number in year, salinity and stability (Fig. 18). S. costatum, C. socialis and C. decipiens were positively correlated to latitude, and the latter two species were also positively correlated to short-wave radiation incident on sea surface along with B. bathyomphala. These species were grouped together in the PCA analysis along with "Tot. D" (Figure 18). S. costatum and B. bathyomphala were also positively correlated to salinity and B. bathyomphala was the only species positively correlated to station depth. The only species in this latter group (S. costatum, C. socialis, C. decipiens and B. bathyomphala) that correlated to diffuse attenuation coefficient and diurnal PAR was C. decipiens. All species in the PCA analysis were positively correlated to the supplementary variable "Tot. D". The species with highest similarity to P. pouchetii according to the number of positive correlations to the same environmental variables were T. nordenskioeldii and P. seriata. They had four positive correlations to environmental variables in common with P. pouchetii. In total P. pouchetii was positively correlated to four environmental variables.

Table 11: Factor coordinates of the Vestfjord archipelago (April 2006, 2007 and 2009) species data (active variables) and environmental data (supplementary variables). The two highest values are shown, highest absolute value is underlined, eigenvalues of correlation matrix and cumulative proportion of total variance explained by each vector of the principal components analysis of the active variables.

Species	Factor	Factor	Factor	Factor	Factor	Factor	Factor	Factor	Factor
Active var.	1	2	3	4	5	6	7	8	9
P. pouchetii		<u>-0.62</u>						0.55	
S. costatum		-0.52			<u>-0.43</u>				
C. socialis	<u>-0.80</u>								-0.45
T. nordenskioeldii		<u>-0.75</u>				0.51			
P. seriata	<u>0.63</u>	<u>-0.35</u>							
F. oceanica			0.61	<u>-0.64</u>					
B. bathyomphala	<u>-0.68</u>						0.60		
C. decipiens	-0.55				<u>0.60</u>				
C. furcellatus		<u>-0.65</u>	-0.61						
Eigenvalue	2.31	1.58	1.12	1	0.74	0.64	0.63	0.56	0.42
Cumulative %	25.76	43.30	55.70	66.76	75	82.13	89.18	95.37	100
Station dept		0.21				-0.17			
Latitude		<u>-0.39</u>				0.16			
Longitude	0.16	<u>0.26</u>							
Sea temp.	<u>0.53</u>							-0.09	
k*	0.23			<u>-0.27</u>					
I_s*		0.33	-0.26						
Q_t^*	<u>-0.50</u>	0.19							
Q_s*	-0.30	<u>0.40</u>							
Day no. in year	0.68			-0.25	5454				
Salinity			0.09	<u>-0.14</u>					
$\Delta \sigma t^*$	0.17	0.29							
Tot. Diatoms	-0.23	<u>-0.58</u>							

^{*} Explanation to environmental variable acronyms; k diffuse attenuation coefficient, I_s diurnal PAR incident on surface, Q_t total heat flux, Q_s short-wave radiation at surface and $\Delta \sigma t$ stability (density difference from 0m to 10m depth). See Materials and Methods for further details on environmental variables.

An overview of positive correlations between species and environmental variables in the PCA analysis for the Barents Sea and East Finnmark and Vestfjord archipelago is given in Table 12, where the three strongest positive correlations to environmental variables are shown for each species.

Table 12: PCA correlations for the Barents Sea and East Finnmark and the Vestfjord archipelago showing species correlation to environmental variables, the three strongest positive correlation to environmental variables in each PCA are shown for each species (**B** Barents Sea and East Finnmark, **V** Vestfjord archipelago and ***denotes the strongest correlation, **second strongest and *third strongest). Species acronyms: **Pp** *Phaeocystis pouchetii*, **Dia** total diatoms, **Fo** *Fragilariopsis oceanica*, **Tn** *Thalassiosira nordenskioeldii* (common for the Barents Sea, East Finnmark and Vestfjord archipelago), **Cs** *Chaetoceros socialis*, **Np** *Navicula pelagica*, **Th** *Thalassiosira hyalina*, **Cdeb** *Chaetoceros debilis*, **Ta** *Thalassiosira antarctica*, **Cc** *Chaetoceros compressus* (Barents Sea and East Finnmark), **Sc** *Skeletonema costatum*, **Ps** *Pseudo-nitzschia seriata*, **Bb** *Bacterosira bathyomphala*, **Cdec** *Chaetoceros decipiens*, **Cf** *Chaetoceros furcellatus* (Vestfjord archipelago). Environmental acronyms: **Std** stations depth (m), **N** latitude (°), **E** longitude (°), **T** sea temperature (°C), **k** diffuse attenuation coefficient, **I**_s diurnal PAR incident on surface, **Q**_t total surface heat flux, **Q**_s short-wave radiation at surface, **Dno** day number in year, **S** salinity ‰, **Δσt** stability (density difference from 0m to 10m depth). See Materials and Methods for further details on variables.

Var.	Pp	Dia	Fo	Cs	Np	Tn	Th	Cdeb	Ta	Cc	Sc	Ps	Bb	Cdec	Cf
Std													V**		
N	V^{**}	V^{***}	B**		B**	B***	B***		B*		V^{**}			V^*	
						V^{***}									
\mathbf{E}		B**	B***	B**	B***		B**		B***						
T	\mathbf{B}^*							B^*				V^{**}			
	V^*														
k		B***	V^*	B***		B**		B***	B^{**}			V^*			V^{***}
						V^*									
I_s															V^{**}
$\mathbf{Q}_{\mathbf{t}}$		V^{**}	B^*		\mathbf{B}^*	B^*	\mathbf{B}^*			B**	V^{***}		V^{***}	V^{***}	
			V^{***}												
$\mathbf{Q}_{\mathbf{s}}$										B^*			V^*	V^{**}	
Dno	B**	B*		B*		V^{**}						V***			V^*
	V***														
S			V^{**}					B**		B***	V^*				
Δσt*															

4. Discussion

The main findings in the present study are as follows: The highest *Phaeocystis pouchetii* dominance (see Materials and Methods, *Phaeocystis* dominance ratio) observed during the sampling periods (2006, 2007 and 2009) in the Barents Sea in May and Vestfjord archipelago in April, was in 2009. High *P. pouchetii* dominance was also observed in East Finnmark which was only sampled in May 2009. In all three areas the highest *P. pouchetii* dominance was generally observed at 10m depth (the three depths investigated each year were 0m, 10m and 50m) during the sampling periods. In 2009 at 10m depth, 58% of the stations were dominated by *P. pouchetii* in the Barents Sea, 50% in Vestfjorden archipelago and 92% in East Finnmark. The year with the highest diatom dominance was in 2006 both in the Barents Sea and Vestfjord archipelago. In both areas diatoms were generally observed to dominate at 0m depth during the sampling periods. In 2006 at 0m depth, 76% of the stations were dominated by diatoms in the Barents Sea and 88% in Vestfjord archipelago. In East Finnmark the diatom dominance was low, 17% at 0m in 2009.

The *Phaeocystis* sequences (18s rRNA) analyzed from the Barents Sea indicated that it could belong to both *P. cordata* and *P. antarctica*. (Table 7). Examined from a morphological point of view this is not likely. *P. cordata* is not observed to have any colonial stage, neither in natural samples nor in culture (Zingone et al. 1999). In case of the colony forming *P. antarctica* it is only reported to be present in Antarctic waters (Schoemann et al. 2005). In addition it is possible to distinguish *P. pouchetii* from *P. antarctica* when they are in their colonial stage. *P. pouchetii* forms lobed cloud-like colonies with cells in packets of four while *P. antarctica* forms globular colonies with cells randomly distributed (Medlin & Zingone 2007). This suggests that the species observed was *P. pouchetii*, but it is clear that more extensive gentical analysis (more genes) can give other suggestions.

The spring bloom in the central Barents Sea has been reported to peak in April and sometimes into May by Evensen (1994) and in May by Ellertsen (1982), Rey and Loeng (1985). However, Sakshaug and Slagstad (1991) and Rey and Loeng (1985) concludes that the spring bloom in the central Barents Sea starts at varying times depending on the vertical stability of the water column and irradiance. According to Sakshaug and Slagstad (1991) the spring bloom can start in early April if the vertical mixing is shallower than 20m. Ice edge blooms takes place at the same time as in the central Barents Sea, in April or May (Hegseth 1992). Data from East Finnmark is scarce, and spring bloom timing may vary. Eilertsen and Frantzen

(2007) and Hegseth et al. (1995) reported the spring bloom in Porsangerfjord to peak during April/May and continue into the summer. Despite great latitudinal differences, the spring bloom in Vestfjord archipelago proper peaks approximately at the same time as in the Barents Sea and East Finnmark, though it may some years peak earlier in shallow areas. Huseby (2002) thus reports spring bloom peaks in late March for Austnesfjord and during April in Henningsværstaumen and Vestfjorden. Spring bloom peaks in late March or early April in this area has also been reported by others e.g. Braarud and Nygaard (1978, 1980). A compilation based on a literature study as well as their own data of the most abundant phytoplankton species in March, April and May (showing maximum cell numbers) from the coast of northern Norway and the Barents Sea is given by Degerlund and Eilertsen (2009). This extensive work summarizes the phytoplankton literature covering a great geographical area over a long time period (1922-2007) giving an overview of the spring bloom peaks and species associated with it, and the conclusions herein are that the most variable timings of the spring blooms are south in the area (Vestfjord archipelago) and in the north (ice edge).

My sampling in the Barents Sea and East Finnmark took place in May, one month later than in the Vestfjord archipelago which was sampled in April. Due to limited availability of resources and vessel-time, the areas and periods sampled in the Barents Sea as mentioned varied somewhat between years. In the Barents Sea the sampling in 2006 and 2007 started five days earlier than in 2009. In addition, the sampling area in 2006 was further north than the other years, contributing to the relative low temperatures observed in 2006. The sampling in 2009 was conducted both in the Barents Sea and East Finnmark. Since I only had data from eastern Finnmark from one year these data were pooled with the Barents Sea data in the PCA analyses. In addition one resoning for this was that eastern Finnmark generally has colder water than exsists further south in northern Norway. In the Vestfjord archipelago the same geographical area was sampled each year. However, the sampling period in 2006 was almost two week earlier than in 2007 and 2009.

The present study is therefore within the time period where the spring bloom event is observed in the Barents Sea, East Finnmark and Vestfjord archipelago. However, the spring bloom event is as mentioned reported to vary between years depending on environmental variables like e.g. stability of the water column and irradiance. It is important to have in mind that the present investigation is a "single point sampling" and that the species present are a result of both the biological and physical condition that has already taken place. However, the

species present vs. abundances and the environmental variables may give us a clue of which stage the spring bloom is in and what environmental regime it takes place in. Degerlund and Eilertsen (2009) used this approach for the Barents Sea and north Norwegian coast. Where species associations i.e. several species "thriving" in the same environment (Tansley 1935, Krebs & Richard 1985) interpreted as positive correlations between species and the correlation of these species to environmental variables can discern what we interpret as an association of early or late spring bloom species (Degerlund & Eilertsen 2009).

As mentioned in the aim of the present study, *P. pouchetii* is known to be an important species in all three areas investigated, and the relative abundance between *P. pouchetii* and diatoms is also known to vary greatly between years. In the following discussion I will focus upon the vertical and horizontal dominance variation between *P. pouchetii* and diatoms in the study area and their correlation to species and environmental variables.

There was a trend for *P. pouchetii* to dominate at 10m and diatoms at 0m in this present study. For simplicity "station dominance" will be used in the following to denote the relative i.e. high or low percent of stations dominated by either P. pouchetii or diatoms. In five of the seven cruises the highest *P. pouchetii* station dominance was observed at 10m station depth. The same accounted for diatoms concerning 0m if the situation observed at 50m in Vestfjord archipelago in 2009 is not taken in to account. The situation in Vestfjord archipelago was not representative for the entire area since abundance data only was taken from the Vestfjorden transect at 50m in 2009. A similar vertical distribution, where P. pouchetii was more abundant in the deeper part of the water column, was observed by Wassmann et al. (1999). They observed P. pouchetii to be most abundant between 25m and 50m in the meandering Polar Front and in the frontal zones whereas in the upper layer P. pouchetii abundance deceased. They reported the situation observed to be in a well developed bloom phase (though no peak bloom phase) based on increasing stratification, moderate to high chlorophyll concentrations and increasingly depleted nutrient concentrations towards the north. They also observed silicate concentration to often be <2μM. Similar vertical distribution patterns (but however much lower abundance) was observed in their remaining transect, including both Atlantic water (pre-bloom stage) and Arctic water (peak bloom) in the central Barents Sea (Wassmann et al. 1999). In the Atlantic water the stratification was weak which is typical for this area (Wassmann et al. 1999). Strong stratification was observed in the Arctic waters and the bloom appeared to be limited by silicate and nitrate (Wassmann et al. 1999). In situations where nutrients and silicate is depleted in the upper stratified layers, P. pouchetii has an advantage over diatoms. P. pouchetii does not need silicate and experiments indicate that diatoms dominate over *P. pouchetii* only when silicate concentrations are above 2µM (Egge & Aksnes 1992), giving P. pouchetii a competitive advantage later in the spring bloom. In addition a positive buoyancy has been reported for P. pouchetii colonies (Skreslet 1988, Schoemann et al. 2005). The ability to adjust their specific weight might play an important role in the competition with diatoms. In stratified waters where nutrients are accessible only below a deep pycnocline, P. pouchetii may possibly acquire neutral buoyancy below the pycnocline. West of Svalbard, Eilertsen et al. (1989) found it evident that the critical depth during the day was below 1% light depth (which in their study varied between 15m and 35m) allowing the phytoplankton to take advantage of the enhanced nutrient concentrations under the pycnocline. The low light intensities associated with greater depths might also act as an advantage for P. pouchetii. Eilertsen (1989) reported P. pouchetii to show great ability to maintain and increase its photosynthetic efficiency at low light intensities. The same tendency has been reported for *Phaeocystis* from Antarctica (Palmisano et al. 1986), where it was shown to be better adapted than diatoms to low light intensities (Arrigo et al. 1999). In addition, Hegarty (1998) reports on Phaeocystis cf. pouchetii growing faster relative to diatoms when nutrients were non-limiting and irradiance was low. This might be the main reasons for the observed dominance of *P. pouchetii* at a greater depth than diatoms.

The highest percent of stations dominated by *Phaeocystis pouchetii* was observed in 2009 in both main areas, the Barents Sea and Vestfjord archipelago. High *P. pouchetii* dominance was also observed in East Finnmark in 2009. However, it was only in the Barents Sea and East Finnmark situations were observed where the percent of stations dominated by *P. pouchetii* exceeded the percent of stations dominated by diatoms. This points to the greater presence of *P. pouchetii* concerning distribution in the Barents Sea and East Finnmark than in Vestfjord archipelago in the periods investigated. The high *P. pouchetii* dominance in East Finnmark in May 2009 is supported by the negative correlation between *P. pouchetii* and latitude (°N) in the PCA analysis for the Barents Sea and East Finnmark. This indicates an increasing abundance of *P. pouchetii* in the southern Barents Sea and East Finnmark. In the PCA analysis for Vestfjord archipelago *P. pouchetii* was positively correlated to latitude (°N) which indicates a greater abundance of *P. pouchetii* in the two northernmost locations sampled, Austnesfjord and Henningsværstraumen. This is especially the case in

Austnesfjorden, supported by that the maximum *P. pouchetii* dominance value was observed in Austnesfjord in 2006 and 2007 at 10m (the depth with the generally highest *P. pouchetii* dominance). In 2009 the maximum *P. pouchetii* dominance value was however observed in Tysfjord at 10m. The explanations to the distribution pattern observed for *P. pouchetii* has to be sought in the physical and biological variables connected to its environment.

P. pouchetii was positively correlated to sea temperatures both in the Barents Sea, East Finnmark and in Vestfjord archipelago. However, this might not be a direct effect of P. pouchetii thriving only at high temperatures since some of the stations with high P. pouchetii dominance in the other years (2006 and 2007) rather had some of the lowest temperatures. The positive correlation to sea temperatures may as well be an effect of the life history strategy of P. pouchetii, indicating a later appearance of P. pouchetii in the succession. After all the sea temperature is tightly coupled to the development of the spring bloom, where relatively higher temperatures indicate a later stage in the spring bloom. If so, the high sea temperatures observed in 2009 in both the Barents Sea and Vestfjord archipelago indicates that the spring bloom is in a late phase. P. pouchetii has been reported to occur later in the spring bloom, where the traditional view is that spring blooms in regions were P. pouchetii blooms occur is usually characterized by a diatom bloom followed by a peak in P. pouchetii colony cells (Riebesell et al. 1995, Wassmann et al. 1999, Rousseaua et al. 2000, Smith et al. 2003). In addition, previous investigations has observed that the spring bloom peaks earlier in coastal water than offshore (Føyn 1929, Huseby 2002) which might explain the high P. pocuhetii dominance observed in East Finnmark. The spring bloom in the sheltered fjord Austnesfjord is as earlier mentionded reported to start ealier than in Henningsværstraumen and Vestfjorden which might be the reason for the observed high P. pouchetii dominance in this fjord in 2006 and 2007. This might also be the case in Tysfjord in 2009 where high P. pouchetii dominance was observed along with the highest temperatures observed in the Vestfjord archipelago indicating a later bloom stage.

A late appearance of *P. pouchetii* in the spring bloom in the Barents Sea and East Finnmark was also supported by the positive correlation between *P. pouchetii* and *Chaetoceros debilis, Chaetoceros socialis* and *Chaetoceros compressus* in the PCA analysis for the area in question. Typically the species succession follows a characteristic pattern in the spring bloom and it is to some degree possible to estimate the stage of a bloom due to successional patterns (Margalef 1958). *Chaetoceros* species and especially *C. socialis* have been reported to have high concentrations late in the spring bloom season in the Barents Sea

(von Quillfeldt 2000). In Vestfjord archipelago *P. pouchetii* was positively correlated to *Pseudo-nitzschia seriata, Thalassiosira nordenskioeldii, Chaetoceros furcellatus* and *Skeletonema costatum. S. costatum* often appears early in the spring bloom in Vestfjord archipelago (March) and along the north Norwegian coast (Huseby 2002, Degerlund & Eilertsen 2009) while *T. nordenskioeldii* and *C. furcellatus* have a somewhat later appearance (Schei 1974, Huseby 2002). *T. nordenskioeldii* might have a more sporadic appearance since it also has been reported as an early spring bloom species along the north Norwegian coast by Degerlund and Eilertsen (2009). *P. seriata* is distributed in temperate to northern cold water regions and Heimdal (1974) observed it, however in small amounts, in early April in Ullsfjord in a spring bloom situation dominated by diatoms and *P. pouchetii*. The two species *T. nordenskioeldii* and *P. seriata* were in addition to *P. pouchetii* positively correlated to sea temperature where *P. seriata* had the strongest correlation to sea temperatures in Vestfjord archipelago.

It seems as if *P. pouchetii* do not appear as late in the spring bloom succession in Vestfjord archipelagio as in the Barents Sea supported by its correlation to both early and late spring bloom species in Vestfjord archipelago. It may rather be more abundante throughout the spring bloom season in Vestfjord archipelago. In addition, *P. pouchetii* was only positively correlated to diurnal PAR incident on sea surface and short-wave radiation incident on sea surface in the PCA analysis for the Barents Sea and East Finnmark, indicating a later appearance in the Barents Sea and East Finnmark than in Vestfjord archipelago.

Other environmental variables which might also indicate a later appearance of P. pouchetii in the spring bloom in the Barents Sea, East Finnmark and Vestfjord archipelago was the positive correlation between P. pouchetii, day number in year and the diffuse attenuation coefficient. However, it is more likely that the positive correlation between P. pouchetii and day number in year is a result of the sampling track which varied greatly between years in the Barents Sea but not so much in Vestfjord archipelago. In Vestfjord following: the Vestfjorden transect, archipelago the sampling track was as Henningsværstraumen, Austnesfjord and Tysfjord, except in 2007 when Austnesfjord was sampled before Henningsværstraumen. In the case of Vestfjord archipelago the positive correlation between P. pouchetii and day number in year indicates a low P. pouchetii abundance in the Vestfjorden transect and an increasing P. pouchetii abundance in Henningsværstrumen, Austnesfjord and Tysfjord. This is supported by the maximum P. pouchetii dominance values observed in Austnesfjord and Tysfjorden as earlier mentioned.

The diffuse attenuation coefficient is known to increase during the spring bloom due to increased abundance of phytoplankton which in turn results in increased release of extracellular organic carbon (Smith 1977, Larsson & Hagström 1979, Iturriaga 1981, Larsson & Hagström 1982, Riemann et al. 1982). As earlier mentioned, *P. pouchetii* is known for its rapid growth and gelatinous colonies consisting of a variety of polysaccharides which probably increases the diffuse attenuation coefficient. The species *P. pouchetii* was positively correlated to in both main areas were also positively correlated to the diffuse attenuation coefficient except from *S. costatum* in Vestfjord archipelago. This again shows the earlier appearance of *S. costatum* in the spring bloom succession and the positive correlation between *P. pouchetii* and both early and later spring bloom species in the Vestfjord archipelago.

The year with the highest percent of stations dominated by diatoms was in 2006 in both the Barents Sea and Vestfjord archipelago. The diatom dominance in East Finnmark in 2009 was low compared to the Barents Sea and especially Vestfjord archipelago. The percent of stations dominated by diatoms was generally higher in Vestfjord archipelago than in the Barents Sea and especially East Finnmark. This points to the greater importance of diatoms in Vestfjord archipelago than in the Barents Sea and especially East Finnmark in the three years investigated. In the PCA analysis for the Barents Sea and East Finnmark "Tot. D" (total diatoms) was positively correlated to longitude (°E). This was also the case for the three species, Navicula pelagica, T. nordenskioeldii and Thalassiosira hyalina, which "Tot. D" had its strongest positive correlation to in the PCA analysis for the Barents Sea and East Finnmark i.e. these species followed the same abundance trend as total diatoms. These three species were in addition to having a positive correlation to longitude (°E) also positively correlated to latitude (°N) along with Fragilariopsis oceanica, C. socialis and Thalassiosira antarctica. This indicates that the most abundant diatom species connected to "Tot. D" in the Barents Sea and East Finnmark in the three years sampled had a higher abundance in northeast, probably at the ice edge which was sampled each year in northeast. All stations situated into the ice drift in the years sampled were dominated by diatoms except for one station in 2006 and 2007 where P. pouchetii dominated. This is supported by that the species from the genera Chaetoceros, Thalassiosira, Fragilariopsis and Navicula are all reported to be predominant in the outermost and thinnest part of the sea ice (Sakshaug et al. 2009). In Vestfjord archipelago "Tot. D" and the three species it had its strongest positive correlation to were positively correlated to latitude (°N) which indicates a greater abundance of diatoms north in the sampling area (Henningsværstraumen and Austnesfjord). In the three years sampled in Vestfjord archipelago the maximum diatom dominance values observed at 0m (the depth with the generally highest diatom dominance) were in Henningsværstraumen in 2006 and 2009 and in Austnesfjord in 2007. Examination of the environmental variables and species connected to "Tot. D" might contribute to explain the proposed distribution pattern in time and space for the main species constituting "Tot. D".

"Tot. D" was negatively correlated to sea temperatures according to the PCA analysis for the Barents Sea and East Finnmark and Vestfjord archipelago. This is supported by that the lowest sea temperatures in both main areas were observed in 2006 i.e. the year with the highest diatome dominance. The negative correlation to sea temperature might indicate that the main species in the "Tot. D" variable had an early appearance in the spring bloom succession. However, in case of the PCA analysis for the Barents Sea and East Finnmark it strengthens the proposed higher abundance of diatoms connected to the low temperatures at the ice edge which was sampled each year. The three species "Tot. D" had its strongest positive correlation to in the PCA analysis for the Barents Sea and East Finnmark (N. pelagica, T. nordenskioeldii and T. hyalina) were also negatively correlated to sea temperatures. This is in agreement with T. hyalina being characterized as a spring species often in the presence of ice and N. pelagica being a true ice algae species (Gran 1902, Eilertsen et al. 1989, Kuznetsov 1992, Quillfeldt et al. 2003). It is therefore reasonable to suggest that the main species in "Tot. D" in the investigated period is abundant in the presence of ice. This is also supported by total diatoms to be dominating at temperatures of -1.46°C in 2006. Temperatures below the ice in Arctic water in ice covered regions of the Barents Sea is reported to be between -1.75°C to -1.9°C in May, values represent range in the sampling area for surface waters (0-1m) (Hegseth 1992). The negative correlation to sea temperature might therefore not solely be associated to early appearance in the spring bloom since T. nordenskioeldii is proposed to be a late spring bloom species along with T. hyalina (compared to the pennate chain-forming Fossula arctica and Fragilariopsis spp.) in an Arctic spring bloom (von Quillfeldt 2000), but rather to the ice bloom situation where low temperatures are connected to the ice edge. Though T. nordenskioeldii and T. hyalina are proposed as being later spring bloom species, they often appear before Chaetoceros spp. (Quillfeldt 2000). This suggests that the main species constituting "Tot. D" blooms ahead of P. pouchetii which was positively correlated to the only three Chaetoceros species in the PCA analysis for the Barents Sea and East Finnmark. However, Phytoplankton connected to an ice edge spring bloom will generally experience low temperatures when following the northward retreat of the ice edge. In addition was "Tot. D" positively correlated to the diffuse attenuation coefficient in the PCA analysis for the Barents Sea and East Finnmark. Hegseth (1992) observed high dominance of silt, clay and nonliving organic matter under ice in samples collected over the Hopen Bank in February/March. When the ice starts to melt in April/May (Hegseth 1992) the silt, clay and nonliving organic matter under ice is released which probably rapidly increases the diffuse attenuation coefficient in the initial stage of the ice edge bloom. It is difficult to say if the positive correlation to the diffuse attenuation coefficient is due to a later appearance of the main diatoms in the spring bloom i.e. high concentration of phytoplankton and release of extracellular organic carbon, or that the main diatoms observed are more abundant in the initial stage of the ice edge bloom. However, the main species constituting "Tot. D" probably appears ahead of the peak of *P. pouchetii* in the spring bloom in the Barents Sea in the investigated period.

The three species "Tot. D" had its strongest positive correlation to in the PCA analysis for the Vestfjord archipelago (S. costatum, C. socialis and T. nordenskioeldii) were also negatively correlated to sea temperatures, except from T. nordenskioeldii. These species are often some of the main species in the spring bloom in Vestfjord archipelago (Braarud & Nygaard 1980, Degerlund & Eilertsen 2009). As earlier mentioned S. costatum is an early species and T. nordenskioeldii is a somewhat later species in the spring bloom succession in Vestfjord archipelago. In the Vestfjord archipelago C. socialis has been reported to belong to the species in early succession, small diatoms (Huseby 2002, Degerlund & Eilertsen 2009). The main species constituting the "Tot. D" belong both to early and late spring bloom species, indicating total diatoms to be more abundant throughout the spring bloom in Vestfjord archipelago than in the Barents Sea. Recall, this was also observed for P. pouchetii in Vestfjord archipelago. This agrees well with the observations made by Føyn (1929), reporting the spring bloom in Vestfjord archipelago to be initiated with *Chaetoceros* spp. and *P*. pouchetii. One reason for this might be that the spring bloom is more "short-lived" in Vestfjord archipelago than in the Barents Sea. This is however true for the fjords located on the west side of Svalbard, Kongsfjord and Hornsund according to Eilertsen et al. (1989) who state that the spring bloom lasts longer in this area (from mid March to early June) than at the north Norwegian coast, where they usually last for about one month (Matthews & Heimdal 1980, Eilertsen 1983). This is probably not connected to the initial nutrient concentration since they are observed comparable in the Spitzbergen fjords and Balsfjord outside Tromsø (Eilertsen & Taasen 1984). Eilertsen et al. (1989) suggest heavy grazing to slow down the progress of the spring bloom and recycled ammonia to prolong the progress. This agrees well with Sakshaug's statement "the late and protracted phytoplankton blooms in the permanently ice-free Atlantic waters may represent good example of "match" whereas the early blooms that arise where sea ice overlies Atlantic water may be textbook examples of mismatch, as are the early spring blooms in Norwegian fjords (Wassmann et al. 1990)". This suggested that phytoplankton generally have a more narrow "peak window" in Vestfjord archipelago compared to the Barents Sea which might be the reason for the observed overlap in peak abundance in Vestfjord archipelago between *P. pouchetii* and diatoms.

The latest species associations suggested for the present study area are *P. pouchetii* associations for the Barents Sea region and *C. socialis* associations along the north Norwegian coast (Degerlund & Eilertsen 2009). Species association names are assigned according to Cleve's (1897) idea of naming the species association after the most predominant species in the area. This is supported by several others (Rey & Loeng 1985, Skjoldal & Rey 1989, Rey 1993, Evensen 1994, Quillfeldt 1996, Rat'kova & Wassmann 2002) suggesting the great importance of *P. pouchetii* in the Barents Sea and diatoms, especially *C. socialis*, along the north Norwegian coast. Degerlund and Eilertsen (2009) observed a tendency for *P. pouchetii* to increase in importance towards the north in their study area which was from Vestfjord archipelago to the Barents Sea. They observed *P. pouchetii* to be most predominant in the northernmost coastal fjords and in the Barents Sea which is in agreement with the present three years study. *P. pouchetii* was not only abundant in the Barents Sea and especially East Finnmark, it was occasionally also the most dominating species in relation to total diatoms in the entire area sampled in the Barents Sea and East Finnmark in 2009.

As earlier mentioned, Sakshaug and Slagstad (1991) and Rey and Loeng (1985) conclude that the spring bloom in the central Barents Sea starts at varying times depending on the vertical stability of the water column and irradiance. However, in the Barents Sea the surface stabilities (0-10m) were generally low in May all years, the only exception was the northernmost station west of Svalbard in 2009. Low stability can result in increased mixed depth. One definition is that the mixed depth related to vertical density distribution is the depth at which a change from the surface σ_t of 1.25 has occurred (Levitus 1982). However, due to the often weakly stratified nature of the water columns in the Barents Sea and East Finnmark (Eilertsen & Skarðhamar 2006) a σ_t change of 0.1 is here used as criterion. The

situation in East Finnmark was rather different, which due to river runoff had high stabilities compared to the Barents Sea.

According to the PCA analysis for the Barents Sea and East Finnmark *P. pouchetii* was positively correlated to stability and total diatoms were negatively correlated to stability. This is supported by that the only station in the Barents Sea and the stations in East Finnmark with surface stability above 0.1 were dominated by *P. pouchetii*. Especially was East Finnmark the main area attributing to the positive correlation between *P. pouchetii* and stability.

P. pouchetii seems to have some competitive advantages over diatoms at low turbulence since it can have positive buoyancy (Skreslet 1988, Schoemann et al. 2005), while diatoms would dominate in relatively turbulent conditions according to Margalef (1978). It is not possible to observe any trend of either P. pouchetii or diatoms being dominant in stratified areas in the Barents Sea since only one station was stratified. However, diatoms were more dominating in 2006 and 2007 than in 2009 and there were no stratification in the two earliest years sampled. In East Finnmark on the other hand the situation observed was probably a well developed spring bloom since a marked stratification of the water column was observed, probably due to river runoff. Hegseth et al. (1995) state that freshwater runoff does not cause any marked stability in the water masses until May/June, when the spring bloom is over in the area proper. In support of this was the observation of *Chaetoceros* spp. spores being common among diatoms present at 50m in East Finnmark which indicates that the peak in diatoms probably had culminated. According to this the spring bloom observed in the near coastal area of East Finnmark in the present study might be in a late bloom phase dominated by P. pouchetii. In addition, previous investigations has observed that the spring bloom peaks earlier in coastal water than offshore as earlier mentioned. This might be the reason for the observed diatom dominance at the offshore stations with low stability and P. pouchetii dominance at the coastal stations with high stability in East Finnmark.

"Tot. D" and the three species it had its strongest positive correlations to in the Barents Sea and East Finnmark were negatively correlated to stability. This is surprising since the main species constituting "Tot. D" were indicated to be most abundant in the ice edge bloom. Ice edge blooms are characterized by a stratified upper water lay due to the low saline melt water. However, the surface stability calculated in the present study was from 0m to 10m while Hegseth (1992) observed a pronounced pycnocline at 20m to 30m during April/May (1986-

1988) as a result of melting of sea ice. It is therefore possible that any stabilization was overlooked when only investigating the stability in the upper 10 meters if this also was the case in the present study.

However, "Tot. D" and the three species it had its strongest positive correlations to were positively correlated to total heat flux in the Barents Sea and East Finnmark. A positive total heat flux value denotes heat loss from air and is referred to as negative heat flux. The thermal regime of the Barents Sea is mainly influenced by two factors, the total heat flux and the water exchange with the adjacent basins (Kuznetsov 1992). The negative heat flux increases the temperature of the sea surface which eventually stabilizes the upper layers of the water column. At the ice edge the melting of ice will also contribute to the stabilization of the upper water column which in turn might trigger the ice edge bloom reported to start in April or May as earlier mentioned. However, "Tot. D" and the three species it had its strongest positive correlation to in the Barents Sea, East Finnmark and Vestfjord archipelago were negatively correlated to stability. Nevertheless, thermal stratification resulting from radiation absorbed by the phytoplankton cells may be weak and difficult to detect (Stramska & Dickey 1993).

In Vestfjord archipelago both *P. pouchetii* and "Tot. D" were negatively correlated to stability. High stabilities, (>1.25 in Vestfjord archipelago) were observed in Tysfjord in 2006 and 2007 and in Austnesfjord in 2007. Surface stabilities most likely developes earlier in these two sheltered fjords than in Henningsværstraumen and Vestfjorden. Thus, the spring bloom might have started earlier in these two fjords and further culminated, leaving low abundance of both *P. pouchetii* and diatoms in the stratified waters of the two fjords in the years in question. Recall, high *P. pouchetii* dominance was observed in these two fjords. However, the maximum *P. pouchetii* dominance values were observed in the years when relatively low stability was observed in the two fjords. i.e. Austnesfjord in 2006 and Tysfjord in 2009. Only exception was the maximum *P. pouchetii* dominance value observed in Austnesfjord in 2007. The lowest stabilities in Vestfjord archipelago were not surprisingly observed in Henningsværstraumen in all three years, and in all three years the stations in Henningsværstraumen had a predominance of diatoms. This is supported by that diatoms would dominate in relatively turbulent conditions according to Margalef (1978).

As in the PCA analysis for the Barents Sea and East Finnmark, "Tot. D" and the three species it had its strongest positive correlations to in the PCA analysis for Vestfjord archipelago were positively correlated to total heat flux, except from *T. nordenskioeldii*.

Stratification is not necessary for the initiation of a spring bloom. In all localities north of Skjomen the spring bloom is reported to take place in unstratified water masses (Schei 1974, Eilertsen et al. 1981b, Eilertsen 1983, Rey & Loeng 1985), in fjords with depths of approximately 200m (Eilertsen & Taasen 1984). Therefore the diatom species observed in an early spring bloom succession will not be positively correlated to stability. In addition, stratification in an early spring bloom succession might be weak and difficult to detect.

There seems to exist little consistency regarding the relative abundance variation between *P. pouchetii* and diatoms. In all years, *P. pouchetii* was present in the periods the areas were investigated and in addition found dominant in some areas, some periods more dominating than others. However, interesting is the ability of this single species, *P. pouchetii*, to dominate over a bulk of different diatom species. The relative abundance variation between *P. pouchetii* and diatoms has great impact on the ecology and economy connected to the areas in question as mentioned in the introduction i.e. *P. pouchetii* has been shown to deter grazers and to be toxic to marine organisms, altering the vertical carbon transport as well as having different nutritional value compared to diatoms. What makes *P. pouhetii* so successful in the competition with the bulk of different diatom species?

Several factors are believed to strengthen the dominance of *P. pouchetii* during a spring bloom. *Phaeocystis* appears to be capable of adaptation to a wide range of growth irradiances (Eilertsen 1989). When the concentration of diatoms and *P. pouchetii* increase, the shelf shading increases. This results in lower irradiance, which can favour *P. pouchetii*. *Phaeocystis* single cells have low sinking rate due to their nanosize (Becquevort & Smith 2001, Peperzak et al. 2003). Colonies of *Phaeocystis* have negative sinking rate which demonstrates their capacity to regulate their buoyancy (Skreslet 1988, Schoemann et al. 2005). Another factor probably making *P. pouchetii* more competitive is their resistance to grazing both due to their large size range and to the toxic life stage associated with *P. pouchetii* (Estep et al. 1990, Schoemann et al. 2005, Veldhuis et al. 2005, Wassmann et al. 2005, Nejstgaard et al. 2007, Rousseau et al. 2007).

As diatom species often can be characterized as early or late spring bloom species, the spring bloom peak in *P. pouchetii* is reported to occur both before and after a peak in diatoms. However, the traditional view is that a peak in diatoms is followed by a peak in *P. pouchetii* as earlier mentioned. An explanation can be that one triggering factor for colony formation in *P. pouchetii* is that solitary cells require a solid substrate for attachment. *P. pouchetii* has

often been observed attached to Chaetoceros spp. setae both in experiment cultures and in natural environments (Kayser 1970, Rousseau et al. 1994 and own observations). A possible explanation to the observed decrease in diatom cell number followed by an increase in P. pouchetii could also be the production and release of the cytotoxic α , β , γ , δ -unsaturated aldehyde 2-trans-4-trans-decadienal (DD) (Hansen & Eilertsen 2007), identified as the most toxic component released by P. pouchetii (Hansen et al. 2004). Laboratory work conducted by Hansen and Eilertsen (2007) shows that division rates for S. costatum, C. sosialis and T. antarctica decreased as concentration of DD increased. However, no conclusions could be drawn considering if DD is present in sufficient amounts to influence diatom growth (Hansen & Eilertsen 2007) since the methods for quantifying polyunsaturated aldehydes (PUAs) are not sensitive enough in field (Casotti et al. 2005). Experiments indicate that diatoms dominate over P. pouchetii only when silicate concentrations are above 2 µM (Egge & Aksnes 1992), giving P. pouchetii a competetive advantage later in spring bloom. This can explain the peak in diatoms followed by the peak in P. pouchetii, but it can not explain the vice versa dominance which also has been observed in early spring in northern Norway (Gaarder 1938, Heimdal 1974, Eilertsen et al. 1981b).

5. Conclusions

The vertical distribution of phytoplankton showed a trend for *Phaeocystis pouchetii* to dominate at 10m and diatoms at 0m in the three main areas sampled. The highest *P. pouchetii* dominance was observed in 2009 in the Barents Sea, East Finnmark and Vestfjord archipelago. Especially high *P. pouchetii* dominance was observed in East Finnmark. Further, *P. pouchetii* appears more important in East Finnmark and in the southern Barents Sea than in the northern Barents Sea and Vestfjord archipelago during present study. In Vestfjord archipelago *P. pouchetii* seemed to be more abundant in northwest, being Henningsværstraumen. However, *P. pouchetii* seemed generally to be more dominating in Austnesfjord during the sampling periods. The highest diatom dominance was observed in 2006 in the Barents Sea and Vestfjord archipelago. Diatoms appeared to be more dominating in the Vestfjord archipelago than in the Barents Sea during the sampling periods. However, diatoms generally seemed to be more abundant than *P. pouchetii* in the northern Barents Sea, especially in northeast at the ice edge in the years sampled. In the Vestfjord archipelago the highest abundance of diatoms seemed to be in northwest (Henningsværstraumen) which also was the area with the generally highest diatom dominance in the sampling periods. *P.*

pouchetii was positively correlated to species known for their later appearance in the spring bloom in the Barents Sea and East Finnmark, indicating a later appearance of *P. pocuhetii*. Total diatoms ("Tot. D") had its three strongest positive correlations to species reported to have peak abundance earlier than the species P. pouchetii was positively correlated to, indicating that the main species constituting "Tot. D" blooms earlier than P. pouchetii. In the Vestfjord archipelago P. pouchetii was positively correlated to both early and late spring bloom species, indicating P. pouchetii to stay abundant throughout the bloom season. As P. pouchetii "Tot. D" had its three strongest positive correlations to both early and late spring bloom species in Vestfjord archipelago, indicating the main species constituting "Tot. D" to stay abundant throughout the bloom season. However, according to the physical parameters the main species constituting "Tot. D" seemed to be more abundant in the early spring bloom compared to P. pouchetii in both the Barents Sea, East Finnmark and Vestfjord archipelago. Concerning the identity of *P. pouchetii*, the genetic analyses performed indicated that it could also belong to both *Phaeocystis cordata* and *Phaeocystis antarctica*. Nevertheless, examined from a morphological point of view, the *Phaeocystis* cell-material collected from the Barents Sea in 2007 and 2009 were identified as *Phaeocystis pouchetii*.

6. Further research

It is rather evident that life-history strategies play an important role in the ecosystem as a whole. Marcus and Boero (1998) stated that the benthic-pelagic coupling is important in an ecological context in enhancing the understanding of ecological patterns of global importance. As Eppley (1986) suggested, dormant life-cycle stages may provide the key to understanding fluctuations in the abundance of planktonic species. This puts larger focus on biological interactions as regulators in addition to the common "physics regulates biology" concepts. For more than 100 years scientists have searched for a "postulated" *Phaeocystis* resting stage, unfortunately with no conclusive success (Scherffel 1899, Scherffel 1900). In one attempt to find the "postulated" resting stage of *Phaeocystis pouchetii*, a monoculture was cultivated and structures looking like tetraspores were found on the surface of the cultivating-column (pers. comment HC. Eilertsen). This bottom stage, possible resting stage, is also mentioned by a Russian author more than 40 years ago (Kashkin 1964). However, the nature of an overwintering form and the colony-forming cell of *Phaeocystis* is still unresolved along with the factors triggering colony formation (Rousseau et al. 2007). It is well known that a significant proportion of marine planktonic diatoms in neritic environments form resting

spores (Garrison 1981). When conditions are preferable and deep mixing is present the spores reach the euphotic zone and germinate. Experiments have shown that spores may have a distinct photoperiodic response, thus day-length may trigger germination of spores and/or the onset of growth (Hollibaugh et al. 1981, Eilertsen 1993, Eilertsen et al. 1995, Hansen & Eilertsen 1995). How evolution has placed *Phaeocystis* "spores germination" in time and space locally will influence competition with diatoms. For the first time a proposed zygote in the form of a nonmotile cell was reported for Phaeocystis in this case P. antarctica (Gaebler-Schwarz et al. 2010). Zygotes are known to form the overwintering life stages as cysts in Dinophyceae and akinetes in Pithophoraceae and it might have the same ecological function in P. antarctica (Gaebler-Schwarz et al. 2010). These proposed zygotes have been observed attached to diatom frustules which may serve as protection against predators (Gaebler-Schwarz et al. 2010). This I have also observed, both during the cruise to the Barents Sea (during present study), in natural samples from Tromsøysundet and in laboratory cultures maintained at the Planktonlab. (AMB). This suggests that the proposed zygote might be involved in the life cycle of P. pouchetii as well. Eilertsen et al. (1981b) experienced that during early spring large amounts of solitary cells (the precursor of the colonial stage) may occur "out of nothing". This was also observed in Tromsøysundet during my Bachelor theses study. At the 15th of March there were no registered *P. pouchetii* in Tromsøysundet while at the 19th of March there were 1.9 x 10⁴ cells 1⁻¹. P. pouchetii might have been overlooked if attached to diatom frustules and when released i.e. at favourable conditions, showed rapid growth characteristic for this species. An understanding of "what is favourable conditions" triggering spore germination, colony formation and massive growth in phytoplankton, will probably be a big step forward in resolving the questions connected to the variation in relative abundance between P. pouchetii and diatoms.

7. References

- Aanesen RT, Eilertsen HC, Stabell OB (1998) Light-induced toxic properties of the marine alga Phaeocystis pouchetii towards cod larvae. Aquatic Toxicology 40:109-121
- Arrigo KR, Robinson DH, Worthen DL, Dunbar RB, DiTullio GR, VanWoert M, Lizotte MP (1999)

 Phytoplankton community structure and the drawdown of nutrients and CO2 in the Southern
 Ocean. Science 283:365-367
- Austin MP, Greig-Smith P (1968) The application of quantitative methods to vegetation survey: II.

 Some methodological problems of data from rain forest. The Journal of Ecology 56:827-844
- Becquevort S, Smith WO (2001) Aggregation, sedimentation and biodegradability of phytoplanktonderived material during spring in the Ross Sea, Antarctica. Deep Sea Research Part II: Topical Studies in Oceanography 48:4155-4178
- Braarud T (1935) The "Øst" expedition to the Denmark Strait 1929. II. The phytoplankton and its conditions of growth. Hvalrådets Skrifter 10:1-173
- Braarud T, Gaarder KR, Nordli O (1958) Seasonal changes in the phytoplankton at various points off the Norwegian west coast (observations at the permanent oceanographic stations, 1945-46). Fiskeridirektoratets skrifter Serie Havundersøkelser (Report on Norwegian Fishery and Marine Investigations) Fiskeridirektoratet, Bergen
- Braarud T, Nygaard I (1978) Phytoplankton observations in offshore Norwegian coastal waters between 62 °N and 69 °N Fiskeridirektoratets skrifter Serie Havundersøkelser. Fiskeridirektoratet, Bergen, p 489-505
- Braarud T, Nygaard I (1980) Phytoplankton observations in offshore Norwegian coastal waters between 62°N and 69°N. 2. Diatom societies from Möre to Vesterålen, March–April 1968–1971. Sarsia 65:93–114
- Brown RA (1990) Meteorology. In: Walker O. Smith J (ed) Polar Oceanography, Part A: Physical Science. Academic Press, Inc., San Diego, p 1-47
- Cao Y, Williams DD, Williams NE (1999) Data transformation and standarization in the multivariate analysis of river water quality. Ecological Applications 9:669-677
- Casotti R, Mazza S, Brunet C, Vantrepotte V, Ianora A, Miralto A (2005) Growth inhibition and toxicity of the diatom aldehyde *2 trans*, *4 trans* decadienal on *Thalassiosira weisfflogii* (Bacillariophyceae) Journal of Phycology 41:7-20
- Cleve PT (1883) Diatoms, collected during the expedition of the Vega. Vega-Expeditionens Vetenskapliga lakttagelser 3:455-517
- Cleve PT (1896) Diatoms from Baffins Bay and Davis Strait. Bihang Kongelige svenska Vetenskaplige Akademie Handlingar 22, Afd. III:1–22
- Cleve PT (1897) A treatise on the Phytoplankton of the Atlantic and its tributaries and on the periodical changes of the plankton of Skagerak, Vol. Upsala Nya Tidnings Aktiebolags Tryckeri
- Cleve PT (1899) Plankton collected with the Swedish expedition to Spitzbergen in 1898. Kongliga Svenska Vetenskaps-Akademiens Handlingar 32:1-151
- Cushing DH (1978) Biological effects of climatic change. Rapports et Proces-Verbaux des Reunions (Denmark) 173:107-116
- Cushing DH (1990) Plankton production and year-class strength in fish populations: and update of the match/mismatch hypothesis. Mar Biol 26:249-293
- Degerlund M, Eilertsen HC (2009) Main Species Characteristics of Phytoplankton Spring Blooms in NE Atlantic and Arctic Waters (68–80°N) Estuarine and Coasts 33:242-269
- Egge JK, Aksnes DL (1992) Silicate as regulating nutrient in phytoplankton competition. Marine ecology progress series Oldendorf 83:281-289
- Eilertsen HC (1983) Planteplankton før og etter vassdragsreguleringen i Skjomen: 1970-1972 og 1977-1979, Vol 4. Rådg. Utv. Skjomenprosjektet. NVE. Rep

- Eilertsen HC (1989) *Phaeocystis pouchetii* (Hariot) Lagerheim, a key species in Arctic marine ecosystems: life history and physiology. Rapp P-v- Réun Cons Int Explor Mer 188:131
- Eilertsen HC (1993) Spring blooms and stratification. Nature 363:24
- Eilertsen HC, Falk-Petersen S, Hopkins CCE, Tande K (1981a) Program for the project, study area, topography, and physical environment. Sarsia 66:25-34
- Eilertsen HC, Frantzen S (2007) Phytoplankton from two sub-Arctic fjords in Northern Norway 2002-2004: I. Seasonal variations in chlorophyll a and bloom dynamics. Marine Biology Research 3:319-332
- Eilertsen HC, Holm-Hansen O (2000) Effects of high latitude UV radiation on phytoplankton and nekton modelled from field measurements by simple algorithms. Polar Research 19(2):173-182
- Eilertsen HC, Raa J (1995) Toxins in seawater produced by a common phytoplankter: Phaeocystis pouchetii. Journal of Marine Biotechnology 3:115-120
- Eilertsen HC, Sandberg S, Tellefsen H (1995) Photoperiodic control of diatom spore growth: a theory to explain the onset of phytoplankton blooms. Marine Ecology Progress Series 116:303-307
- Eilertsen HC, Schei B, Taasen JP (1981b) Investigations on the plankton community of Balsfjorden, Northern Norway. The phytoplankton 1976-1978. Abundance, species composition, and succession. Sarsia 66:129-141
- Eilertsen HC, Skarðhamar J (2006) Temperatures of north Norwegian fjords and coastal waters: Variability, significance of local processes and air-sea heat exchange. Estuarine, Coastal and Shelf Science 67:530-538
- Eilertsen HC, Taasen JP (1984) Investigations on the plankton community of Balsfjorden, nothern Norway. The phytoplankton 1976-1978. Environmental factors, dynamics of growth, and primary production. Sarsia 69:1-15
- Eilertsen HC, Taasen JP, Weslawski JM (1989) Phytoplankton studies in the fjords of West Spitzbergen: Physical environment and production in spring and summer. Journal of Plankton Research 11:1245-1260
- Eilertsen HC, Wyatt T (2000) Phytoplankton models and life history strategies. South African Journal of Marine Science 22:323-338
- Ellertsen B (1982) Økologiske undersøkelser nær iskanten i Barentshavet somrene 1979 og 1980. Fisken og Havet (1982) 3:31-83
- Eppley RW (1986) Plankton dynamics of the Southern California Bight, Vol. Springer-Verlag
- Estep KW, Nejstgaard JC, Skjoldal HR, Rey F (1990) Predation by copepods upon natural populations of Phaeocystis pouchetii as a function of the physiological state of the prey. Marine ecology progress series Oldendorf 67:235-249
- Evensen A (1994) Planteplankton i Barentshavet: Artssammensetinig og sukksesjon. Cand. Scient. Thesis, University of Tromsø.153 pp
- Fernandez E, Serret P, De Madariaga I, Harbour DS, Davies AG (1992) Photosynthetic carbon metabolism and biochemical composition of spring phytoplankton assemblages enclosed in microcosms: the diatom-Phaeocystis sp. succession. Marine ecology progress series Oldendorf 90:89-102
- Frouin R, Ligner DW, Gautier C, Baker KS, Smith RC (1989) A simple analytical formula to compute clear sky total and photosynthetically active solar irradiance at the ocean surface. Journal of Geophysical Research 94 (7):9731-9742
- Furevik T (2001) Annual and interannual variability of Atlantic Water temperatures in the Norwegian and Barents Seas: 1980-1996. Deep Sea Research Part I: Oceanographic Research Papers 48:383-404
- Furnes GK, Sundby S (1981) Upwelling and wind-induced circulation in Vestfjorden. . In: The Norwegian Coastal Current, Proceedings of the Norwegian Coastal Current Symposium, Geilo, 9–12 September, 1980, Vol 1, p 152-177

- Føyn BR (1929) Investigations of the Phytoplankton at Lofoten March-April 1922-1927. Skr Nor Vidensk Akad Oslo 1 Mat-Naturv Klasse 1928 10:1-71
- Gaarder KR (1938) Phytoplankton studies from the Tromsø district 1930-31. Tromse Museums Årshefter, Natur Historisk Avdeling 11 (55):1-59
- Gaebler-Schwarz S, Davidson A, Assmy P, Chen J, Henjes J, Nöthig EM, Lunau M, Medlin LK (2010) A new cell stage in the haploid diploid life cycle of the colony forming Haptophyte *Phaeocystis antarctica* and its ecological implications. Journal of Phycology 46:1006–1016
- Garrison DL (1981) Monterey Bay phytoplankton. II. Resting spore cycles in coastal diatom populations. Journal of Plankton Research 3:137-156
- Gill AE (1982) Atmosphere Ocean Dynamics., Vol 30. Academic Press Inc., London
- Gran HH (1900) Hydrographic-biological studies of the North Atlantic Ocean and the coast of Nordland. Report on Norwegian Fishery and Marine Investigations 1(5) 1–92
- Gran HH (1902) Das Plankton des Norwegischen Nordmeeres. Report on Norwegian Fishery and Marine Investigations 2 (5):1–222
- Gran HH (1904) Die Diatomeen der arktischen Meere. I Teil. Die Diatomeen des Planktons. Fauna Arctica 3:509-554
- Gran HH (1927) The production of plankton in the coastal waters off Bergen March–April 1922. Report on Norwegian Fishery and Marine Investigations 3(8):1–74
- Gran HH (1930) The spring growth of the plankton at Møre in 1928–29 and at Lofoten in 1929 in relation to its limiting factors. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I Matematisk-Naturvidenskabelig Klasse 5:1–77
- Haberman KL, Ross RM, Quetin LB (2003) Diet of the Antarctic krill (Euphausia superba Dana): II. Selective grazing in mixed phytoplankton assemblages. Journal of Experimental Marine Biology and Ecology 283:97-113
- Hamm CE (2000) Architecture, ecology and biogeochemistry of Phaeocystis colonies. Journal of Sea Research 43:307-315
- Hansen E, Eilertsen HC (2007) Do the polyunsaturated aldehydes produced by Phaeocystis pouchetii (Hariot) Lagerheim influence diatom growth during the spring bloom in Northern Norway?

 Journal of Plankton Research 29:87-96
- Hansen E, Ernstsen A, Eilertsen HC (2004) Isolation and characterisation of a cytotoxic polyunsaturated aldehyde from the marine phytoplankter Phaeocystis pouchetii (Hariot) Lagerheim. Toxicology 199:207-217
- Hansen GA, Eilertsen HC (1995) Modelling the onset of phytoplankton blooms: a new approach. Ecology of fjords and coastal waters:73-83
- Hegarty SG, Villareal TA (1998) Effects of light level and N:P supply ratio on the competition between Phaeocystis cf. pouchetii (Hariot) Lagerheim (Prymnesiophyceae) and five diatom species. Journal of Experimental Marine Biology and Ecology 226:241-258
- Hegseth EN (1992) Sub-ice algal assemblages of the Barents Sea- Species composition, chemical composition, and growth rates. Polar Research 12:485-496
- Hegseth EN (1997) Phytoplankton of the Barents Sea the end of a growth season. Polar Biology 17:235-241
- Hegseth EN, Svendsen H, Hellum von Quillfeldt C (1995) Phytoplankton in fjords and coastal waters of nothern Norway: environmental conditions and dynamics of the spring bloom. In: Skjodal HR, Hopkins C, Erikstad KE, Leinas HP (eds) Ecology of fjords and coastal waters Elsevier Science, Amsterdam:45-72
- Heimdal B (1974) Composition and abundance of phytoplankton in the Ullsfjord area, North Norway. Astarte 7:17-42
- Heimdal BR (1983) Phytoplankton and nutrients in the waters north-west of Spitzbergen in the autumn of 1979. Journal of Plankton Research 5:901-915

- Heimdal BR (1989) Arctic Ocean phytoplankton. In Herman Y (ed): The arctic seas: climatology, oceanography, and biology Van Nostrand Reinhold, New York:193-222
- Henderson-Sellers B (1986) Calculating the surface energy balance for Lake and reservoir Modeling: A review. Rev Geophys 24(3):625-649
- Hollibaugh JT, Seibert DLR, Thomas WH (1981) Observations on the survival and germination of resting spores of three Chaetoceros (Bacillariophyceae) species. J Phycol 17:1-9
- Hopkins TS (1991) The GIN Sea-A synthesis of its physical oceanography and literature review 1972-1985. Earth-Science Reviews 30:175-318
- Huseby S (2002) The phytoplankton spring bloom dynamics in the Lofoten area, Nothern Norway. Cand. Scient. thesis. Norges Fiskerihøgskole, Universitetet i Tromsø:118 pp.
- Ingvaldsen RB, Asplin L, Loeng H (2004) Velocity field of the western entrance to the Barents Sea. Journal of Geophysical Research 109:12
- Iqbal M (1983) An introduction to solar radiation. , Vol. Academic.
- Iturriaga R (1981) Phytoplankton photoassimilated extracellular products; heterotrophic utilization in marine environment. in: Rheinheimer, G et al (Ed) (1981) Lower Organisms and their Role in the Food Web: Proceedings of the 15th European Marine Biology Symposium, Kiel, Damp 2000, Federal Republic of Germany (September 29-October 3, 1980) Kiel Meeresforsch (Sonderh), 5 European Marine Biology Symposia 15:318-324
- Jahnke J, Baumann MEM (1987) Differentiation between Phaeocystis pouchetii (Har.) Lagerheim and Phaeocystis globosa Scherffel. I. Colony shapes and temperature tolerances. Hydrobiol Bull 21:141-147
- Jørgensen E (1905) The protist plankton and the diatoms in bottom samples. Bergens Museums Skrifter 7:3–254
- Kashkin NI (1964) On the winter deposits of phytoplankton in the sub-littoral. Trudy O/ceanol Inst A/cad Nauk USSR 65:49-57
- Kayser H (1970) Experimental-ecological investigations on Phaeocystis poucheti (Haptophyceae): cultivation and waste water test. Helgoland Marine Research 20:195-212
- Krebs CJ, Richard LW (1985) Ecology: The Experimental Analysis of Distribution and Abundance. Bios 56:236-238
- Kuznetsov LL (1992) Phytoplankton of the Barents Sea. Institute of Marine Biology, USSR Academy of Science, Dalnie Zelntzy Russian Academy of Sciences, Apatity
- Lagerheim G (1896) Über Phaeocystis pouchetii (Hariot) Lagerheim, eine Plankton-Flagellate. Övers K Vetensk-Akad Förh 4: 277–288
- Lancelot C (1995) The mucilage phenomenon in the continental coastal water of teh North Sea. Vollenweider, RA, Rinaldi, A (Eds) The Science of the Total Environment, Special volume on Marine Mucilages 165:83-102
- Lancelot C, Rousseau V (1994) Ecology of Phaeocystisdominated ecosystems: the key role of colony forms. Leadbeater BSc, Green JC (eds) The Haptophyte algae Systematics Association 51:229-245
- Larsson U, Hagström A (1979) Phytoplankton exudate release as an energy source for the growth of pelagic bacteria. Marine biology 52:199-206
- Larsson U, Hagström Å (1982) Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophication gradient. Marine biology 67:57-70
- Levitus S (1982) Climatological atlas of the world ocean. NOAA Prof
- Pap 13:173 pp
- Loeng H (1991) Features of the physical oceanographic conditions of the Barents Sea. Polar Research 10:5-18
- Lutter S (1989) Phytoplankton Dynamics and Sedimentation Processes During Spring and Summer in Balsfjorden, Nothern Norway. Polar Biol 10:113-124

- Marcus NH, Boero F (1998) Minireview: The Importance of Benthic-Pelagic Coupling and the Forgotten Role of Life Cycles in Coastal Aquatic Systems. Limnology and Oceanography 43:763-768
- Margalef R (1958) Temporal succession and spatial heterogeneity in phytoplankton. Perspectives in marine biology, University of California Press:323-348
- Margalef R (1978) Life-forms of phytoplankton as survival alternatives in unstable environments. Oceanologica acta 134:493-509
- Matthews JBL, Heimdal B (1980) Pelagic productivity and food chains in fjord systems. In: Freeland HJ, Farmer DM, Levings CD (eds) Fjord Oceanography, Vol Nato Conference Series VI: Marine Sciences. . Plenum Publ. Corp., New York, p 377-398 pp.
- Medlin L, Zingone A (2007) A taxonomic review of the genus Phaeocystis. Biogeochemistry 83:3-18 Mitchelson-Jacob G, Sundby S (2001) Eddies of Vestfjorden, Norway. Continental Shelf Research 21:1901-1918
- Nejstgaard JC, Frischer ME, Simonelli P, Troedsson C, Brakel M, Adiyaman F, Sazhin AF, Artigas LF (2008) Quantitative PCR to estimate copepod feeding. Marine biology 153:565-577
- Nejstgaard JC, Tang KW, Steinke M, Dutz J, Koski M, Antajan E, Long JD (2007) Zooplankton grazing on Phaeocystis: a quantitative review and future challenges. Biogeochemistry 83:147-172
- Nichols PD, Skerratt JH, Davidson A, Burton H, McMeekin TA (1991) Lipids of cultured Phaeocystis pouchetii: signatures for food-web, biogeochemical and environmental studies in Antartica and the Southern Ocean. Phytochemistry 30:3209-3214
- Ottersen G, Chr N (2001) Atlantic climate governs oceanographic and ecological variability in the Barents Sea. Limnology and Oceanography 46:1774-1780
- Palmisano AC, SooHoo JB, SooHoo SL, Kottmeier ST, Craft LL, Sullivan CW (1986) Photoadaptation in Phaeocystis pouchetii advected beneath annual sea ice in McMurdo Sound, Antarctica. Journal of Plankton Research 8:891-906
- Pedersen OP, Tande KS, Pedersen T, Slagstad D (2009) Advection and retention as life trait modulators of capelin larvae-A case study from the Norwegian coast and the Barents Sea. Fisheries Research 97:234-242
- Peperzak L, Colijn F, Koeman R, Gieskes WWC, Joordens JCA (2003) Phytoplankton sinking rates in the Rhine region of freshwater influence. Journal of Plankton Research 25:365-383
- Pohnert G (2000) Wound-activated chemical defense in unicellular planktonic algae. Angewandte Chemie International Edition 39:4352-4354
- Pohnert G (2002) Phospholipase A2 activity triggers the wound-activated chemical defense in the diatom Thalassiosira rotula. Plant physiology 129:103-111
- Quillfeldt CH (1996) Ice Algae and Phytoplankton in North Norwegian and Arctic Waters: Species Composition, Succession and Distribution. Department of Aquatic Biology, The Norwegian College of Fishery Science, Phd Thesis, University of Tromsø
- Quillfeldt CH (2000) Common Diatom Species in Arctic Spring Blooms: Their Distribution and Abundance. Botanica Marina 43:499-516
- Quillfeldt CH (2001) Identification of some easily confused common diatom species in arctic spring blooms. Botanica Marina 44:375-389
- Quillfeldt CH, Ambrose WG, Clough LM (2003) High number of diatom species in first-year ice from the Chukchi Sea. Polar Biology 26:806-818
- Quinn GP, Keough MJ (2009) Experimental Design and Data Analysis for Biologists, Vol 8. University Press, United Kingdom, Cambridge
- Rat'kova TN, Wassmann P (2002) Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea. Journal of Marine Systems 38:47-75
- Reigstad M, Wassmann P (2007) Does Phaeocystis spp. contribute significantly to vertical export of organic carbon? Biogeochemistry 83:217-234

- Rey F (1993) Planteplanktonet og dets primærproduksjon i det nordlige Barentshavet, Vol 10. Havforskningsinstituttet
- Rey F, Loeng H (1985) The influence of ice and hydrographic conditions on the development of phytoplankton in the Barents Sea. In: In: J.S. Gray and M.E. Christiansen (Editors). Marine Biology of Polar Regions and Effects of Stress on Marine Organisms. Wiley C (ed), p 49-63
- Riebesell U, Reigstad M, Wassmann P, Noji T, Passow U (1995) On the trophic fate of Phaeocystis pouchetii (hariot): VI. Significance of Phaeocystis-derived mucus for vertical flux Netherlands Journal of Sea Research 33:193-203
- Riemann B, Sondergaard M, Schierup HH, Bosselmann S, Christensen G, Hansen J, Nielsen B (1982)

 Carbon metabolism during a spring diatom bloom in the eutrophic Lake Mossoe. Int Rev

 Gesamten Hydrobiol 67:145-185
- Rousseau V, Chrétiennot-Dinet MJ, Jacobsen A, Verity P, Whipple S (2007) The life cycle of Phaeocystis: state of knowledge and presumptive role in ecology. Biogeochemistry 83:29-47
- Rousseau V, Vaulot D, Casotti R, Cariou V, Lenz J, Gunkel J, Baumann M (1994) The life cycle of Phaeocystis (Prymnesiophyceae): evidence and hypotheses. Journal of marine systems 5:23-39
- Rousseaua V, Becquevorta S, Parenta J-Y, Gasparinib S, Darob M-H, Tackxb M, Lancelota C (2000)

 Trophic efficiency of the planktonic food web in a coastal ecosystem dominated by
 Phaeocystis colonies. Journal of Sea Research 43:357–372
- Sakshaug E (1972) Phytoplankton investigations in Trondheimsfjord, 1963–1966. Det Kongelige Norske Videnskabers Selskab Skrifter 1:1–56
- Sakshaug E, Johnsen GH, Kovacs KM, (eds) (2009) Ecosystem Barents Sea, Vol. Tapir Acad. Press, Trondheim, 587 pp
- Sakshaug E, Slagstad D (1991) Light and productivity of phytoplankton in polar marine ecosystems: a physiological view. Polar Research 10:69-86
- Sandberg S (1996) Våroppblomstringens dynamikk i en fjord-kyst gradient i Balsfjorden og Malangensystemet 1993. Cand. Scient. thesis., Universitetet i Tromsø.
- Sars GO (1879) Undersøkelser over loddefisket i Finmarken. Indberetninger til Departementet for det indre. Departementet for det indre, Christiania, Norway:17-32
- Savage RE (1932) Phaeocystis and herring shoals. The Journal of Ecology 20:326-340
- Schei B (1974) Phytoplankton investigations in Skjomen, a fjord in North Norway, 1970-1971. Astarte 7:43-59
- Scherffel A (1899) Phaeocystis globosa nov. sp. (Vorläufige Mittheilung). Berichte der Deutschen Botanischen Gesellschaft 17:317-318
- Scherffel A (1900) Phaeocystis globosa nov. Spec. Nebst einigen Betrachtungen über die Phylognie niederer, insbesondere brauner Organismen, Vol 4. Lipsius & Tischer
- Schoemann V, Becquevorta S, Stefelsb J, Rousseaua V, Lancelota C (2005) Phaeocystis blooms in the global ocean and their controlling mechanisms: a review Journal of Sea Research 53:43-66
- Skjoldal HR, Rey F (1989) Pelagic production and variability of the Barents Sea ecosystem. In:
 Sherman K, Alexander LM, editors Biomass yields and geography of large marine ecosystems
 AAAS selected Symposium 111 American Association for the Advancement of Sciences
 Boulder, CO: Westview Press:241–286
- Skofteland E (1985) Ferskvannstilførsel til kysten før og etter regulering. Vassdragsreguleringers innvirkning på fjorder
- Skreslet S (1988) Buoyancy in Phaeocystis pouchetii (Hariot) Lagerheim. Journal of Experimental Marine Biology and Ecology 119:157-166
- Smayda TJ (1958) Phytoplankton studies around Jan Mayen Island March-April 1955. Nytt Magasin for Botanikk 6:75-96
- Smayda TJ (1980) Phytoplankton species succession. The physiological ecology of ohytoplankton Studies in ecology 7, ed, I Morris:493-570

- Smayda TJ (1997) What is a Bloom? A Commentary. Limnology and Oceanography 42:1132-1136
 Smith SD, Anderson RJ, Hartog GD, Topham DR, Perkins RG (1983) Air investigations of a polynya in the Canadian archipelagos, structure of turbulence and heat flux. Journal of Geophysical Research 88:2900-2910
- Smith WO (1977) Primary production off the coast of northwest Africa: excretion of dissolved organic matter and its heterotrophic uptake. Deep Sea Research 24:35-47
- Smith WO, Dennett MR, Mathot S, Caronc DA (2003) The temporal dynamics of the flagellated and colonial stages of Phaeocystis antarctica in the Ross Sea Elsevier Science
- Sournia A, Chrétiennot-Dinet M-J, Ricard M (1991) Marine phytoplankton: how many species in the world ocean? Journal of Plankton Research 13:1093-1099
- Stabell OB, Aanesen RT, Eilertsen HC (1999) Toxic peculiarities of the marine alga Phaeocystis pouchetii detected by in vivo and in vitro bioassay methods. Aquatic Toxicology 44:279-288
- Stramska M, Dickey TD (1993) Phytoplankton bloom and the vertical thermal structure of the upper ocean. Journal of Marine Research 51:819-842
- Svendsen H (1991) Preliminary results from a hydrophysical investigation of Porsangerfjord, Altafjord and adjacent coastal waters, June-August 1990., Geophysical institute, Bergen
- Svendsen H, Thompson R (1978) Wind-driven circulation in a fjord. Journal of Physical Oceanography 8:703-712
- Sælen OH (1950) The hydrography of some fjords in Northern Norway. Annual Reports of Tromsø Museum 70:102
- Sætre R, Mork M (1981) The Norwegian Coastal Current., Vol I og II. University of Bergen, Geilo Tansley AG (1935) The use and abuse of vegetational concepts and terms. Ecology 16:284-307
- Throndsen J, Heimdal BR (1976) Primary production, phytoplankton and light in Straumsbukta near Tromsø. Astarte 9:51-60
- Tomas CR, Hasle GR (1997) Identifying marine phytoplankton, Vol. Academic Press, San Diego Utermöhl H (1958) Zur Vervollkommung der quantitativen Phytoplanktonmethodik. Mitteillungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 9:1-38
- van Rijssel M, Janse I, Noordkamp KJB, Gieskes WWC (2000) An inventory of factors that affect polysaccharide production by *Phaeocystis globosa*. J Sea Res 43:297-306
- Veldhuis MJW, Brussaard CPD, Noordeloos AAM (2005) Living in a Phaeocystis colony: a way to be a successful algal species. Harmful Algae 4:841-858
- Verity PG, Smayda TJ (1989) Nutritional value of Phaeocystis pouchetii (Prymnesiophyceae) and other phytoplankton for Acartia spp.(Copepoda): ingestion, egg production, and growth of nauplii. Marine Biology 100:161-171
- Verity PG, Zirbel MJ, Nejstgaard JC (2007) Formation of very young colonies by Phaeocystis pouchetii from western Norway. Aquatic Microbial Ecology 47:267-274
- von Quillfeldt CH (2000) Common Diatom Species in Arctic Spring Blooms: Their Distribution and Abundance. Botanica Marina 43:499-516
- Wassmann P, Ratkova T, Andreassen I, Vernet M, Pedersen G, Rey F (1999) Spring Bloom

 Development in the Marginal Ice Zone and the Central Barents Sea. Marine Ecology 20:321346
- Wassmann P, Ratkova T, Reigstad M (2005) The contribution of single and colonial cells of Phaeocystis pouchetii to spring and summer blooms in the north-eastern North Atlantic. Harmful algae 4:823-840
- Wassmann P, Vernet M, Mitchell BG, Rey F (1990) Mass sedimentation of Phaeocystis pouchetii in the Barents Sea. Mar Ecol Prog Ser 66:183-195
- Weisse T, Tande K, Verity P, Hansen F, Gieskes W (1994) The trophic significance of Phaeocystis blooms. Journal of Marine Systems 5:67-79
- Wolfe GV (2000) The chemical defense ecology of marine unicellular plankton: constraints, mechanisms, and impacts. The Biological Bulletin 198:225-244

Zingone A, Chrétiennot Dinet MJ, Lange M, Medlin L (1999) Morphological and genetic characterization of Phaeocystis cordata and P. jahnii (Prymnesiophyceae), two new species from the Mediterranean Sea. Journal of Phycology 35:1322-1337

Appendix A

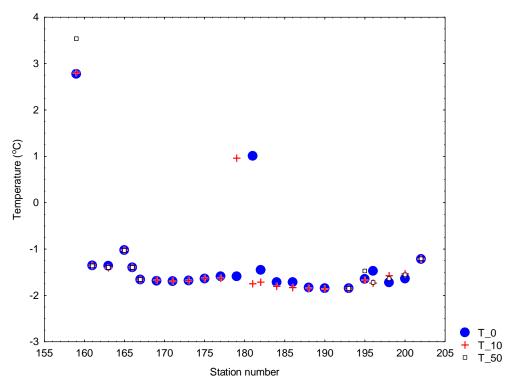


Figure 1A: Sea temperatures plotted against station number at 0m, 10m and 50m in the Barents Sea in May 2006.

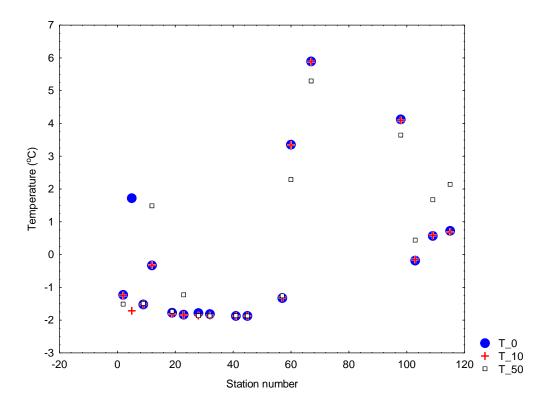


Figure 2A: Sea temperatures plotted against station number at 0m, 10m and 50m in the Barents Sea in May 2007.

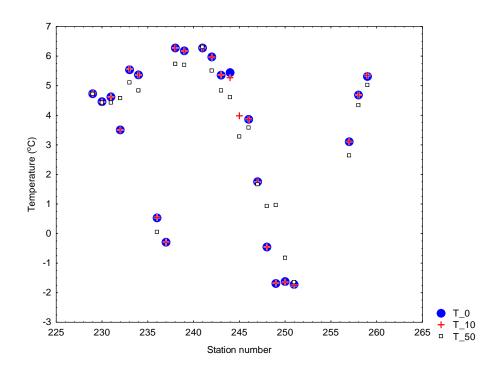


Figure 3A: Sea temperatures plotted against station number at 0m, 10m and 50m in the Barents Sea in May 2009.

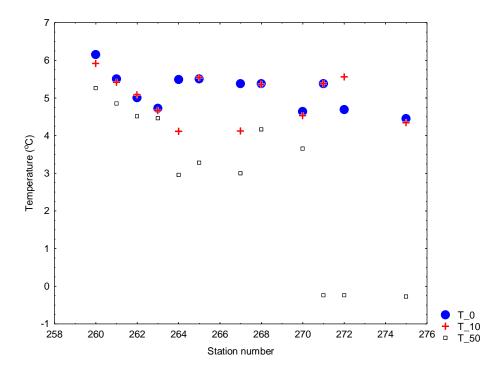


Figure 4A: Sea temperatures plotted against station number at 0m, 10m and 50m in East Finnmark in May 2009.

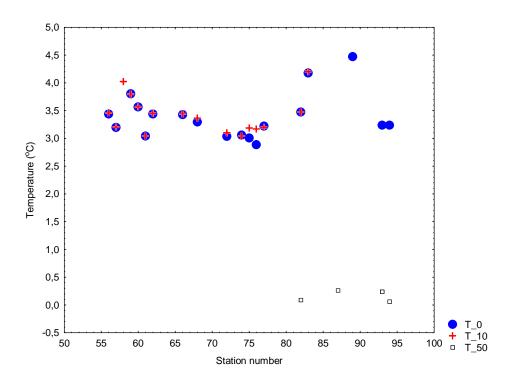


Figure 5A: Sea temperatures plotted against station number at 0m, 10m and 50m in the Vestfjord archipelago in April 2006.

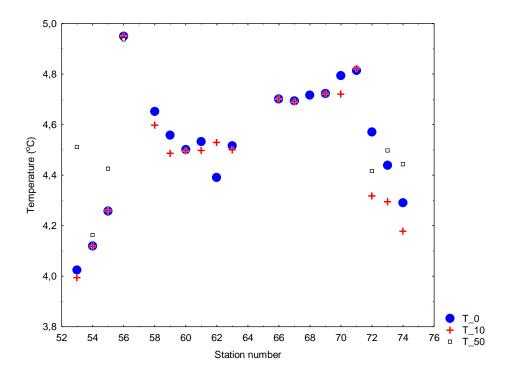


Figure 6A: Sea temperatures plotted against station number at 0m, 10m and 50m in the Vestfjord archipelago in April 2007. Note missing 0m temperature for station 56, values from 5m was used instead.

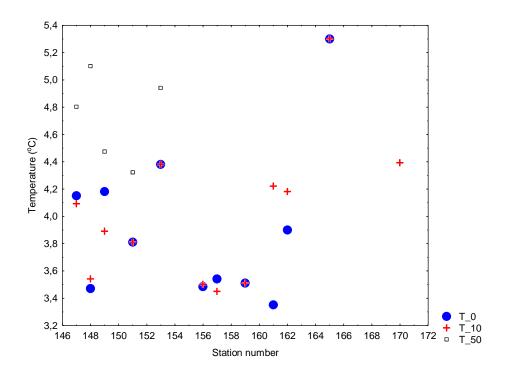


Figure 7A: Sea temperatures plotted against station number at 0m, 10m and 50m in the Vestfjord archipelago in April 2009.

Appendix B

Table 1B: An overview showing sampling stations in the Barents Sea in May 2006, 2007 and 2009.

ID. All 0	verview show	ing sampinig sta	uons m un	e Darents Sea i
Station	Latitude (°)	Longitude (°)	Date	Time (UTC)
159	80.13	9.58	10.05.06	07:14
161	80.84	9.34	10.05.06	14:45
163	81.55	9.36	10.05.06	20:24
165	81.31	13.76	11.05.06	03:05
166	81.48	15.83	11.05.06	06:05
167	81.73	15.79	11.05.06	12:00
169	81.77	15.84	11.05.06	19:10
171	81.73	15.80	11.05.06	23:16
173	81.73	15.80	12.05.06	03:02
175	81.73	15.80	12.05.06	06:57
177	81.66	15.60	12.05.06	11:05
179	81.15	18.80	12.05.06	19:00
181	80.69	29.22	13.05.06	06:19
182	80.92	30.51	13.05.06	13:00
184	80.88	30.30	13.05.06	16:56
186	80.90	29.91	13.05.06	21:04
188	80.90	29.38	14.05.06	00:59
190	80.85	29.74	14.05.06	05:53
193	80.02	28.95	14.05.06	14:02
195	79.60	31.09	14.05.06	20:09
196	79.07	33.34	15.05.06	02:02
198	78.30	31.91	15.05.06	07:02
200	78.30	31.91	15.05.06	13:00
202	76.56	27.40	15.05.06	19:34
2	75.51	20.02	10.05.07	18:00
5	75.54	22.38	10.05.07	22:01
9	75.51	24.50	11.05.07	02:05
12	76.46	28.92	11.05.07	11:21
19	77.94	31.76	12.05.07	06:20
23	78.02	32.98	12.05.07	12:56
28	78.08	33.90	12.05.07	21:01
32	78.07	33.94	13.05.07	01:03
41	77.98	33.70	13.05.07	10:05
45	77.98	33.73	13.05.07	13:57
57	74.93	21.51	15.05.07	05:07
60	74.24	18.98	15.05.07	11:03
67	73.87	18.63	15.05.07	17:47
98	77.19	13.73	18.05.07	07:00
103	77.78	12.29	18.05.07	12:07
109	78.21	11.17	18.05.07	17:14
115	78.69	10.26	18.05.07	23:03
229	77.99	9.03	15.05.09	02:23
230	77.72	9.68	15.05.09	09:34
	Station 159 161 163 165 166 167 169 171 173 175 177 181 182 184 186 188 190 193 195 196 198 200 202 2 5 9 12 19 23 28 32 41 45 57 60 67 98 103 109 115 229	Station Latitude (°) 159 80.13 161 80.84 163 81.55 165 81.31 166 81.48 167 81.73 169 81.77 171 81.73 173 81.73 175 81.66 179 81.15 181 80.69 182 80.92 184 80.88 186 80.90 190 80.85 193 80.02 195 79.60 196 79.07 198 78.30 200 78.30 202 76.56 2 75.51 5 75.54 9 75.51 12 76.46 19 77.94 23 78.02 28 78.08 32 78.07 41 77.98 57	Station Latitude (°) Longitude (°) 159 80.13 9.58 161 80.84 9.34 163 81.55 9.36 165 81.31 13.76 166 81.48 15.83 167 81.73 15.79 169 81.77 15.84 171 81.73 15.80 173 81.73 15.80 175 81.66 15.60 179 81.15 18.80 181 80.69 29.22 182 80.92 30.51 184 80.88 30.30 186 80.90 29.91 188 80.90 29.91 188 80.90 29.93 190 80.85 29.74 193 80.02 28.95 195 79.60 31.09 196 79.07 33.34 198 78.30 31.91 202 76.56 <td>159 80.13 9.58 10.05.06 161 80.84 9.34 10.05.06 163 81.55 9.36 10.05.06 165 81.31 13.76 11.05.06 166 81.48 15.83 11.05.06 167 81.73 15.79 11.05.06 169 81.77 15.84 11.05.06 171 81.73 15.80 12.05.06 173 81.73 15.80 12.05.06 175 81.73 15.80 12.05.06 179 81.15 18.80 12.05.06 181 80.69 29.22 13.05.06 182 80.92 30.51 13.05.06 184 80.88 30.30 13.05.06 188 80.90 29.91 13.05.06 188 80.90 29.91 13.05.06 193 80.02 28.95 14.05.06 195 79.60 31.09 14.05.06 196</td>	159 80.13 9.58 10.05.06 161 80.84 9.34 10.05.06 163 81.55 9.36 10.05.06 165 81.31 13.76 11.05.06 166 81.48 15.83 11.05.06 167 81.73 15.79 11.05.06 169 81.77 15.84 11.05.06 171 81.73 15.80 12.05.06 173 81.73 15.80 12.05.06 175 81.73 15.80 12.05.06 179 81.15 18.80 12.05.06 181 80.69 29.22 13.05.06 182 80.92 30.51 13.05.06 184 80.88 30.30 13.05.06 188 80.90 29.91 13.05.06 188 80.90 29.91 13.05.06 193 80.02 28.95 14.05.06 195 79.60 31.09 14.05.06 196

2009	231	77.47	10.97	15.05.09	15:58
2009	232	77.03	11.25	15.05.09	23:00
2009	233	76.64	13.06	16.05.09	07:08
2009	234	76.40	14.33	16.05.09	13:05
2009	236	74.38	19.96	17.05.09	21:38
2009	237	74.32	19.14	18.05.09	17:26
2009	238	74.31	15.80	19.05.09	14:18
2009	239	74.07	15.46	19.05.09	21:56
2009	241	73.23	16.37	20.05.09	14:25
2009	242	73.30	19.26	20.05.09	23:49
2009	243	73.40	22.05	21.05.09	06:38
2009	244	73.80	24.59	21.05.09	13:30
2009	245	74.25	26.98	21.05.09	20:09
2009	246	74.92	28.88	22.05.09	02:55
2009	247	75.64	29.92	22.05.09	09:26
2009	248	76.40	30.61	22.05.09	17:05
2009	249	77.14	31.27	22.05.09	22:59
2009	250	77.34	30.96	23.05.09	03:35
2009	251	77.72	30.92	23.05.09	12:38
2009	257	74.87	27.49	25.05.09	08:34
2009	258	74.00	27.17	25.05.09	14:17
2009	259	72.85	26.68	25.05.09	20:57

Table 2B: An overview showing sampling stations in East Finnmark in May 2009.

Year	Station	Latitude (°)	Longitude (°)	Date	Time (UTC)
2009	260	71.69	26.47	26.05.09	03:57
2009	261	71.05	26.67	26.05.09	18:32
2009	262	70.96	29.07	27.05.09	01:33
2009	263	70.46	31.00	27.05.09	01:45
2009	264	69.78	30.71	27.05.09	13:38
2009	265	69.81	30.41	28.05.09	07:03
2009	267	69.68	30.41	28.05.09	11:03
2009	268	70.03	29.97	28.05.09	15:37
2009	270	70.11	28.94	28.05.09	20:43
2009	271	70.87	26.27	29.05.09	14:58
2009	272	70.20	25.27	29.05.09	22:32
2009	275	70.12	25.18	30.05.09	09:08

Table 3B: An overview showing sampling stations in the Vestfjord archipelago in April 2006, 2007 and 2009.

Year			Longitude (°)		Time (UTC)
2006	56	68.35	15.99		18:28
2006	57	68.17	15.28		21:35
2006	58	68.00	14.52	02.04.06	00:40
2006	59	67.80	13.78	02.04.06	03:35
2006	60	67.56	13.27	02.04.06	20:10
2006	61	68.15	14.20	02.04.06	23:10
2006	62	68.15	14.20		23:10
2006	66	68.15	14.20	03.04.06	07:02
2006	68	68.15	14.20		16:01
2006	72	68.33	14.73	03.04.06	20:30
2006	74	68.33	14.73	03.04.06	00:03
2006	75	68.33	14.73	04.04.06	04:30
2006	76	68.33	14.73	04.04.06	08:00
2006	77	68.33	14.73	04.04.06	06:07
2006	82	67.90	16.26	05.04.06	07:31
2006	83	67.86	16.20	05.04.06	15:37
2006	87	67.82	16.48	05.04.06	23:26
2006	89	67.82	16.48	06.04.06	08:20
2006	93	68.06	16.13	07.04.06	06:01
2006	94	68.06	16.13	07.04.06	10:00
2007	53	68.35	16.00	12.04.07	18:53
2007	54	68.20	15.19		21:31
2007	55	68.06	14.39	13.04.07	01:33
2007	56	67.86	13.65	13.04.07	05:05
2007	58	68.34	14.73	13.04.07	13:13
2007	59	68.34	14.73	13.04.07	17:02
2007	60	68.34	14.73		21:06
2007	61	68.34	14.73	14.04.07	01:01
2007	62	68.34	14.73		05:05
2007	63	68.34	14.73	14.04.07	09:10
2007	66	68.24	14.20	14.04.07	19:06
2007	67	68.24	14.21	14.04.07	23:02
2007	68	68.24	14.21	15.04.07	02:57
2007	69	68.24	14.21	15.04.07	07:05
2007	70	68.24	14.21	15.04.07	11:00
2007	71	68.24	14.21	15.04.07	14:58
2007	72	67.82	16.48	18.04.07	07:06
2007	73	67.86	16.39	18.04.07	10:43
2007	74	67.90	16.26	18.04.07	18:15
2009	147	68.35	15.99	15.04.09	06:18
2009	148	68.20	15.29	15.04.09	09:00
2009	149	68.00	14.51	15.04.09	13:20
2009	151	67.81	13.78	15.04.09	16:18
2009	153	67.56	13.28	15.04.09	18:51
2009	156	68.16	14.14	16.04.09	23:40

2009	157	68.17	14.14 17.04.09	03:28
2009	159	68.16	14.13 17.04.09	07:42
2009	161	68.33	14.73 17.04.09	23:31
2009	162	68.33	14.73 18.04.09	03:26
2009	165	67.82	16.47 19.04.09	06:22
2009	170	67.87	16.34 19.04.09	15:05

Appendix C

- Table 1C: "central" P. pouchetii literature. The list is incomplete and compiled from various sources.
- Aanesen, R.T., Eilertsen, H.C. and Stabell, O.B. (1998) Light-induced toxic properties of the marine alga Phaeocystis pouchetii towards cod larvae. Aquat. Toxicol. 40: 109-121.
- Admiraal, W. and Venekamp, L.A.H. (1986) Significance of tintinnid grazing during blooms of Phaeocystis pouchetii (Haptophyceae) in Dutch coastal waters. Neth. J. Sea Res. 20: 61-66.
- Aksnes, D.L. and Egge, J.K. (1991) A theoretical model for nutrient uptake in phytoplankton. Mar. Ecol. Prog. Ser. 70: 65-72.
- Al-Hasan, R.H., Ali, A.M., Radwan, S.S. (1990) Lipids, and their constituent fatty acids, of Phaeocystis sp. from the Arabian Gulf. Mar. Biol. 105: 9-14.
- Anderson, L.J.W. and Sweeney, B.M. (1977) Diel changes in sedimentation characteristics of Ditylum brightwelli: changes in cellular lipid and effects of respiratory inhibitors and ion-transport modifiers. Limnol. Oceanogr. 22: 539-552.
- Anderson, L.J.W. and Sweeney, B.M. (1978) Role of inorganic ions in controlling sedimentation rate of a marine centric diatom Ditylum brightwellii. J. Phycol. 14: 204-214.
- Anderson, P. (1996) Design and Implementation of some Harmful Algal Monitoring Systems. UNESCO, Paris.
- Apstein, C. (1904) Die Schatzungsmethode in der Planktonforschung. Wissenschaftlige Meeresunters. Abteilung Kiel. Neue Folge, Band VIII: 105 123.
- Armonies, W. (1989) Occurrence of meiofauna in Phaeocystis seafoam. Mar. EcolProg. Ser. 53: 305-309.
- Arrigo, K.R., Robinson, D.H., Worthen, D.L., Dunbar, R.B., DiTullio, G.R., van Woert, M. and Lizotte, M.P. (1999) Phytoplankton community structure and the drawdown of nutrients and CO2 in the Southern Ocean. Science 283: 365-367.
- Atkins, P.W. (1999) Physical Chemistry, Oxford University Press, Oxford.
- Atkinson, L.P., Paffenhöfer, G.-A. and Dunstan, W.M. (1978) The chemical and biological effect of a Gulf Stream intrusion off St. Augustine, Florida. Bull. Mar. Science 28: 667-679.
- Bakker, C., Herman, P.M.J. and Vink, M. (1990) Changes in seasonal succession of phytoplankton induced by the storm-surge barrier in the Oosterschelde (SW Netherlands). J. Plankton Res. 12: 947-972.
- Bakker, C., Herman, P.M.J. and Vink, M. (1994) A new trend in the development of the phytoplankton in the Oosterschelde (SW Netherlands) after the construction of a storm-surge barrier. Hydrobiologia 282/283: 79 100.
- Bannister, T.T. (1990) Comparison of Kiefer-Mitchell and Bannister-Laws algal models. Limnol. Oceanogr. 35: 972-979.
- Barnard, W.R., Andreae, M.O. and Iverson, R.L. (1984) Dimethylsulfide and Phaeocystis poucheti in the southeastern Bering Sea. Cont. Shelf Res. 3: 103-113
- Bätje,M. and Michaelis,H. (1986) Phaeocystis pouchetii blooms in the East Frisian coastal waters (German Bight, North Sea). Mar. Biol. 93: 21-27.
- Baumann, M.E.M., Lancelot, C., Brandini, F.P., Sakshaug, E. and John, D.M. (1994) The taxonomic identity of the cosmopolitan prymnesiophyte Phaeocystis: a morphological and ecophysiological approach. J. Mar. Syst. 5: 5-22.
- Bautista,B.R.P. Harris,P., Tranter,R.G. and Harbour,D. (1992) In situ copepod feeding and grazing rates during a spring bloom dominated by Phaeocystis sp. in the English Channel. J. Plankton Res. 14: 691-703
- Beardall, J., Johnston, A. and Raven, J. (1998) Environmental regulation of CO2-concentrating mechanisms in microalgae. Can. J. Bot. 76: 1010-1017.
- Becquevort, S., Rousseau, V. and Lancelot, C. (1998) Major and comparable roles for free-living and attached bacteria in the degradation of Phaeocystisderived organic matter in Belgian coastal waters of the North Sea. Aquat. Microb. Ecol. 14: 39-48.
- Berges, J.A. and Falkowski, P.G. (1998) Physiological stress and cell death in marine phytoplankton:

- Induction of proteases in response to nitrogen or light limitation. Limnol.Oceanogr. 43: 129-135.
- Beukema, J.J. and Cadée, G.C. (1991) Growth rates of the bivalve Macoma balthica in the Wadden Sea during a period of eutrophication: relationships with concentrations of pelagic diatoms and flagellates. Mar. Ecol. Prog. Ser. 68: 249-256.
- Bidle, K.D. and Azam, F. (1999) Accelerated dissolution of diatom silica by marine bacterial assemblages. Nature 397: 508-512.
- Bienfang, P.K. (1981a) Sinking rates of heterogeneous, temperate phytoplankton populations. J. Plankton Res. 3: 235-253.
- Bienfang, P.K. (1981b) SETCOL- a technologically simple and reliable method for measuring phytoplankton sinking rates. Can. J. Fish. Aquat. Sci. 38: 1289-1294.
- Bienfang, P.K. (1982) Phytoplankton sinking-rate dynamics in enclosed experimental ecosystems. In: G.D.Grice and M.R.Reeve (eds): Marine mesocosms. Springer Verlag New-York: 261-275.
- Billard,C. (1994) Life cycles. In: J.C.Green B.S.C.Leadbeater (eds.): The Haptophyte Algae. Clarendon Press, Oxford: 167-186.
- Billen,G. and Fontigny,A. (1987) Dynamics of a Phaeocystis-dominated spring bloom in Belgian coastal waters. II. Bacterioplankton dynamics. Mar. Ecol. Prog. Ser. 37: 249-257.
- Boalch,G.T. (1984) Algal blooms and their effects on fishing in the English Channel. Hydrobiologia 116/117: 449-452.
- Boalch,G.T. (1987) Recent blooms in the western English Channel. Rapp. P.-v. Réun. Cons. Int. Explor. Mer. 87: 94-97.
- Bonin, D.J., Maestrini, S.Y. and Leftley, J.W. (1981) The role of phytohormones and vitamins in species succession of phytoplankton. In: T.Platt (ed.) Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci.: 210: 310-322.
- Booth,B.C., Lewin,J. and Norris,R.E. (1982) Nanoplankton species predominant in the subarctic Pacific in May and June 1978. Deep-Sea Res. 29: 185-200.
- Brand,L. (1984) The salinity tolerance of forty-six marine phytoplankton isolates. Est. Coast. Shelf Science 18: 543-556.
- Brussaard, C.P.D., Riegman, R., Noordeloos, A.A.M., Cadée, G.C., Witte, H., Kop, A.J., Nieuwland, G., van Duyl, F.C. and Bak, R.P.M. (1995) Effects of grazing, sedimentation and phytoplankton cell lysis on the structure of a coastal pelagic food web. Mar. Ecol. Prog. Ser. 123: 259-271.
- Brussaard, C.P.D., Gast, G.J., van Duyl, F.C. and Riegman, R. (1996) Impact of phytoplankton bloom magnitude on a pelagic microbial food web. Mar. Ecol. Prog. Ser. 144: 211-221.
- Brussaard, C.P.D., Noordeloos, A.A.M. and Riegman, R. (1997). Autolysis kinetics of the marine diatom Ditylum brightwellii (Bacillariophyceae) under nitrogen and phosphorus limitation and starvation. J. Phycol. 33: 980-987.
- Brzezinski, M.A., and Nelson, D.M. (1988) Differential cell sinking as a factor influencing diatom species composition for limiting nutrients. J. Exp. Mar. Biol. Ecol. 119: 179-200.
- Buck, K.R. and Garrison, D.L. (1983) Protists from the ice-edge region of the Weddell Sea. Deep-Sea Res. 30: 1261-1277.
- Bullen,G.E. (1908) Plankton studies in relation to the western mackerel fishery. J. Mar. Biol. Assoc. 8: 269-302.
- Buma, A.G.J., Bano, N., Veldhuis, M.J.W. and Kraay, G.W. (1991) Comparison of the pigmentation of two strains of the prymnesiophyte Phaeocystis sp. Neth. J. Sea Res. 27: 173-182.
- Buma, A.G.J., Noordeloos, A.A.M. and Larsen, J. (1993) Strategies and kinetics of photoacclimation in three antarctic nanophytoflagellates. J. Phycol. 29: 407-417.
- Burkill, P.H., Mantoura, R.F.C.C., Llewellyn, A. and Owens, N.J.P. (1987) Microzooplankton grazing and selectivity of phytoplankton in coastal waters. Mar. Biol. 93: 581-590.
- Butler, J.N. (1992) Alkalinity titration in seawater: how can the data be fitted to an equilibrium model? Mar. Chem. 38: 251-288.
- Cadée,G.C. (1982) Tidal and seasonal variation in particulate and dissolved organic carbon in the

- western Dutch Wadden Sea and Marsdiep tidal inlet. Neth. J. Sea Res. 15: 228-249.
- Cadée,G.C. (1986) Recurrent and changing seasonal patterns in phytoplankton of the westernmost inlet of the Dutch Wadden Sea from 1969 to 1985. Mar. Biol. 93: 281-289.
- Cadée,G.C. and Hegeman,J. (1986) Seasonal and annual variation in Phaeocystis pouchetii (Haptophyceae) in the westernmost inlet of the Wadden Sea during the 1973 to 1985 period. Neth. J. Sea Res. 20: 29-36.
- Cadée,G.C. (1990) Increase of Phaeocystis blooms in the westernmost inlet of the Wadden Sea, the Marsdiep, since 1973. In: C.Lancelot, G.Billen and H.Barth (eds.) Eutrophication and algal blooms in North Sea coastal zones. Commission of the European Communities, Brussels: 105-112.
- Cadée, G.C. (1991a) Phaeocystis colonies wintering in the water column? Neth. J. Sea Res. 28: 227-230.
- Cadée, G.C. (1991b) Phytoplankton variability in the Marsdiep, 1980-1990. ICES Variability Symp. Paper no.14 session 2. ICES mar. Sci. Symp. 1991: 1-7.
- Cadée,G.C. and Hegeman,J. (1991a) Historical phytoplankton data of the Marsdiep. Hydrobiol. Bull. 24: 111-118.
- Cadée,G.C. and Hegeman,J. (1991b) Phytoplankton primary production, chlorophyll and composition, organic carbon and turbidity in the Marsdiep in 1990 compared with foregoing years. Hydrobiol. Bull. 25: 29-35.
- Cadée,G.C. (1992) Trends in Marsdiep phytoplankton. Neth. Inst. Sea Res. Publication Series 20: 143-149.
- Cadée, G.C. and Hegeman, J. (1993) Persisting high levels of primary production at declining phosphate concentrations in the Dutch coastal area (Marsdiep). Neth. J. Sea Res. 31: 147-152.
- Cadée, G.C. (1996) Accumulation and sedimentation of Phaeocystis globosa in the Dutch Wadden Sea. J. Sea Res. 36: 321-327.
- Cariou, V., Casotti, R., Birrien, J.-L. and Vaulot, D. (1994) The initiation of Phaeocystis colonies. J. Plankton Res. 16: 457-470.
- Chadwick, H.C. (1885) Foul water. Nature 32: 245.
- Chang, F.H. (1984a) The mucilage-producing Phaeocystis pouchetii (Prymnesiophyceae), cultured from the "Tasman Bay slime". New Zealand J. of Mar. and Freshw. Res. 17: 165-168.
- Chang, F.H. (1984b) The ultrastructure of Phaeocystis pouchetii (Prymnesiophyceae) vegetative colonies with special reference to the production of new mucilaginous envelope. New Zealand J. of Mar. and Freshw. Res. 18: 303-308.
- Chen,C.Y. and Durbin,E.G. (1994) Effects of pH on the growth and carbon uptake of marine phytoplankton. Mar. Ecol. Prog. Ser. 109: 83-94.
- Chin,W-C., Orellana,M.V. and Verdugo,P. (1998) Spontaneous assembly of marine dissolved organic matter into polymer gels. Nature 391: 568-572.
- Chrétiennot-Dinet, M-J., Giraud-Guille, M-M., Vaulot, D., Puteaux, J-L., Saito, Y. and Chanzy, H. (1997) The chitinous nature of filaments ejected by Phaeocystis (Prymnesiophyceae). J. Phycol. 33: 666-672.
- Chrétiennot-Dinet,M-J. (1999) An enigma in marine nanoplankton. In: J.Seckbach (ed.) Enigmatic microorganisms and life in extreme environments. Kluwer Academic Publishers. The Netherlands: 205-213.
- Chu,S.P. (1946) The utilisation of organic phosphorus by phytoplankton. J. Mar. Biol. Assoc. UK. 26: 285-295.
- Claustre, H., Poulet, S.A. Williams, R., Marty, J.-C., Coombs, S., Ben Mlih, F., Hapette, A.M. and Martin-Jezequel, V. (1990) A biochemical investigation of a Phaeocystis sp. bloom in the Irish Sea. J. Mar. Biol. Assoc. U.K. 70: 197 207.
- Cleve, P.T. (1900a) The plankton of the North Sea, the English Channel and the Skagerak in 1898. Kongl. Svenska Vetenskaps Akadamiens Handlingar. 32(8): 1-53.
- Cleve, P.T. (1900b) The plankton of the North Sea, the English Channel and the Skagerak in 1899. Kongl. Svenska Vetenskaps Akadamiens Handlingar 31(2): 1-77.
- Colijn, F. (1982) Light absorption in the waters of the Ems-Dollard estuary and its consequences for the

- growth of phytoplankton and microphytobenthos. Neth.J.Sea Res. 15: 196-216.
- Colijn, F. (1983) Primary production in the Ems-Dollard estuary. Ph.D. Thesis. University of Groningen.
- Cushing, D.H. (1990) Recent studies on long-term changes in the sea. Freshwater Biology 23: 71-84.
- Dangeard,P. (1934) Sur la présence en France du Phaeocystis globosa Scherffel. Bull. Soc. Bot. Fr. 81: 143-145.
- Davidson, A.T. (1985) Phaeocystis. B.Sc. Thesis. University of Tasmania.
- Davidson, A.T. and Marchant, H.J. (1987) Binding of manganese by Antarctic Phaeocystis pouchetii and the role of bacteria in its release. Mar. Biol. 95: 481-487.
- Davidson,A.T. and Marchant,H.J. (1992) The biology and ecology of Phaeocystis pouchetii (Prymnesiophyceae). In: F.E.Round and D.J.Chapman (eds.) Progress in phycological research. Biopress, Bristol: 1 45.
- Davies, A.G., de Madariaga, I., Bautista, B., Fernández, E., Harbour, D.S., Serret, P. and Tranter, P.R.G. (1992) The ecology of a coastal Phaeocystis bloom in the north-western English Channel in 1990. J. Mar. Biol. Assoc. UK. 72: 691-708.
- de Kok,J.M. (1996) A two-layer model of the Rhine plume. J. Mar. Syst. 8: 269284. de Madariaga,I. (1992) Interspecific differences in the photosynthetic carbon metabolism of marine phytoplankton. Mar. Biol. 114: 509-515.
- de Ruijter, W.P.M., Visser, A.W. and Bos, W.G. (1997) The Rhine outflow: A prototypical pulsed discharge plume in a high energy shallow sea. J. Mar. Syst. 12: 263-276.
- de Vries,I., Duin,R.N.M., Peeters,J.C.H., Los,F.J., Bokhorst,M. and Laane,R.W.P.M. (1998) Patterns and trends in nutrients and phytoplankton in Dutch coastal waters: comparison of time series analysis, ecological model simulation, and mesocosm experiments. ICES J. mar. Science 55: 620-634.
- Degens, E.T., Guillard, R.R.L., Sackett, W.M. and Hellebust, J.A. (1968) Metabolic fractionation of carbon isotopes in marine plankton -I. Temperature and respiration experiments. Deep-Sea Res. 15: 1-9.
- Delsman,H.C. (1914a) Resume über Planktonbeobachtungen an Bord des Leuchtschiffes "Haaks" May-Dezember 1910. In: Bulletin Planctonique pour les années 1908-1911, deuxieme partie. Cons. perm. Int. explor. Mer: 112-113.
- Delsman,H.C. (1914b) Übersicht über die quantitativen Planktonfange auf dem Feuerschiff "Haaks" (Holland) 1911. In: Bulletin Planctonique pour les années 1908-1911, deuxieme partie. Cons. perm. Int. explor. Mer: 114 116.
- Demers, S., Roy, S., Gagnon, R. and Vignault, C. (1991) Rapid light-induced changes in cell fluorescence and in xanthophyll-cycle pigments of Alexandrium excavatum (Dinophyceae) and Thalassiosira pseudonana (Bacillariophyceae): a photo-protection mechanism. Mar. Ecol. Prog. Ser. 76: 185-193.
- Dienst der Hydrografie van de Koninklijke Marine (1976) Stroomatlas Noordzee, zuidelijke deel. 's Gravenhage.
- DiTullio,G.R., Grebmeier,J.M., Arrigo,K.R., Lizotte,M.P., Robinson,D.H., Leventer,A., VanWoert,M.L. and Dunbar,M.B. (2000) Rapid and early export of Phaeocystis antarctica blooms in the Ross Sea, Antarctica. Nature 404: 595-598.
- Dodge, J.D. (1985) Marine Dinoflagellates of the British Isles. Her Majesty's Stationary Office, London.
- Doering, P.H., Oviatt, C.A., Beatty, L.L., Banzon, V.F., Rice, R., Kelly, S.P., Sullivan, B.K. and Frithsen, J.B. (1989) Structure and function in a model coastal ecosystem: silicon, the benthos and eutrophication. Mar. Ecol. Prog. Ser. 52: 287-299.
- Drebes, G. (1974) Marines Phytoplankton. Georg Thieme Verlag, Stuttgart.
- Duin,R.N.M. and W.D.Bil (1988) Berekening primaire produktie op de HP1000. National Institute for Coastal and Marine Management/RIKZ. Report GWAO-88.1313.
- Eberlein, K., Leal, M.T., Hammer, K.D., Hickel, W. (1985) Dissolved organic substances during a Phaeocystis pouchetii bloom in the German Bight (North Sea). Mar. Biol. 89: 311-316.
- Edvardsen,B., Eikrem,W., Green,J.C., Andersen,R.A., Moon-van der Staay,S.Y. and Medlin,L.K. (2000) Phylogenetic reconstructions of the Haptophyta inferred from 18S ribosomal DNA sequences and available morphological data. Phycologia 39: 19-35.

- Egge, J.K. and Aksnes, D.L. (1992) Silicate as regulating nutrient in phytoplankton competition. Mar. Ecol. Prog. Ser. 83: 281-289.
- Egge, J.K. (1993) Nutrient control of phytoplankton growth: Effects of macronutrient composition (N, P, Si) on species succession. Ph.D. Thesis, University of Bergen, Norway.
- Eilers, P.H.C. and Peeters, J.C.H. (1988) A model for the relationship between light intensity and the rate of photosynthesis of phytoplankton. Ecol. Modell. 42: 199-215.
- Eilertsen, H.C. (1989) Phaeocystis pouchetii (Hariot) Lagerheim, a key species in Arctic marine ecosystems: Life history and physiology. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 188: 131.
- Eilertsen,H.C., Taasen,J.P. and Weslawski,J.M. (1989) Phytoplankton studies in the fjords of West Spitzbergen: physical environment and production in spring and summer. J. Plankton Res. 11: 1245-1260.
- Eilertsen, H.C. and Raa, J. (1995) Toxins in seawater produced by a common phytoplankter: Phaeocystis pouchetii. J. mar. biotechnol. 3: 115-119.
- Eilertsen, H.C., Sandberg, S. and Tøllefsen, H. (1995) Photoperiodic control of diatom spore growth: a theory to explain the onset of phytoplankton blooms. Mar. Ecol. Prog. Ser. 116: 303-307.
- Elzenga, J.T.M., Prins, H.B.A. and Stefels, J. (2000) The role of extracellular carbonic anhydrase activity in inorganic carbon utilization of Phaeocystis globosa (Prymnesiophyceae): A comparison with other marine algae using the isotopic disequilibrium technique. Limnol. Oceanogr. 45: 372-380.
- Eppley, R.W., Holmes, R.W. and Strickland, J.D.H. (1967) Sinking rates of marine phytoplankton measured with a fluorometer. J. Exp. Mar. Biol. Ecol. 1: 191-208.
- Eppley, R.W. (1972) Temperature and phytoplankton growth in the sea. Fish. Bull. 70: 1063-1085.
- Escaravage, V., Peperzak, L., Prins, T.C., Peeters, J.C.H. and Joordens, J.C.A. (1995) The development of a Phaeocystis sp. bloom in a mesocosm experiment in relation to nutrients, irradiance and coexisting algae. Ophelia 42: 55-74.
- Estep,K.W., Davis,P.G., Hargraves,P.E. and Sieburth,J.M. (1984) Chloroplast containing microflagellates in natural populations of north Atlantic nanoplankton, their identification and distribution; including a description of five new species of Chrysochromulina (Prymnesiophyceae) Protistologica 20: 613-634.
- Falkowski, P.G., Dubinsky, Z. and Wyman, K. (1985) Growth-irradiance relationships in phytoplankton. Limnol. Oceanogr. 30: 311-321.
- Falkowski, P.G. and Raven, J.A. (1997) Aquatic Photosynthesis, Blackwell Science, Malden (USA).
- Fernandez, E., Serret, P. de Madariaga, I., Harbour, D.S. and Davies, A.G. (1992) Photosynthetic carbon metabolism and biogeochemical composition of spring phytoplankton assemblages enclosed in microcosms: the diatom-Phaeocystis succession. Mar. Ecol. Prog. Ser. 90: 89-102.
- Fisher, T.R., Harding, L.W., Stanley, D.W. and Ward, L.G. (1988) Phytoplankton nutrients and turbidity in the Chesapeake, Delaware, and Hudson estuaries. Estuar. Coast. Shelf Sci. 24: 61-93.
- Flynn,K.J. and Davidson,K. (1993) Predator-prey interactions between Isochrysis galbana and Oxyrrhis marina. I. Changes in particulate δ^{13} C. J. Plankton Res. 15: 455-463.
- Fogg,G.E. (1975) Algal Cultures and Phytoplankton Ecology. The University of Wisconsin Press, Wisconsin.
- Fransz,H.G. and Gieskes,W.W.C. (1984) The unbalance of phytoplankton and copepods in the North Sea. Rapp. P.-v. Réun. Cons. Int. Explor. Mer. 183: 218-225.
- Fransz,H.G., Gonzalez,S.R., Cadée,G.C. and Hansen,F.C. (1992) Long-term change of Temora longicornis (Copepoda, Calanoida) abundance in a Dutch tidal inlet (Marsdiep) in relation to eutrophication. Neth. J. Sea Res. 30: 23 32.
- Furnas, M.J. (1990) In situ growth rates of marine phytoplankton: approaches to measurement, community and species growth rates. J. Plankton Res. 12: 1117-1151.
- Gaebler-Schwarz S, Davidson A, Assmy P, Chen J, Henjes J, Nöthig EM, Lunau M, Medlin LK (2010) A new cell stage in the haploid diploid life cycle of the colony forming Haptophyte *Phaeocystis antarctica* and its ecological implications. Journal of Phycology 46:1006–1016

- Garrison, D.L. and Thomsen, H.A. (1993) Ecology and biology of ice biota. Berichte zur Polarforschung 121: 68-74.
- Gasparini, S., Daro, M.H., Antajan, E., Tackx, M., Rousseau, V., Parent, J-Y. and Lancelot, C. (2000) Mesozooplankton grazing during the Phaeocystis globosa bloom in the southern bight of the North Sea. J. Sea Res. 43: 345-356.
- Gavis, J. and Ferguson, J.F. (1975) Kinetics of carbon dioxide uptake by phytoplankton at high pH. Limnol. Oceanogr. 20: 211-221.
- Gibson, J.A.E., Garrick, R.C., Burton, H.R. and McTaggart, A.R. (1990) Dimethylsulfide and the alga Phaeocystis pouchetii in antarctic coastal waters. Mar. Biol. 104: 339-346.
- Gieskes, W.W.C. (1972) Phytoplankton and primary productivity studies in the Southern Bight of the North Sea, eastern part, in 1972. Annales Biologiques 29: 54-61.
- Gieskes, W.W.C. and Kraay, G.W. (1975) The phytoplankton spring bloom in Dutch coastal waters of the North Sea. Neth. J. Sea Res. 9: 166-196.
- Gieskes, W.W.C. and Kraay, G.W. (1977) Continuous plankton records: Changes in the plankton of the North Sea and its eutrophic southern bight from 1948 to 1975. Neth. J. Sea Res. 11: 334-364.
- Gieskes, W.W.C. and Kraay, G.W. (1984) Phytoplankton, its pigments, and primary production at a central North Sea station in May, July and September 1981. Neth. J. Sea Res. 18: 51-70.
- Gillbricht, M. (1988) Phytoplankton and nutrients in the Helgoland region. Helgolander Meeresunters. 42: 435-467.
- Goldmann, J.C. and Carpenter, E.J. (1974) A kinetic approach to the effect of temperature on algal growth Limnol. Oceanogr. 19: 756-766.
- Gran,H.H. (1902) Das Plankton des Norwegischen Nordmeeres von biologischen und hydrographischen Gesichtspunkten behandelt. Report on Norwegian Fishery- and Marine-Investigations 2: 1-222.
- Grasshoff,K., Ehrhardt,M. and Kremling,K. (1983) Methods of seawater analysis. Verlag Chemie, Weinheim.
- Green,J.C. and Pienaar, R.N. (1977) The taxonomy of the order Isochrysidales (Prymnesiophyceae) with special reference to the genera Isochrysis Parke, Dicrateria Parke and Imantonia Reynolds. J. Mar. Biol. Ass. UK. 57: 7-17.
- Green, J.C. and Jordan, R.W. (1994) Systematic history and taxonomy. In: J.C.Green and B.S.C.Leadbeater (eds.) The Haptophyte Algae. Clarendon Press, Oxford: 1-21.
- Grimm, N., Weisse, T. (1985) Die Temperaturabhängigkeit des Wachtums von Phaeocystis pouchetii (Haptophyceae) in Batchkulturen. Helgoländer Meeresunters. 39: 201-211.
- Grøntved,J. (1960) Planktological contribution IV. Taxonomic and productional investigations in shallow coastal waters. Meddelelser fra Danmarks Fiskeri og Havundersogelser 3: 1-17.
- Guillard,R.R.L. and Hellebust,J.A. (1971) Growth and the production of extracellular substances by two strains of Phaeocystis poucheti. J. Phycol. 7: 330-338.
- Hagmeier, E. (1961) Plankton-Äquivalente. Auswertungen von chemischen und mikroskopischen Analysen. Kieler Meeresf. 17: 32-47.
- Hagmeier,E. (unpublished) Cell (or organism) volume to carbon relationships conversion list for flex plankton studies. Hallegraeff,G.M. (1983) Scale-bearing and loricate nanoplankton from the east Australian current. Bot. Mar. 26: 493-515.
- Hamel, G. (1930) Chlorophycées des côtes françaises. Revue Algologique 5: 154.
- Hamm CE (2000) Architecture, ecology and biogeochemistry of Phaeocystis colonies. Journal of Sea Research 43:307-315
- Hamm, C.E., Simson, D.A., Merkel, R. and Smetacek, V. (1999) Colonies of Phaeocystis globosa are protected by a thin but tough skin. Mar. Ecol. Prog. Ser. 187: 101-111.
- Hansen E, Eilertsen HC (2007) Do the polyunsaturated aldehydes produced by Phaeocystis pouchetii (Hariot) Lagerheim influence diatom growth during the spring bloom in Northern Norway? Journal of Plankton Research 29:87-96
- Hansen E, Ernstsen A, Eilertsen HC (2004) Isolation and characterisation of a cytotoxic

- polyunsaturated aldehyde from the marine phytoplankter Phaeocystis pouchetii (Hariot) Lagerheim. Toxicology 199:207-217
- Hansen,B., Bjornsen,P.K. and Hansen,P.J. (1994) The size ratio between planktonic predators and their prey. Limnol. Oceanogr. 39: 395-403.
- Hansen, F.C. and van Boekel, W.H.M. (1991) Grazing pressure of the calanoid copepod Temora longicornis on a Phaeocystis dominated spring bloom in a Dutch tidal inlet. Mar. Ecol. Prog. Ser. 123: 123-129.
- Hansen, F.C. and van Boekel, W.H.M. (1992) Lysis induced decline of a Phaeocystis spring bloom and coupling with the microbial foodweb. Mar. Ecol. Prog. Ser. 81: 269-276.
- Hansen, F.C., Reckermann, M., Klein Breteler, W.C.M., Riegman, R. (1993) Phaeocystis blooming enhanced by copepod predation on protozoa: evidence from incubation experiments. Mar. Ecol. Prog. Ser. 102: 51-57.
- Hansen,G. and Larsen,J. (1992) Dinoflagellater i Danske farfande. In: H.A.Thomsen (ed.) Plankton i de indre Danske farfande. MiljØfministeriet MiljØstyrelsen, KØbenhavn: 45-155.
- Harrison, P.J., Turpin, D.H., Bienfang, P.K. and Davies, C.O. (1986) Sinking as a factor affecting phytoplankton species succession: the use of selective loss semi-continuous cultures. J. Exp. Mar. Biol. Ecol. 99: 19-30.
- Hegarty,S.G. and Villareal,T.A. (1998) Effects of light level and N:P supply ratio on the competition between Phaeocystis cf. pouchetii (Hariot) Lagerheim (Prymnesiophyceae) and five diatom species. J. Exp. Mar. Biol. Ecol. 226: 241-258.
- Heimdal, B.R. (1989) Arctic Ocean Phytoplankton. In: Y.Herman (ed.) The Arctic Seas. Climatology, Oceanography, Geology, and Biology. van Nostrand Reinhold Company, New York: 193-222.
- Hensen, V. (1887) Über die Bestimmung des Plankton's oder des im Meere treibenden Materials an Pflanzen und Thieren; nebst Anhang. In: Fünfter Bericht der Kommission zur wissenschaftlichen Untersuchung der Deutschen Meere, in Kiel für die Jahre 1882 bis 1886. Paul Parey, Berlin: 1-109.
- Hessen, D.O. and van Donk, E. (1993) Morphological changes in Scenedesmus induced by substances released from Daphnia. Arch. Hydrobiol. 127: 129 140.
- Hibberd, D.J. (1980) Prymnesiophytes (= Haptophytes). In: E.R.Cox (ed.) Phytoflagellates. Elsevier, Amsterdam: 273-317.
- Hinga,K.R., Arthur,M.A., Pilson,M.E.Q. and Whitaker,D. (1994) Carbon isotope fractionation by marine phytoplankton in culture: The effects of CO2 concentration, pH, temperature, and species. Global Biogem. Cycles 8: 91-102.
- Hinga,K.R. (1992) Co-occurrence of dinoflagellate blooms and high pH in marine enclosures. Mar. Ecol. Prog. Ser. 86: 181-187.
- Hoek, P.P.C. (1898) Het zoologisch station der Nederlandsche Dierkundige Vereeniging in 1897. Tijdschrift Ned. Dierk. Ver. 2: 3-18.
- Hoepffner, N. and Haas, L.W. (1990) Electron microscopy of nanoplankton from the North Pacific Central Gyre. J. Phycol. 26: 421-439.
- Hofstraat, J.W. van Zeijl, W.J.M., de Vreeze, M.E.J., Peeters, J.C.H., Peperzak, L., Colijn, F. and Rademaker, M. (1994) Phytoplankton monitoring by flow cytometry. J. Plankton Res. 16: 1197-1224.
- Huang, C., Dong, Q. and Zheng, L. (1999) Taxonomic and ecological studies on a large scale Phaeocystis pouchetii bloom in the southeast coast of China during late 1997. Oceanologia et Limnologia Sinica 30: 581-590.
- Huiting, A.M. (1995) Can Phaeocystis colonies play a joke on Stokes' law? M.Sc. Thesis, University of Wageningen.
- Huthnance, J.M. (1997) The PROFILE project: an overview. J. Mar. Syst. 12: 249-261.
- Inouye,I. (1990) Phaeocystis pouchetii (Hariot) Lagerheim. In: Y.Fukuyo, H.Takano, M.Chihara and K.Matsuoka (eds.) Red Tide Organisms in Japan. Uchida Rokakuho, Tokyo: 366-367.
- Jackson, G.A. (1989) Simulating chemosensory responses of marine microorganisms. Limnol. Oceanogr. 32: 1253-1266.

- Jackson, G.A. (1990) A model of the formation of marine algal flocs by physical coagulation processes. Deep-Sea Res. 37: 1197-1211.
- Jacobsen A, Veldhuis MJW (2005) Growth characteristics of flagellated cells of Phaeocystis pouchetii revealed by diel changes in cellular DNA content. Harmful algae 4:811-82
- Jacobsen, A., Bratbak, G. and Heldal, M. (1996) Isolation and characterization of a virus infecting Phaeocystis pouchetii (Prymnesiophyceae). J. Phycol. 32: 923-927.
- Jago, C.F., Bale, A.J., Green, M.O., Howarth, M.J., Jones, S.E., McCave, I.N., Millward, G.E., Morris, A.W., Rowden, A.A. and Williams, J.J. (1994) Resuspension processes and seston dynamics, southern North Sea. In: H. Charnock et al. (eds) Understanding the North Sea system. Chapman and Hall, London: 97-113.
- Jahnke, J. and Baumann, M.E.M. (1987) Differentiation between Phaeocystis pouchetii (Har.) Lagerheim and Phaeocystis globosa Scherffel I. Colony shapes and temperature tolerances. Hydrobiol. Bull. 21: 141-147.
- Jahnke, J. (1989) The light and temperature dependence of growth rate and elemental composition of Phaeocystis globosa Scherffel and P. pouchetii (Har.) Lagerh. in batch cultures. Neth. J. Sea Res. 23: 15-21.
- Janse, I. van Rijssel, M., van Hall, P-J., Gerwig, G.J., Gottschal, J.C. and Prins, R.A. (1996) The storage glucan of Phaeocystis globosa (Prymnesiophyceae) cells. J. Phycol. 32: 382-387.
- Janse, I. van Rijssel, M., Ottema, A. and Gottschal, J.C. (1999) Microbial breakdown of Phaeocystis mucopolysaccharides. Limnol. Oceanogr. 44: 1447-1457.
- Janse,I. (2000) C in the sea. Production and microbial breakdown of Phaeocystis polysaccharides. Ph.D. Thesis. University of Groningen.
- Jaworksi, G.H.M., Talling, J.F. and Heaney, S.I. (1981) The influence of carbon dioxide-depletion on growth and sinking rate of two planktonic diatoms in culture. Br. phycol. J. 16: 395-410.
- Jenkinson, I.R. (1986) Halosphaera viridis, Ditylum brightwellii and other phytoplankton in the northeastern North Atlantic in spring: sinking rising and relative abundance. Ophelia 26: 233-253.
- Jenkinson,I.R. and Wyatt,T. (1992) Selection and control of Deborah numbers in plankton ecology. J. Plankton Res. 14: 1697-1721.
- Jenkinson, I.R. (1993) Bulk-phase viscoelastic properties of seawater. Oceanol. Acta 16: 317-334.
- Jennes, M.I. and Duineveld, G.C.A. (1985) Effects of tidal currents on chlorophyll a content of sandy sediments in the southern North Sea. Mar. Ecol. Prog. Ser. 21: 283-287.
- Johnson, K.S., Pytkowicz, R.M. and Wong, C.S. (1979) Biological production and the exchange of oxygen and carbon dioxide across the sea surface in Stuart Channel, British Columbia. Limnol. Oceanogr. 24: 474-482.
- Johnson, R.A. and Wichern, D.W. (1998) Applied multivariate statistical analysis. Prentice-Hall, Upper Saddle River.
- Johnson, T.O. and Smith, W.O. (1986) Sinking rates of phytoplankton assemblages in the Wedell Sea marginal ice zone. Mar. Ecol. Prog. Ser. 33: 131-137.
- Johnston, A.M. and Raven, J.A. (1992) Effect of aeration rates on growth rates and natural abundance 13C/12C ratio of Phaeodactylum tricornutum. Mar. Ecol. Prog. Ser. 87: 295-300.
- Jones, P.G.W. and Haq, S.M. (1963) The distribution of Phaeocystis in the eastern Irish sea. J. Cons. Intern. Expl. Mer 28: 8-20.
- Joordens, J.C.A., Souza, A.J., Heins, C., Visser, A.W. and Peperzak, L. (1995) Rhine Cruise Data Report 1994. National Institute for Coastal and Marine Management/RIKZ Report OS-95.118X.
- Kamermans, P. (1994) Nutritional value of solitary cells and colonies of Phaeocystis sp. for the bivalve Macoma balthica (L.) Ophelia 39: 35-44.
- Karp-Boss, L., Boss, E. and Jumars, P.A. (1996) Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. Oceanogr. Mar. Biol. Ann. Rev. 34: 71-107
- Karsten,G. (1905) Das Phytoplankton des Antarktischen Meeres nach dem Material der deutschen Tiefsee-Expedition 1898-1899. In: (C.Chun, ed.)

- Wissenschaftliche Ergebnisse der deutschen Tiefsee-expedition auf dem Dampfer "Valdivia" 1898-1899.Gustaf Fischer Verlag, Jena.
- Kashkin, N.I. (1963) Materials on the ecology of Phaeocystis pouchetii (Hariot) Lagerheim, 1893 (Chrysophyceae) II. Habitat and specifications of biogeographical characteristics. Okeanologiya, Moscow 3: 697-705.
- Kashkin, N.I. (1964) Information about the ecology of Phaeocystis pouchetii (Hariot) Lagerheim, 1893 (Chrysophyceae) in coastal waters of the North Atlantic. Murmanskogo Morskogo Biol. Inst. 5: 16-36.
- Kat,M. (1977) Four years phytoplankton investigations in the Dutch coastal area 1973-1976. ICES C.M.1977/L: 2.
- Kat,M. (1982) The sequence of the principal phytoplankton blooms in the Dutch coastal area. ICES C.M.1982/L: 22.
- Kayser,H. (1970) Experimental-ecological investigations on Phaeocystis poucheti (Haptophyceae): cultivation and waste water test. Helgoländer wiss. Meeresunters. 20: 195-212.
- Kirk,J.T.O. (1994) Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge.
- Kornmann, P. (1955) Beobachtungen an Phaeocystis-Kulturen. Helgoländer wiss. Meeresunters. 5: 218-233.
- Kromkamp, J. and Walsby, A.E. (1990) A computer model of buoyancy and vertical migration in cyanobacteria. J. Plankton Res. 12: 161-183.
- Kwint,R.L.J. (1997) The origin of DMS(P)cies. A survey of the sources and sinks of the two dimethylated sulphur compounds betadimethylsulphoniopropionate (DMSP) and dimethylsulphide (DMS). Ph.D.Thesis, University of Groningen.
- Laanbroek, H.J., Verplanke, J.C., de Visscher, P.R.M. and de Vuyst, R. (1985) Distribution of phyto-and bacterioplankton growth and biomass parameters, dissolved inorganic nutrients and free amino acids during a spring bloom in the Oosterschelde basin, The Netherlands. Mar. Ecol. Prog. Ser. 25: 1-11.
- Laevastu, T. (1963) Serial atlas of the marine environment. Folio 4. Surface water types of the North Sea and their characteristics. American Geographic Society.
- Lagerheim, G. (1893) Phaeocystis, nov. gen., grundadt pa Tetraspora Poucheti Har. Botaniska Notiser. 32-33
- Lagerheim, G. (1896) Über Phæocystis Poucheti (Har.) Lagerh., eine Plankton-Flagellate. Öfvers. af Vet. Akad. Förhandl. 53: 277-288.
- Lampert, W., Rothhaupt, K.O. and von Elert, E. (1994) Chemical induction of colony formation in a green alga (Scenedesmus acutus) by grazers (Daphnia). Limnol. Oceanogr. 39: 1543-1550.
- Lancelot, C. and Mathot, S. (1985) Biochemical fractionation of primary production by phytoplankton in Belgian coastal waters during short and long-term incubations with 14C-bicarbonate. II. Phaeocystis pouchetii colonial populations. Mar. Biol. 86: 227-232.
- Lancelot, C., Mathot, S. and Owens, N.J.P. (1986) Modelling protein synthesis, a step to an accurate estimate of net primary production: Phaeocystis pouchetii colonies in Belgian coastal waters. Mar. Ecol. Prog. Ser. 32: 193 202.
- Lancelot, C. and Mathot, S. (1987) Dynamics of a Phaeocystis-dominated spring bloom in Belgian coastal waters. I. Phytoplankton activities and related parameters. Mar. Ecol. Prog. Ser. 37: 239-248.
- Lancelot, C., Billen, G., Sournia, A., Weisse, T., Colijn, F., Veldhuis, M.J.W., Davies, A. and Wassman, P. (1987) Phaeocystis blooms and nutrient enrichment in the continental coastal zones of the North Sea. Ambio 16: 38 46.
- Lancelot, C., Billen, G. and Barth, B. (1991) The dynamics of Phaeocystis blooms in nutrient enriched coastal zones. Water Pollution Research Report 23, pp. 1-106.
- Lancelot, C. and Rousseau, V. (1994) Ecology of Phaeocystis: the key role of colony forms. In: J.C.Green and B.S.C.Leadbeater (eds.) The Haptophyte Algae. Clarendon Press, Oxford: 229-245.
- Lancelot, C., Keller, M.D., Rousseau, V., Smith, W.O., Mathot, S. (1998) Autecology of the marine haptophyte Phaeocystis sp. In: D.M. Anderson, A.D. Cembella and G.M. Hallegraeff (eds.) Physiological

- Ecology of Harmful Algal Blooms. NATO ASI series G41: 209-224.
- Langdon, C. (1988) On the causes of interspecific differences in the growth- irradiance relationship for phytoplankton. II. A general review. J. Plankton Res. 10: 1291-1312.
- Larsen, J. and Moestrup, Ø (1989) Guide to toxic and potentially toxic marine algae. The Fish Inspection Service, Ministry of Fisheries, Luna-Tryk, Copenhagen.
- Lazier, J, R, N. and Mann, K.H. (1989) Turbulence and the diffusive layers around small organisms. Deep-Sea Res. 36: 1721-1733
- Leadbeater, B.S.C. (1972) Identification, by means of electron microscopy, of nanoplankton flagellates from the coast of Norway. Sarsia 49: 107-124.
- Leewis, R.J. (1985) Phytoplankton off the Dutch coast. Ph.D. Thesis, University of Nijmegen.
- Lubbers, G.W., Gieskes, W.W.C., Castilho del, P. Salomons, W. and Bril, J. (1990) Manganese accumulation in the high pH microenvironment of Phaeocystis sp. (Haptophyceae) colonies from the North Sea. Mar. Ecol. Prog. Ser. 59: 285-293.
- Lubchenco, J. and Cubit, J. (1980) Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. Ecology 61: 676 687.
- Lüning, K. (1981) Light. In C.S.Loblan and M.J.Wynne (eds.) The biology of seaweeds. Blackwell Scientific Publications, Oxford: 326-330. Lürling, M. (1999) The smell of water. Grazer-induced colony formation in Scenedesmus. Ph.D.Thesis, University of Wageningen.
- Mann, K.H. and Lazier, J.R.N. (1991) Dynamics of Marine Ecosystems. Blackwell Scientific Publication, Oxford.
- Manton,I. and Leadbeater,B.S.C. (1974) Fine-structural observations on six species of Chrysochromulina from wild Danish marine nanoplankton including a description of C.campanulifera sp. nov. and a preliminary summary of the nanoplankton as a whole. Det Kongelige Danske Videnskabs Selskab Biologiske Skrifter 20: 1-26.
- Marchant, H.J. and Davidson, A.T. (1991) Possible impacts of ozone depletion on trophic interactions and biogenic vertical carbon flux in the southern ocean. In: G.Weller, C.L.Wilson, and B.A.B.Severin (eds.) Proceedings of the International Conference on the Role of Polar Regions in Global Change. Geophysical Institute, Fairbanks: 397-400.
- Marchant, H.J., Davidson, A.T. and Kelly, G.J. (1991) UV-B protecting compounds in the marine alga Phaeocystis pouchetii from Antarctica. Mar. Biol. 109: 391-395.
- Marchant, H.J. and Thomsen, H.A. (1994) Haptophytes in polar waters. In J.C.Green and B.S.C.Leadbeater (eds.) The Haptophyte Algae. Clarendon Press, Oxford: 209-228.
- Margalef,R. (1978a) Phytoplankton communities in upwelling areas. The example of NW Africa. Oecologia aquatica 3: 97-132.
- Margalef,R. (1978b) Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta 1: 493-509.
- Marra, J., Langdon, C. and Knudson, C.A. (1995) Primary production, water column changes, and the demise of a Phaeocystis bloom at the Marine Light-Mixed Layers site (59°N, 21°W) in the Northeast Atlantic Ocean. J. Geophys. Res. 100: 6633-6643.
- Marshall, H.G. and Lacouture, R. (1986) Seasonal patterns of growth and composition of phytoplankton in lower Chesapeake Bay and vicinity. Estuar. Coast. Shelf Sci. 23: 115-130.
- Matrai, P.A., Vernet, M., Hood, R., Jennings, A., Brody, E., and Saemundsdóttir, S. (1995) Light-dependence of carbon and sulfur production by polar clones of the genus Phaeocystis. Mar. Biol. 124: 157 167.
- McLaughlin, J.J.A. (1958) Euryhaline chrysomonads: nutrition and toxigenesis in Prymnesium parvum, with notes on Isochrysis galbana and Monochrysis lutheri. J. Protozool 5: 75-81.
- Medlin L, Zingone A (2007) A taxonomic review of the genus Phaeocystis. Biogeochemistry 83:3-18
- Medlin,L.K., Lange,M. and Baumann,M.E.M. (1994) Genetic differentiation among three colony-forming species of Phaeocystis: further evidence for the phylogeny of the Prymnesiophyta. Phycologia 33: 199-212.

- Meyer, A.A., Tackx, M. and Daro, N. (2000) Xanthophyll cycling in Phaeocystis globosa and Thalassiosira sp: a possible mechanism for species succession. J. Sea Res. 43: 373-384.
- Moestrup, Ø. (1979) Identification by electron microscopy of marine nanoplankton from New Zealand, including the description of four new species. New Zealand Journal of Botany 17: 61-95.
- Moestrup,Ø. (1994) Economic aspects: 'blooms, nuisance species, and toxins. In: J.C.Green and B.S.C.Leadbeater (eds.) The Haptophyte Algae. Clarendon Press, Oxford: 265-285.
- Moisan, T.A., Olaizola, M. and Mitchell, B.G. (1998) Xantophyll cycling in Phaeocystis antarctica: changes in cellular fluorescence. Mar. Ecol. Prog. Ser. 169: 113-121.
- Moisan, T.A. and Mitchell, B.G. (1999) Photophysiological acclimation of Phaeocystis antarctica Karsten under light limitation. Limnol. Oceanogr. 44: 247-258.
- Moore, J.K. and Villareal, T.A. (1996) Buoyancy and growth characteristics of three positively buoyant marine diatoms. Mar. Ecol. Prog. Ser. 132: 203-213.
- Morris, A.W. (1971) Trace metal variation in sea water of the Menai Straits caused by a bloom of Phaeocystis. Nature 233: 427-428.
- Nedwell, D.B., Shabbeer, M.T. and Harrison, R.M. (1994) Dimethyl sulphide in North Sea waters and sediments. Estuar. Coast. Shelf Sci. 39: 209-217.
- Nichols PD, Skerratt JH, Davidson A, Burton H, McMeekin TA (1991) Lipids of cultured Phaeocystis pouchetii: signatures for food-web, biogeochemical and environmental studies in Antartica and the Southern Ocean. Phytochemistry 30:3209-3214
- Nielsen, M.V. and Tønseth, C.P. (1991) Temperature and salinity effect on growth and chemical composition of Gyrodinium aureolum Hulburt in culture. J. Plankton Res. 13: 389-398.
- Nielsen, M.V. (1992) Irradiance and daylength effects on growth and chemical composition of Gyrodinium aureolum Hulburt in culture. J. Plankton Res. 14: 811-820.
- Noordkamp, D.J.B., Gieskes, W.W.C., Forney, L.J., Gottschal, J.C. and van Rijssel, M. (2000) Acrylate in Phaeocystis colonies does not affect the surrounding bacteria. J. Sea Res. 43: 287-296.
- Novarino, G., Mills, D.K. and Hannah, F. (1997) Pelagic flagellate populations in the southern North Sea, 1988-89. I. Qualitative observations. J. Plankton Res. 19: 1081-1109.
- Officer, C.B. and J.H.Ryther (1980) The possible importance of silicon in marine eutrophication. Mar. Ecol. Prog. Ser. 3: 83-91. Orton, J.H. (1923) The so-called "Baccy-juice" in the waters of the Thames oyster-beds. Nature 111: 773.
- Osinga,R., Kwint,R.L.J., Lewis,W.E., Kraay,G.W., Lont,J.D., Lindeboom,H.J. and van Duyl,F.C. (1996) Production and fate of dimethylsufide and dimethylsulfoniopropionate in pelagic mesocosms: the role of sedimentation. Mar. Ecol. Prog. Ser. 131: 275-286.
- Osinga,R., de Vries,K.A., Lewis,W.E., van Raaphorst,W., Dijkhuizen,L. and van Duyl,F.C. (1997) Aerobic degradation of phytoplankton debris dominated by Phaeocystis sp. in different physiological stages of growth. Aquat. Microb. Ecol. 12: 11-19.
- Ostenfeld, C.H. (1904) Phaeocystis pouchetii (Hariot) Lagerh. and its zoospores. Arch. Protistenk. 3: 295-302
- Ostenfeld,C.H. (1910) Halosphaera and flagellata. Bulletin trimestriel des résultats acquis pendant les croisières périodiques et dans la périodes intermédiaires. Cons. Perm.inter. explor. Mer. Première Partie: 20-29.
- Owens, N.J.P., Cook, D., Colebrook, M., Hunt, H. and Reid, P.C. (1989) Long term trends in the occurrence of Phaeocystis sp. in the North-east Atlantic. J. Mar. Biol. Assoc. UK. 69: 813-821.
- Palmisano,A.C., Beeler Soohoo,J., Soohoo,S.L., Kottmeyer,S.T., Craft,L.L., Sullivan,C.W. (1986) Photoadaptation in Phaeocystis pouchetii advected beneath annual sea ice in McMurdo Sound, Antarctica. J. Plankton Res. 8: 891-906.
- Parke, M., Green, J.C. and Manton, I. (1971) Observations on the fine structure of zoids of the genus Phaeocystis (Haptophyceae). J. Mar. Biol. Assoc. UK 51: 927-941.
- Passow, U. (1991) Species-specific sedimentation and sinking velocities of diatoms. Mar. Biol. 108: 449-455.

- Passow, U. and Wassmann, P. (1994) On the trophic fate of Phaeocystis pouchetii (Hariot): IV. The formation of marine snow by P.pouchetii. Mar. Ecol. Prog. Ser. 104: 153-161.
- Peeters, J.C.H. and Peperzak, L. (1990) Nutrient limitation in the North Sea: A bioassay approach. Neth. J. Sea Res. 26: 61-73.
- Peeters, J.C.H., Haas, H.A. and Peperzak, L. (1991a) Eutrofiëring, primaire produktie en zuurstofhuishouding in de Noordzee. National Institute for Coastal and Marine Management/RIKZ. Report GWAO-91.083.
- Peeters, J.C.H., Haas, H., Peperzak, L., Wetsteyn, L.P.M.J. (1991b) Limiting factors for phytoplankton in the North Sea. Wat. Sci. Tech. 24: 261-267.
- Peeters, J.C.H., Haas, H.A., Peperzak, L. and de Vries, I. (1993) Nutrients and light as factors controlling phytoplankton biomass on the Dutch continental shelf (North Sea) in 1988-1990. National Institute for Coastal and Marine Management/RIKZ. Report GWAO-93.004.
- Peng,T., Takahashi,T., Broecker,W.S. and Olafsson,J. (1987) Seasonal variability of carbon dioxide, nutrients and oxygen in the northern North Atlantic surface water: observations and a model. Tellus 39: 439-458.
- Peperzak, L. (1991). Fytoplankton in de Oosterschelde. National Institute for Coastal and Marine Management/RIKZ. Report GWAO-90.13114.
- Peperzak, L. and Peeters, J.C.H. (1991) Bioassay of nutrient pollution in the North Sea. Wat. Sci. Tech. 24: 319-320.
- Peperzak, L. (1993) Daily irradiance governs growth rate and colony formation of Phaeocystis (Prymnesiophyceae). J. Plankton Res. 15: 809-821.
- Peperzak, L., Verreussel, R., Zonneveld, K.A.F., Zevenboom, W. and Dijkema, R. (1996a) The distribution of flagellate cysts on the Dutch continental shelf (North Sea) with emphasis on Alexandrium spp. and Gymnodinium catenatum. In: T.Yasumoto, Y.Oshima and Y.Fukuyo (eds): Harmful and Toxic Algal Blooms, UNESCO, Paris: 169-172.
- Peperzak, L., Snoeijer, G.J., Dijkema, R., Gieskes, W.W.C., Joordens, J., Peeters, J.C.H., Schol, C., Vrieling, E.G. and Zevenboom, W. (1996b) Development of a Dinophysis acuminata bloom in the river Rhine plume (North Sea). In: T. Yasumoto, Y.Oshima and Y.Fukuyo (eds): Harmful and Toxic Algal Blooms, UNESCO, Paris: 273-276.
- Peperzak, L., Colijn, F., Gieskes, W.W.C. and Peeters, J.C.H. (1998) Development of the diatom-Phaeocystis spring bloom in the Dutch coastal zone of the North Sea: the silicon depletion versus the daily irradiance threshold hypothesis. J. Plankton Res. 20: 517-537.
- Peperzak, L., Duin, R.N.M., Colijn, F. and Gieskes, W.W.C. (2000a) Growth and mortality of flagellates and non-flagellates cells of Phaeocystis globosa (Prymnesiophyceae). J. Plankton Res. 22: 107-119.
- Peperzak, L., Gieskes, W.W.C., Duin, R. and Colijn, F. (2000b) The vitamin B requirement of Phaeocystis globosa (Prymnesiophyceae). J. Plankton Res. 22: 1529-1537.
- Peperzak, L., Colijn, F., Vrieling, E.G., Gieskes, W.W.C. and Peeters, J.C.H. (2000c) Observations of flagellates in colonies of Phaeocystis globosa (Prymnesiophyceae); a hypothesis for their position in the life cycle. J. Plankton Res. 22: 2181-2203.
- Petri, G. and Vareschi, E. (1997) Utilization of Phaeocystis globosa colonies by young Mytilus edulis. Arch. Fish. Mar. Res. 45: 77-91.
- Pielou, E.C. (1969) An introduction to mathematical ecology. Wiley-InterScience, New York.
- Pienaar, R.N. (1991) Thread formation in the motile cells of Phaeocystis. Electronmikroskopievereniging van Suidelike Afrika 21: 135-136.
- Pienaar, R.N. and Copper, G.A. (1991) Ultrastructure of the motile disc-bearing phase of Phaeocystis. J. Phycol. Suppl. 27: 59.
- Pieters, H., Kluytmans, J.H. and Zandee, D.I. (1980) Tissue composition and reproduction of Mytilus edulis in relation to food availability. Neth. J. Sea Res. 14: 349-361.
- Pingree, R.D. and Griffiths, D.K. (1978) Tidal fronts on the shelf seas around the British isles. J. Geophys. Res. 83: 4615-4622.

- Pintner, I.J., Provasoli, L. (1963) Nutritional characteristics of some chrysomonads. In: C.H. Oppenheimer (ed.) Symp. Mar. Microbiol. Thomas and co, Springfield III.: 114-121.
- Pitcher, G.C., Walker, D.R. and Mitchell-Innes, B.A. (1989) Phytoplankton sinking rate dynamics in the southern Benguela upwelling system. Mar. Ecol. Prog. Ser. 55: 261-269.
- Ploug, H., Stolte, W., Epping, E.H.G. and Jorgensen, B.B. (1999a) Diffusive boundary layers, photosynthesis, and respiration of the colony-forming plankton algae, Phaeocystis sp. Limnol. Oceanogr. 44: 1949-1958.
- Ploug, H., Stolte, W. and Jorgensen, B.B. (1999b) Diffusive boundary layers of the colony-forming plankton alga, Phaeocystis sp. implications for nutrient uptake and cellular growth. Limnol. Oceanogr. 44: 1959-1967.
- Pouchet, M.G. (1892) Sur une algue pélagique nouvelle. Compt. Rend. Hebd. Séances Mém. Soc. Biol. 44: 34-36.
- Prins,T.C., Escaravage,V., Goosen,N., Haas,H.A. and Pouwer,A.J. (1993) Carbon, Nitrogen, Phosphorus and Silicon mass balances in two mesocosm experiments. In: J.C.H.Peeters, J.C.A.Joordens, A.C.Smaal and P.H.Nienhuis (eds.) The impact of marine eutrophication on phytoplankton and benthic suspension feeders: results of a mesocosm pilot study. National Institute for Coastal and Marine Management/RIKZ. Report GWAO93.039: 71-95.
- Prins, T.C., Dankers, N. and Smaal, A.C. (1994) Seasonal variation in the filtration rates of a semi-natural mussel bed in relation to seston composition. J. Exp. Mar. Biol. Ecol. 176: 69-86.
- Provasoli, L., McLaughlin, J.J.A., Droop, M.R. (1957) The development of artificial media for marine alga. Archiv. f. Mikrobiologie 25: 392-428.
- Provasoli, L. and Carlucci, A.F. (1974) Vitamins and growth regulators. In: W.D.P.Stewart (ed.) Algal Physiology and Biochemistry. Blackwell Scientific Publications, Oxford: 741-787.
- Putt, M., Miceli, G., Stoecker, D.K. (1994) Association of bacteria with Phaeocystis sp. in McMurdo Sound, Antarctica. Mar. Ecol. Prog. Ser. 105: 179-189.
- Radach,G. and Berg,J. (1986) Trends in der konzentrationen der Nährstoffe und des Phytoplanktons in der Helgoländers Bocht (Helgoland Reede Daten). Ber. Biol. Anst. Helgoland 2: 1-63.
- Radach,G., Berg,J. and Hagmeier,E. (1990) Long-term changes of the annual cycles of meteorological, hydrographic, nutrient and phytoplankton time series at Heligoland and at LV Elbe 1 in the German Bight. Cont. Shelf Res. 10: 305-328.
- Rahmel, J., Bätje, M., Michaelis, H. and Noack, U. (1995) Phaeocystis globosa and the phytoplankton succession in the East Frisian coastal waters. Helgoländer Meeresunters. 49: 399-408.
- Ramani, P., Cardinali, S., Cabrini, M. and del Negro, P. (1994) Thread-like appendages of Phaeocystis in the Gulf of Trieste (Northern Adriatic Sea) G. Bot. Ital. 128: 1065-1067.
- Raven, J.A. and Johnston, A.M. (1991) Mechanisms of inorganic carbon acquisition in marine phytoplankton and their implications for the use of other resources. Limnol. Oceanogr. 36: 1701-1714.
- Redfield,A.C, Ketchum,B.H. and Richards,F.A. (1963) The influence of organisms on the composition of seawater. In: M.N.Hill (ed.) The Sea. Interscience Publishers, New York: 26-77.
- Reid, P.C., Lancelot, C., Gieskes, W.W.C., Hagmeier, E., Weichart, G. (1990) Phytoplankton of the North Sea and its dynamics: a review. Neth. J. Sea Res. 26: 295-331.
- Reynolds, C.S. (1993) The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge.
- Rick, H.-J. and Aletsee, L. (1989) The distribution of the haptophyte Phaeocystis pouchetii (Hariot) Lagerheim and Phaeocystis globosa Scherffel in the North Sea during May, June 1986 and February, March 1987. Meeresforsch. 32: 169-176.
- Riebesell, U. (1989) Comparison of sinking and sedimentation rate measurements in a diatom winter/spring bloom. Mar. Ecol. Prog. Ser., 54: 109-119.
- Riebesell, U. (1992) The formation of large marine snow and its sustained residence in surface waters. Limnol. Oceanogr. 37: 63-76.
- Riebesell, U. (1993) Aggregation of Phaeocystis during phytoplankton spring blooms in the southern

- North Sea. Mar. Ecol. Prog. Ser. 96: 281-289.
- Riebesell, U., Wolf-Gladrow, D.A. and Smetacek, V. (1993) Carbon dioxide limitation of marine phytoplankton growth rates. Nature 361: 249-251.
- Riebesell, U., Reigstad, M., Wassmann, P., Noji, T. and Passow, U. (1995) On the trophic fate of Phaeocystis pouchetii (Hariot): VI. Significance of Phaeocystis-derived mucus for vertical flux. Neth. J. Sea Res. 33: 193-203.
- Riegger, L. and Robinson, D. (1997) Photoinduction of UV-absorbing compounds in Antarctic diatoms and Phaeocystis antarctica. Mar. Ecol. Prog. Ser. 160: 13-25.
- Riegman,R., Colijn,F., Malschaert,J.F.P., Kloosterhuis,H.T. and Cadée,G.C. (1990) Assessment of growth rate limiting nutrients in the North Sea by the use of nutrient-uptake kinetics. Neth. J. Sea Res. 26: 53-60.
- Riegman, R. (1991) Mechanisms behind eutrophication induced novel algal blooms. Report 1991-9, Netherlands Institute for Sea Research, Texel, The Netherlands.
- Riegman, R., Noordeloos, A.A.M. and Cadée, G.C. (1992) Phaeocystis blooms and eutrophication of the continental coastal zones of the North Sea. Mar. Biol. 112: 479-484.
- Riegman, R., Kuipers, B.R., Noordeloos, A.A.M. and Witte, H.J. (1993a) Size-differential control of phytoplankton and the structure of plankton communities. Neth. J. Sea Res. 31: 255-265.
- Riegman,R., Rowe,A., Noordeloos,A.A.M. and Cadée,G.C. (1993b) Evidence for eutrophication induced Phaeocystis blooms in the Marsdiep area (The Netherlands). In: T.J.Smayda. and Y.Shimizu (eds.) Toxic Phytoplankton in the Sea, Elsevier, Amsterdam.
- Riegman, R. and van Boekel, W.H.M. (1996) The ecophysiology of Phaeocystis globosa: a review. J. Sea Res. 35: 235-242.
- Reigstad M, Wassmann P (2007) Does Phaeocystis spp. contribute significantly to vertical export of organic carbon? Biogeochemistry 83:217-234
- Riley,G.A. (1957) Phytoplankton of the North Central Sargasso Sea, 1950-52. Limnol.Oceanogr. 2: 252-270.
- Rogers, S.I. and Lockwood, S.J. (1990) Observations on coastal fish fauna during a spring bloom of Phaeocystis pouchetii in the Eastern Irish Sea. J. Mar. Biol. Ass. UK. 70: 249-253.
- Rousseau V, Chrétiennot-Dinet MJ, Jacobsen A, Verity P, Whipple S (2007) The life cycle of Phaeocystis: state of knowledge and presumptive role in ecology. Biogeochemistry 83:29-47
- Rousseau, V., Mathot, S. and Lancelot, C. (1990) Calculating carbon biomass of Phaeocystis sp. from microscopic observations. Mar. Biol. 107: 305-314.
- Rousseau, V., Vaulot, D., Casotti, R., Cariou, V., Lenz, J., Gunkel, J. and Baumann, M.E.M. (1994) The life cycle of Phaeocystis (Prymnesiophyceae): evidence and hypotheses. J. Mar. Syst. 5: 23-39.
- Rousseau, V., Becquevort, S., Partent, J.-Y., Gasparini, S., Daro, M.-H., Tackx, M. and Lancelot, C. (2000) Trophic efficiency of the planktonic food web in a coastal ecosystem dominated by Phaeocystis colonies. J. Sea Res. 43: 357-372.
- Rijkswaterstaat (1991) Veilig Getij. De effecten van waterbouwkundige werken op het getijdemilieu van de Oosterschelde. Nota GWWS-91.088 / AX-91.091. Dienst Getijdewateren en Directie Zeeland, Middelburg. 132 pp.
- Savage RE (1932) Phaeocystis and herring shoals. The Journal of Ecology 20:326-340
- Savage, R.E. (1930) The influence of Phaeocystis on the migrations of the herring. Fishery Investigations, series 2, 12: 1-14.
- Savage, R.E. and Hardy, A.C. (1934) Phytoplankton and the herring. Part I, 1921-1932. Fishery Investigations, series 2, 14: 1-73.
- Scherffel,A. (1899) Phaeocystis globosa n.sp. (Vorläufige Mittheilung). Berichte der Deutschen Botanischen Gesellschaft 17: 317-318.
- Scherffel,A. (1900) Phaeocystis globosa nov. spec. nebst einigen Betrachtungen Über die Phylogenie niederer, insbesondere brauner Organismen. Wissenschaftliche Meeresuntersuchungen Abteilung Helgoland N.F. Bd.4: 1 29.

- Schoemann V, Becquevorta S, Stefelsb J, Rousseaua V, Lancelota C (2005) aeocystisblooms in the global ocean and their controlling mechanisms: a review Journal of Sea Research 53:43-6
- Schoemann, V., de Baar, H.J.W., de Jong, J.T.M. and Lancelot, C. (1998) Effects of phytoplankton blooms on the cycling of manganese and iron in coastal waters Limnol. Oceanogr. 43: 1427-1441.
- Seber, G.A.F. (1984) Multivariate Observations. John Wiley and Sons, New York.
- Shanks, A. and Walters, K. (1996) Feeding by a heterotrophic dinoflagellate (Noctiluca scintillans) in marine snow. Limnol. Oceanogr. 41: 177-181.
- Sieburth, J.McN. (1960) Acrylic acid, an "antibiotic" principle in Phaeocystis blooms in Antarctic waters. Science 132: 676-677.
- Sikes, C.S., Roer, R.D. and Wilbur, K.M. (1980) Photosynthesis and coccolith formation: Inorganic carbon sources and net inorganic reaction of deposition. Limnol. Oceanogr. 25: 248-261.
- Simpson, J.H. and Souza, A.J. (1995) Semidiurnal switching of stratification in the region of freshwater influence of the Rhine. J. Geophys. Res. 100: 7037 7044.
- Slocum, C.J. (1980) Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. J. Exp. Mar. Biol. Ecol. 46: 99-110.
- Smaal,A.C. and Twisk,F. (1997) Filtration and absorption of Phaeocystis cf. globosa by the mussel Mytilus edulis L. J. Exp. Mar. Biol. Ecol. 209: 33-46.
- Smayda, T.J. (1970) The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol. Ann. Rev. 8: 353-414.
- Smayda, T.J. (1973) The Growth of Skeletonema costatum during a Winter -Spring Bloom in Narragansett Bay, Rhode Island. Norw. J. Bot. 20: 219 247.
- Smayda, T.J. (1978) From phytoplankters to biomass. In: A.Sournia, (ed.) Phytoplankton Manual. UNESCO, Paris: 273-279.
- Smayda, T.J. (1990) Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. In: E.Granéli, B.Sundström, L.Edler and D.M.Anderson (eds): Toxic Marine Phytoplankton. Elsevier Science, Amsterdam: 29-41.
- Smetacek, V.S. (1985) Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Mar. Biol. 84: 239-251.
- Smith, W.O.Jr., Codispoti, L.A., Nelson, D.M., Manley, T., Buskey, E.J., Niebauer, H.J. and Cota, G.F. (1991) Importance of Phaeocystis blooms in the high-latitude ocean carbon cycle. Nature 352: 514-516.
- Smith WO, Dennett MR, Mathot S, Caronc DA (2003) The temporal dynamics of the flagellated and colonial stages of Phaeocystis antarctica in the Ross Sea Elsevier Science 50:605-617
- Sournia, A. (1982) Form and function in marine phytoplankton. Biol. Rev. 57: 347-394.
- Sournia, A. (1991) Phaeocystis (Prymnesiophyceae). In A.Sournia et al. (eds.) Le phytoplankton nuisible des côtes de France. IFREMER/CNS: 91-100.
- Spencer, C.P. (1981) Studies on Phaeocystis, a planktonic alga forming blooms in Liverpool Bay. Vol. 2. Marine Science Laboratories, University of Wales: 1-80.
- Stabell OB, Aanesen RT, Eilertsen HC (1999) Toxic peculiarities of the marine alga Phaeocystis pouchetii detected by in vivo and in vitro bioassay methods. Aquatic Toxicology 44:279-288
- Stefels, J. and van Boekel, J.H.M. (1993) Production of DMS from dissolved DMSP in axenic cultures of the marine phytoplankton species Phaeocystis sp. Mar. Ecol. Prog. Ser. 131: 307-313.
- Stefels,J. (1997) The smell of the Sea. Production of dimethylsulphoniopropionate and its conversion into dimethylsulphide by the marine phytoplankton genus Phaeocystis. Ph.D. Thesis, University of Groningen.
- Stein, J.R. (1975) Phycological Methods. Cambridge University Press, Cambridge.
- Strickland, J.D.H. and Parsons, T.R. (1972) A practical handbook of seawater analysis. Fisheries Research Board of Canada, Bulletin 167 (Second edition), Ottawa.
- Stuart, V., Sathyendranath, S., Head, E.J.H., Platt, T., Irwin, B. and Maas, H. (2000) Bio-optical characteristics of diatom and prymnesiophyte populations in the Labrador Sea. Mar. Ecol. Prog. Ser. 201: 91-106.
- Stumm, W. and Morgan, J.J. (1996) Aquatic Chemistry. John Wiley and Sons, New York.

- Swift, D.G. (1980) Vitamins and phytoplankton growth. In I.Morris (ed.) The physiological ecology of phytoplankton. Blackwell Scientific Publications, Oxford: 329-368.
- Tande, K.S. and Båmstedt, U. (1987) On the trophic fate of Phaeocystis pouchetii. I. Copepod feeding rates on solitary cells and colonies of P. pouchetii. Sarsia 72: 313-320.
- Tang, E.P.Y. and Peters, R.H. (1995) The allometry of algal respiration. J. Plankton Res. 17: 303-315.
- Taraldsvik, M. and Myklestad, S.M. (2000) The effect of pH on growth rate, biochemical composition and extracellular carbohydrate production of the marine diatom S. costatum. Eur. J. Phycol. 35: 189-194.
- Tett,P.B., Joint,I.R., Purdie,D.A., Baars,M., Oosterhuis,S., Daneri,G., Hannah,F., Mills,D.K., Plummer,D., Pomroy,A.J., Walne,A.W. and Witte,H.J. (1993) Biological consequences of tidal stirring gradients in the North Sea. Phil. Trans. R. Soc. Lond. A, 343: 493-508.
- Thingstad, T.F. and Sakshaug, E. (1990) Control of phytoplankton growth in nutrient recycling ecosystems. Theory and terminology. Mar. Ecol. Prog. Ser. 63: 261-272.
- Thingstad, T.F. and Billen, G. (1994) Microbial degradation of Phaeocystis material in the water column. J. Mar. Syst. 5: 55-65.
- Thompson, I.C. (1885) Foul water. Nature 32: 271-272.
- Thomsen, H.A. (1978) Nanoplankton from the Gulf of Elat (= Gulf of 'Aqaba), with particular emphasis on choanoflagellates. Israel Journal of Zoology 27: 34-44.
- Thoresen, S.S., Clayton, J.R. Jr., Ahmed, S.I. (1984) The effect of short-term fluctuations in pH on NO3-uptake and intracellular constituents in Skeletonema costatum (Grev.) Cleve. J. Exp. Mar. Biol. Ecol. 83: 149-157.
- Throndsen,J. (1978) Preservation and storage. In: A.Sournia (ed.) Phytoplankton manual, UNESCO, Paris: 69-74.
- Tillmann, U. and Hesse, K-J. (1998) On the quantitative importance of heterotrophic microplankton in the northern German Wadden Sea. Estuaries. 21: 585-596.
- Utermöhl,H. (1958) Zur Vervollkommnung der quantitativen Phytoplankton Methodik. Mitt. int. Verein. Limnol. 9: 1-39.
- Valero, M., Richerd, S., Perrot, V. and Destombe, C. (1992) Evolution of alternation of haploid and diploid phases in life cycles. TREE 7: 25-29.
- van Alphen,S.J.L.J., de Ruijter,W.P.M. and Borst,J.C. (1988) Outflow and three-dimensional spreading of Rhine river water in the Netherlands coastal zone. In: J.Dronkers and W.van Leussen (eds) Physical Processes in Estuaries. Springer-Verlag, Berlin: 70-92.
- van Bennekom, A.J., Gieskes, W.W.C. and Tijssen, S.B. (1975) Eutrophication of Dutch coastal waters. Proc. R. Soc. London Ser. B, 189: 359-374.
- van Bennekom,A.J. and Wetsteyn,F.J. (1990) The winter distribution of nutrients in the Southern Bight of the North Sea (1961-1978) and in the estuaries of the Scheldt and the Rhine/Meuse. Neth.J.Sea Res. 25: 75-87.
- van Bleijswijk,J.D.L., Kempers,R.S., Veldhuis,M.J. and Westbroek,P. (1994) Cell and growth characteristics of types A and B of Emiliania huxleyi (Prymnesiophyceae) as determined by flow cytometry and chemical analyses. J. Phycol. 30: 230-241.
- van Boekel, W.H.M. (1991) Ability of Phaeocystis sp. to grow on organic phosphates: direct measurements and prediction with the use of an inhibition constant. J. Plankton Res. 13: 959-970.
- van Boekel, W.H.M. (1992a) Interactions of Phaeocystis sp. with organic compounds and the microbial foodweb. Ph.D.Thesis, University of Groningen.
- van Boekel, W.H.M. (1992b) Phaeocystis colony mucus components and the importance of calcium ions for colony stability. Mar. Ecol. Prog. Ser. 87: 301-305.
- van Boekel, W.H.M., Hansen, F.C., Riegman, R. and Bak, R.P.M. (1992) Lysis-induced decline of a Phaeocystis spring bloom and coupling with the microbial foodweb. Mar. Ecol. Prog. Ser. 81: 269-276.
- van Breemen,P.J. (1904) Het Plankton der Noordzee in 1903. Jaarboek van het Rijksinstituut voor het Onderzoek der Zee. Helder: 52-59.

- van Breemen, P.J. (1905) Plankton van Noordzee en Zuiderzee. Ph.D. Thesis, University of Amsterdam.
- van den Hoek,C., Mann,D.G. and Jahns,H.M. (1995) Algae. An introduction to phycology. Cambridge University Press, Cambridge.
- van der Giessen, A., de Ruijter, W.P.M. and Borst, J.C. (1990) Three-dimensional current structure in the Dutch coastal zone. Neth. J. Sea Res. 25: 45-55.
- van der Tol,M.W.M. and Joordens,J.C.A. (1993) Modelling of a phytoplankton community in a pelagic mesocosm. In: J.C.H. Peeters, J.C.A. Joordens, A.C. Smaal and P.H. Nienhuis (eds.) The impact of marine eutrophication on phytoplankton and benthic suspension feeders: results of a mesocosm pilot study. National Institute for Coastal and Marine Management/RIKZ. Report GWAO-93.039: 96-128.
- van der Veer,H.W., van Raaphorst,W. and Bergman,M.J.N. (1989) Eutrophication of the Dutch Wadden Sea: external nutrient loadings of the Marsdiep and Vliestroom basin. Helgoländer Meeresunters. 43: 501-515.
- van de Werff,A., and Huls,H. (1957-1974) Diatomeeënflora van Nederland. Otto Koeltz Science Publishers, Koenigstein. van Duyl,F.C., Gieskes,W.W.C., Kop,A.J. and Lewis,W.E. (1998) Biological control of short-term variations in the concentration of DMSP and DMS during a Phaeocystis spring bloom. J.Sea Res. 40: 221-231.
- van Ierland, E.T. and Peperzak, L. (1984) Separation of marine seston and density determination of marine diatoms by density gradient determination. J. Plankton Res. 6: 29-44.
- van Leeuwenhoek, A. (1676) Letter to "d'Heer Henrij Oldenburgh secretaris van de Roijale Societeit a. Londen", Delft, 18pp.
- van Rijssel, M., Hamm, C.E. and Gieskes, W.W.C. (1997) Phaeocystis globosa (Prymnesiophyceae) colonies: hollow structures built with small amounts of polysaccharides. Eur. J. Phycol. 32: 185-192.
- van Rijssel M, Janse I, Noordkamp KJB, Gieskes WWC (2000) An inventory of factors that affect polysaccharide production by *Phaeocystis globosa*. J Sea Res 43:297-306
- Vaulot, D., Birrien, J.-L., Marie, D., Casotti, R., Veldhuis, M.J.W., Kraaij, G.W. and Chrétiennot-Dinet, M.-J. (1994) Morphology, ploidy, pigment composition, and genome size of cultured strains of Phaeocystis (Prymnesiophyceae). J. Phycol. 30: 1022-1035.
- Veldhuis, M.J.W. and Admiraal, W. (1985) Transfer of photosynthetic products in gelatinous colonies of Phaeocystis pouchetii (Haptophyceae) and its effect on the measurement of excretion rate. Mar. Ecol. Prog. Ser. 26: 301-304.
- Veldhuis MJW, Brussaard CPD, Noordeloos AAM (2005) Living in a Phaeocystis colony: a way to be a successful algal species. Harmful Algae 4:841-858
- Veldhuis, M.J.W., F. Colijn and L.A.H. Venekamp (1986) The spring bloom of Phaeocystis pouchetii (Haptophyceae) in Dutch coastal waters. Neth. J. Sea Res. 20: 37-48.
- Veldhuis, M.J.W. (1987) The eco-physiology of the colonial alga Phaeocystis pouchetii. Ph.D. Thesis, University Groningen.
- Veldhuis, M.J.W. and Admiraal, W. (1987) Influence of phosphate depletion on the growth and colony formation of Phaeocystis pouchetii. Mar. Biol. 95: 47 54.
- Veldhuis, M.J.W., Colijn, F. and Admiraal, W. (1991) Phosphate utilization in Phaeocystis pouchetii (Haptophyceae). Mar. Ecol. 12: 53-62.
- Verity, P.G. (1986) Grazing of phototrophic nanoplankton by microzooplankton in Narragansett Bay. Mar. Ecol. Prog. Ser. 29: 105-115.
- Verity, P.G. and Villareal, T.A. (1986) The relative food value of diatoms, dinoflagellates, flagellates, and cyanobacteria for tintinnid ciliates. Arch. Protistenkd. 131: 71-84.
- Verity, P.G., Villareal, T.A. and Smayda, T.J. (1988a) Ecological investigations of blooms of colonial Phaeocystis pouchetii I. Abundance, biochemical composition, and metabolic rates. J. Plankton Res. 10: 219-248.
- Verity, P.G., Villareal, T.A. and Smayda, T.J. (1988b) Ecological investigations of blooms of colonial Phaeocystis pouchetii. II. The role of life cycle phenomena in bloom termination. J. Plankton Res. 10:

- 749-766.
- Verity, P.G. and T.J. Smayda (1989) Nutritional value of Phaeocystis pouchetii (Prymnesiophyceae) and other phytoplankton for Acartia spp. (Copepoda): ingestion, egg production and growth of nauplii. Mar. Biol. 100: 161-171.
- Verity, P.G. (1991) Feeding in planktonic protozoans: evidence for non-random acquisition of prey. J. Protozool. 38: 69-76.
- Verity, P.G., Smayda, T.J. and Sakshaug, E. (1991) Photosynthesis, excretion, and cell growth rates of Phaeocystis colonies and solitary cells. Polar. Res. 10: 117-128.
- Verity, P.G. and Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar. Ecol. Prog. Ser. 130: 277-293.
- Verity,P.G., Paffenhöfer,G.-A., Wallace,D., Sherr,E. and Sherr,B. (1996) Composition and biomass of plankton in spring on the Cape Hatteras shelf, with implications for carbon flux. Cont. Shelf Res. 16: 1087-1116.
- Villareal, T.A. (1992) Buoyancy properties of the giant diatom Ethmodiscus. J. Plankton Res. 14: 459-463. Vogel, S. (1996) Life in moving fluids. Princeton University Press, Princeton.
- Vollenweider, R.A., Rinaldi, A. and Montanari, G. (1992) Eutrophication, structure and dynamics of a marine coastal system: Results of ten years monitoring along the Emilia Romagna coast (Northwest Adriatic Sea). In: R.A. Vollenweider, R. Marchetti and R. Viviani (eds.) Marine Coastal Eutrophication, Elsevier, Amsterdam: 63-106.
- Waite, A.M., Bienfang, P.K. and Harrison, P.J. (1992a) Spring bloom sedimentation in a subarctic ecosystem. I. Nutrient sensitivity. Mar. Biol., 114: 119-129.
- Waite, A.M., Thompson, P.A. and Harrison, P.J. (1992b) Does energy control the sinking rate of marine diatoms? Limnol. Oceanogr. 37: 468-477.
- Wassman, P., Vernet, M., Mitchell, B.G. and Rey, F. (1990) Mass sedimentation of Phaeocystis pouchetii in the Barents Sea. Mar. Ecol. Prog. Ser. 66: 183 195.
- Wassmann,P. (1994) Significance of sedimentation for the termination of Phaeocystis blooms. J. Mar. Syst. 5: 81-100.
- Wassmann P, Ratkova T, Reigstad M (2005) The contribution of single and colonial cells of Phaeocystis pouchetii to spring and summer blooms in the north-eastern North Atlantic. Harmful algae 4:823-840
- Weisse, T., Grimm, N., Hickel, W. and Martens, P. (1986) Dynamics of Phaeocystis pouchetii blooms in the Wadden Sea of Sylt (German Bight, North Sea). Est. Coast. Shelf Sci. 23: 171-182.
- Weisse, T. and Scheffel-Möser, U. (1990a) Morphometric characteristics and carbon content of Phaeocystis cf. pouchetii (Prymnesiophyceae). Bot. Mar. 33: 197-203.
- Weisse, T. and Scheffel-Möser, U. (1990b) Growth and grazing loss rates in single-celled Phaeocystis sp. (Prymnesiophyceae). Mar. Biol. 106: 153-158.
- Weisse, T., Tande, K., Verity, P., Hansen, F. and Gieskes, W. (1994) The trophic significance of Phaeocystis blooms. J. Mar. Syst. 5: 69-79.
- Wulff,A. (1933) Über Hydrografie und Oberflächenplankton nebst Verbreitung von Phaeocystis in der Deutschen Bucht im Mai 1933. Berichte der Deutschen wissenschaftlichen Kommission Meeresforschung, Neue Folge 230: 343-350.
- Yamaguchi, M. and Honjo, T. (1989) Effects of temperature, salinity and irradiance on the growth of the noxious red tide flagellate Gymnodinium nagasakiense (Dinophyceae). Nippon Suisan Gakkaishi 55: 2029-2036.
- Yoder, J.A. (1979) Effect of temperature on light-limited growth and chemical composition of Skeletonema costatum (Bacillariophyceae). J. Phycol. 15: 362-370.
- Zingone,A., Chrétiennot-Dinet,M.-J., Lange,M. and Medlin,L. (1999) Morphological and genetic characterization of Phaeocystis cordata and P. jahnii (Prymnesiophyceae), two new species from the Mediterranean Sea. J. Phycol. 35: 1322-1337.