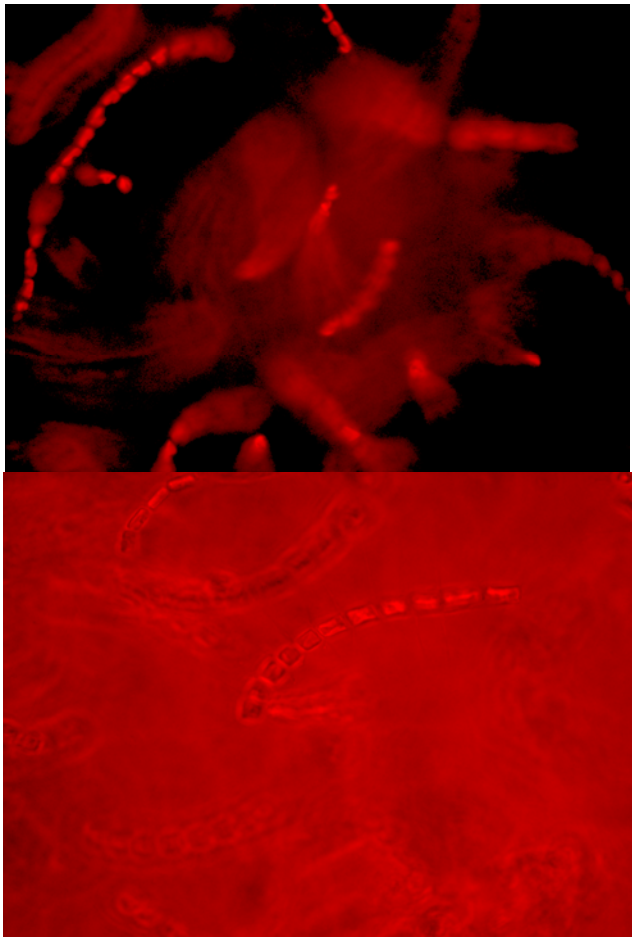
The Importance of Morphological/Physiological Heterogeneity as Adaptive Strategies in Stocks of Common Northern/Arctic Phytoplankton Species with Special Focus on the Common Diatom *Chaetoceros socialis*



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CONTENTS

ABSTRACT

The cosmopolitan, centric diatom *Chaetoceros socialis* was investigated in terms of its validity as a single species characterized by its morphology, physiology and distribution. A database was constructed using my own and published literature distribution observations of *C. socialis* in Northern Norway, the Atlantic, Arctic and Barents Sea. From this range of observations, it is possible to establish that *C. socialis* is found at temperatures ranging from -1.86°C to +13.6°C. Observations have been made between March and November with the greatest number of observations of *C.Socialis* being during March. Experiments were carried out under laboratory conditions with mono cultures of *C. socialis* grown at 2°C and 7°C. When cells were examined after cleaning, a significant difference in apical axis size was observed between cells which were grown at 2°C and those grown at 7°C. No significant difference was observed in growth rates between the cells grown at 2°C and 7°C. The morphology of the cleaned cells was observed to be different from the ‘standard’ or ’type’ for this species which leads one to question the present definition of *C. socialis* as a species.

1. INTRODUCTION

The underlying reason why taxonomy is important is that the physiological behaviour of individual species determines how ecosystems function. Ecosystems consist of taxonomic entities, and this was probably the reason Aristotle (evolution.berkeley.edu 2006) sought to define the *differentio specifica* - the specific difference between groups of organisms and defined species. Grouping “comparable” organisms in entities has been the basis of all ecological activities, even if Aristotle did not formulate this clearly.

The emergence of the species concept is linked to evolutionary theories; it is therefore necessary to understand how and why the theories of evolution and species concepts arose. The concept of species was present long before Carl Linnaeus‘(1707 - 1778) taxonomy system was established. He is however credited as the ‘Father of Taxonomy’, therefore for the purposes of this thesis this is where I will begin. Linnaeus defined three kingdoms: plants, animals and rocks. Linnaeus' system of classification was based on reproductive organs and resulted in many groupings that in some instances seemed unnatural. Similar reproductive organs do not necessarily suggest association between two (or more) organisms. Linnaeus recognised that this produced an "artificial” classification. Jean Baptiste Pierre Antoine de Monet Chevalier de Lamarck (1744 - 1829) suggested that adaptive changes in a species may, as a result of environmental influence, be passed on to their offspring (“lamarckism”). In, “The Origin of Species” Darwin (1859), claimed that all organisms evolve continuously through random mutations and that the best adaptation to the prevailing environmental/biological conditions will survive. The mechanisms for ‘mutations’ were not brought into focus until Gregor Mendel (1866) and his work with pea plants. Mendel’s work showed that there were two main genes associated with each phenotypic trait and the

combination in which these were inherited from the parental gametes determined the offspring's phenotypic features. Later research has shown that this is in fact a much more complex process. Theodosius Dobzhansky (evolution.berkeley.edu 2006) combined the study of genetics and natural history in an effort to find a unified explanation of how evolution happens. This was known as 'The Modern Synthesis'. The Modern Synthesis brings together genetics, palaeontology, systematics, and many other sciences, e.g. molecular biology, into one explanation of evolution.

No single encompassing definition of species exists and many different 'schools' of classification are active today. Irreversible divergence, distinct ecological niche and inability to interbreed are often used to describe a 'species'. There are also numerous examples of how the incorporation of molecular techniques has led either to the redefinition of a species, or to a lack of agreement on what a species is. For example for the classification of bacteria the three previously named properties of a species are insufficient. Bacteria can be defined by 'ecotypes' (Cohan 2002), i.e. populations which occur in the same ecological niche, identified by molecular techniques. Within the bacterial world one species may in fact contain many ecotypes which function in a similar fashion as a genus (Cohan 2002).

Diatoms have been very successful in terms of evolutionary diversification, and may contain 10,000 – 12,000 recognised species. Diatoms share several characteristics distinguishing them from other algae; they are single celled organisms where the protoplast is enclosed within a rigid lidded silica box – the frustule. Diatoms are also characterised by gametic meiosis in addition to mitosis, and the reduction of the flagella apparatus. (Graham and Wilcox 2000).

The classification of diatoms is: Kingdom: Protista, Eukaryota: Aconta (without flagella), Class: Bacillariophyceae (diatoms).

Diatoms have a fossil record from the middle Cretaceous period through to the Cenozoic period and reflect a fundamentally different evolutionary trait from higher plants. It is thought that eukaryotic phytoplankton i.e. diatoms, dinoflagellates and haptophytes were formed when a non-photosynthetic eukaryote engulfed and acquired a chloroplast from a photosynthetic eukaryote (Falkowski 2004). Observations, such as those of Baarud (1951), support the idea that phytoplankton species are not specific to one area or even one type of area, Baarud even suggested that ecotypes or races of phytoplankton may exist.

In 1912 Gran carried out work on the taxonomy of diatoms based on cell morphology, using light microscopy. Less attention was given in this work to the metabolism and contents of the cell. The introduction of electron microscopy revealed new morphological aspects of the diatoms. Simonsen (1979) used electron microscopy to introduce a classification system based on both light and electron microscopy but still firmly based on cell morphology. The more recent use of the transmission electron microscope (TEM) and the scanning electron microscope (SEM) did not reveal other applicable structures. However the previous observations are better explained using TEM and SEM (Fryxell 1983).

According to Mann (1999) species definition is still 'messy'. The concept of separate genetic entities in one population, caused by temporal segregation, has been shown in the diatom *Pseudo-nitzschia galaxiae* (Cerino 2005). Although phenotypic plasticity is not a problem for taxonomic classification, such plasticity is of importance when considering the ecological functioning of diatoms.

Some diatom species seem to exhibit morphological plasticity, making morphologically based species determination dubious. *Thalassiosira gravida* grown at 17°C has the morphology of a typical *T. rotula,* however at 3°C it acquires the morphology of *T. gravida,*

(Syvertsen 1977). In a sample of *Ditylum brightwellii*, isolated from field samples, 23 of the 24 isolates studied were genetically distinct (Ryneason and Armbrust 2000). Obviously a certain level of critical consideration is required when deciding the meaning of 'genetically distinct.' However the authors do go on to comment that this number is remarkable considering that diatoms reproduce daily to create genetically identical individuals. Diatoms can also vary significantly in genetic terms within a single population. The measured genetic diversity in this study reflected an underlying physiological diversity (Ryneason and Armbrust 2000). This could suggest that genetic diversity also has consequences for the physiological behaviour of a species, and is therefore important if a species is to be determined by its physiology. The constant realignment of the genetic composition of a population may also explain why the dynamics of diatom blooms are so difficult to predict despite years of study (Ryneason and Armbrust 2000). Some phytoplankton species have been shown to be able to adapt their physiology to their environments. For instance, the chlorophyte *Dunaliella teriolecta* has been shown to have the ability to redistribute the enzyme RuBisCO between the pyrenoid and the stroma in response to light and shade. This response is seen at the population level rather than at an individual cell level (Lin and Carpenter 1997). Phytoplankton communities may reveal an astonishing biodiversity; whereas classical competition theory suggests that only a few competing species should survive. It would seem that this 'competitive chaos' promotes biodiversity (Huisman et al 2001).

Separated 'strains' of phytoplankton do not necessarily have uniform characteristics, in that each strain does not necessarily correspond to particular 'species' criteria. Montressor (2003) observed that varying the light intensity did not cause standard variation in the maximum growth rate amongst the strains.

Rynearson and Armbrust (2000) found that the isolates displayed relative different growth rates both within and between light intensities. *Thalasiosira rotula* has an ability to produce polyunsaturated aldehydes and it has been observed (Pohnert 2005) that different clones/strains of this species produce variations in their toxicity when subjected to similar conditions. Phytoplankton strains from two hydrographically different areas have also been shown to be identical for common molecular markers yet displayed functional differences (Lowe et al 2005). When mapping and considering the whole genome of the diatom *Thalassiosira Pseudonana,* indications were found in the genome that 'novel' changes had occurred to the chloroplast protein translocation system, when compared to that found in plants (Armbrust *et al* 2004). Some species are impossible to separate based on morphological differences alone (Knowlton 1993) and these are termed sibling and cryptic species.

Diatoms normally reproduce by vegetative division during blooms. It is commonly accepted that while some of the cells maintain their size, others become progressively smaller and the end result is thought to be sexual reproduction taking place (Garrison 1984). This process may also lead to the formation of resting spores. Cell size in a population is restored through auxosporulation, although this is rarely observed in situ. Information on reproduction cycles in the natural environment is scarce (Mann 1988, Round et al 1990). The limited investigations that have been carried out suggest that within a population sexual reproduction is a nearly synchronous event. According to Mann (1988) this occurs within a restricted size window with a periodicity varying form 2 to 40 years. The average cells size within laboratory cultures is also reported to decrease with time (Cerino et al 2005, Mann 1988). Other examinations of interspecific phytoplankton cell size suggest that there are

physiological differences between large and small phytoplankton (see e.g. Popp et al. 1998).

1.1 *Chaetoceros socialis* (Lauder 1864)

Species of the genus *Chaetoceros* are considered an integral component of the ecology of all seas (Rines et al 2003). An important member of the *Chaetoceros* genus is *Chaetoceros socialis,* which was first described in 1864 by Henry Scott Lauder using samples collected in the waters around Hong Kong, during his time as an Assistant Surgeon with the Royal Navy.

> *'Chætoceros socialis, filaments slender, aggregated, embedded in gelatine, with wavy, spirally dotted awns, some of which are more elongated, and converge to a common centre'*
> *Lauder(1864)*

A detailed description of the distribution of *C.socialis* globally is not available in the literature. An examination of early Norwegian articles concerning phytoplankton reveals that *C.socialis* was the prominent species during the springtime, with figures in the region of 3,000,000 cells l^{-1} including resting spores being found in Vesterålen (Føyn 1928), Balsfjorden and Malangen (Gaarder 1932). Føyn (1928) also comments that *C. socialis* is one of the prime forms of phytoplankton of the early spring bloom and that *C.socialis* occurred at such high densities that it was difficult to count. Føyn also mentions that *C.socialis* occurs at the same time as *Phyaeocystis pouchetii.* Gaarder's and Føyn's papers also report the presence of many resting spores during the bloom. In Narragansett Bay, Canada, *C. socialis* was a year round occupant. The maximum diversity

amongst *Chaetoceros* species coincided with a period of increased mixing in the water column (Shevchenko et al 2004). During the spring bloom *Chaetoceros* species follows the smaller faster growing species such as *Skeletonema sp.* (Shevchenko et al 2004, Margalef 1967, Guillard et al 1977, Smayda 1980).

In terms of distribution *C. socialis* is found in geographic areas as diverse as the Mediterranean and the Arctic (Eilertsen and Wyatt 2000). Other members of the *Chaetoceros* family have proved difficult to separate, for example *C. socialis* and *C. socialis var*. *radians* are difficult to separate but are characterised by occurring at different times of year in all localities (Hellum von Quilfeldt 1996). Hargraves (1979) found four different types of resting spores for *C. socialis.* The foregoing could be either an indication of adaptation to various niches by different members of the family or some form of environmental pressure forcing the evolution of different strains.

When considering modelling and production studies it is important not to assume that a set of species have the same characteristics or exhibit the same behaviours in different environments. Verity (1996) stressed the importance of not only understanding individual species but also variations within individual species and the role this plays in larger ecosystems. This theme is central to the purpose of this thesis.

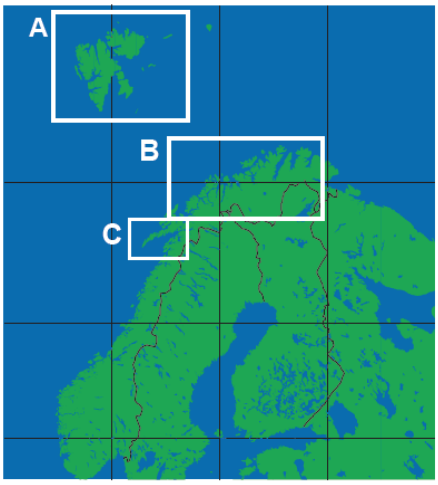
2. MATERIALS AND METHODS

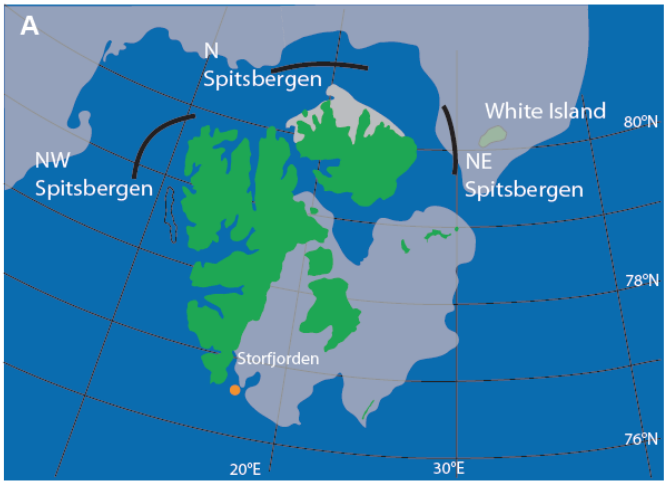
2.1 Field investigations

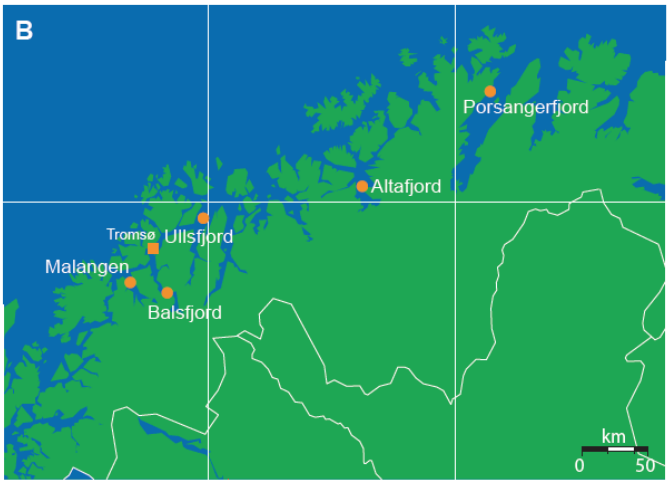
Sampling was performed during cruises with R/V “Johan Ruud” (100 ft.) and R/V “Jan Mayen” (186 ft.). Samples were collected from five different regions (Table 1, Figure 1): Arctic Barents Sea, Polar Front, Atlantic Barents Sea and North Norwegian coast. Tromsø Sound was also monitored over the entire spring season by sampling the sea water intake at the Norwegian College of Fishery Science, Tromsø (Table 1).

Table 1. Overview of sampling: CTD= Conductivity, Temperature and Depth, WB = Water bottles, L=Irradiance, M=Meteorology, P= Photographs for measurements of cell size.

Location	Sampling dates	Stations Number	Depth (m)	Sampling
Alta midtre vest	20/02/06	26	0, 10, 50, 340	CTD, WB, L, M
Ullsfjord sør av Karlsoy	20/02/06	14	0, 10, 50, 250	CTD, WB, L, M
Porsangnes vest	21/02/06	36	0, 10, 50, 205	CTD, WB, L, M
Ullsfjord nord av Jøvik	22/02/06	17	0, 10, 50, 205	CTD, WB, L, M
Blasfjord Berg	23/02/06	7	0, 10, 62	CTD, WB, L, M
Malangen Hekkingen	23/02/06	48	0, 10, 50, 427	CTD, WB, L, M
Tromsøysund	03-06-13-15-20-22-27/03/06 18-24-26/04/06 02/05/06	15, 16, 31, 32, 34, 35, 37, 47, 60, 61	1-3	WB,L,M
Vestfjorden	01-02/04/2006	1, 2, 3, 4, 5	0, 5, 10, 20, 30, 40, 60, bottom	CTD, WB, L, M
Henningsvæstraumenn	02-03/04/2006	6, 49, 50, 51	0, 5, 10, 15, 20, 25, 30, 40	CTD, WB, L, M
Austnesfjorden	03-04/04/2006	37, 38, 39, 40, 41	0, 5, 10, 15, 20	CTD, WB, L, M
Hadselsfjorden	05704/2006	18, 19	0, 5, 10, 20, 30, 40, 60, 120	CTD, WB, L, M
Tysfjorden	05-07/04/2006	20, 21, 22, 23, 24, 25	0, 10, 20, 30, 40, 50, 60, bottom	CTD, WB, L, M
Balsfjord Berg	18/04/06	27	0, 5, 10, 20, 30, 50	CTD, WB, L, M
Malangen	18/04/06	28	0, 5, 10, 20, 30, 50	CTD, WB, L, M
NW Spitzbergen	10-11/05/2006	8, 9, 10, 11	0, 1, 2, 5, 10, 20, 30, 50	CTD, WB, L, M
N Spitzbergen	11-13/05/2006	12, 13, 42, 43, 44, 45, 47, 52, 53	0, 1, 2, 5, 10, 20, 30, 50	CTD, WB, L, M, P
White Island	13-14/05/06	54, 55, 56, 57, 58	0, 1, 2, 5, 10, 30	CTD, WB, L, M
NE Spitzbergen	14-15705/2006	59, 62, 63, 64, 65, 66	0, 5, 10, 20, 30, 50	CTD, WB, L, M







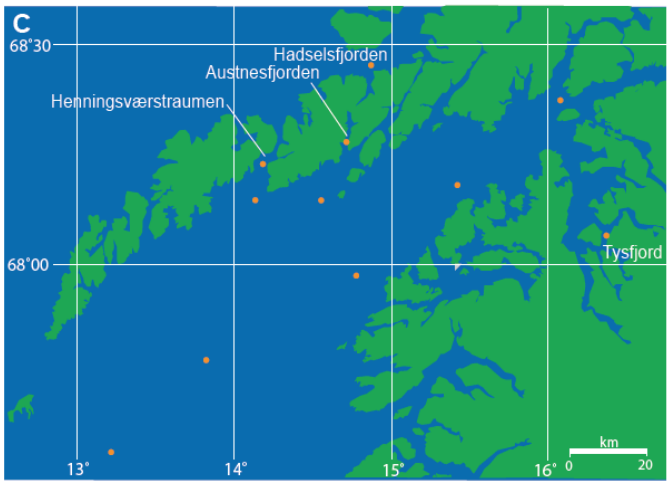


Figure 1. Map of the sampling areas: *A = Svalbard area (ice cover in grey for early June 2006), B = Northern Norwegian Coast, C= Lofoten area*

Meteorological parameters (air temperature °C, Air pressure mB, humidity %, wind speed ms^{-1}, wind direction, visibility km and cloud cover on a scales of 1-9.) were recorded at each station. The following hydrographical and biological parameters: conductivity, temperature, depth (from pressure) and fluorescence (FL) were measured with a CTD (Seabird Electronics 9 plus 6800 m) at each station. Water samples were collected using 5 l "Niskin" water bottles attached to the CTD (Jan Mayen). From each of the bottles water samples for analysis of pH and thereby C content, and samples for quantitative species analysis were taken, while qualitative phytoplankton samples were taken using a 25 µm mesh size phytoplankton net that was hauled from depths determined by the indications of fluorescence from the CTD, i.e. hauls were taken from just below the chlorophyll (FL) maximum. Samples were counted after 2 hours sedimentation using the Utermöhl (1931) technique applying single 50 ml and 2 ml 4 well Nunclon counting chambers. Samples which could not be counted immediately were preserved using 20% formalin neutralised with hexamine in the ratio of 100ml : 2ml.

Water samples (5 or 10ml depending upon the density) were filtered onto Whatman 25 mm GF/C filters whereafter Chlorophyll *a* analysis was performed according to the method of Holm-Hansen and Reimann (1978) using methanol as the extractant. The samples were extracted for at least 4h at 4°C in the dark and thereafter measured on a calibrated Turner Designs 700 Fluorometer. The following equations were used to compute Chl*a* and phaeophytine;

$$\text{µg Chl}a\ \text{l}^{-1} = \frac{\left[0.0001938 \times \left(R_a - R_b\right)\right]}{V}$$

$$\text{µg Phaeophytine l}^{-1} = \frac{\left[0.0001938 \times \left(2.72 * R_b - R_a\right)\right]}{V}$$

(Where R_a = fluorometer reading before adding HCl, R_b = fluorometer reading after adding to 2 drops of 10% HCl, V = volume of filtered seawater in litres.)

2.2 Laboratory Experiments

Monocultures of *Chaetoceros socialis* were adapted for two weeks to two different light intensities (10 and 50 µmol quanta m^{-2} s^{-1}) at two different temperatures (2°C and 7°C) and cultivated in double filtered sea water enriched with Gaillard's (f/2) growth medium (0.25ml per litre) and silicate '(0.66ml per litre). The *C. socialis* cells were germinated in December 2003 from sediment collected in Austnesfjorden, Lofoten. Water samples of all the replicates were collected and left in 2ml Nunclon 4-well chambers for at least 2 hours to sediment in the dark and cold (fridge). Counts of the chambers (cells $^{-l}$) were made using an inverted Leica microscope. Cells were counted at the start and the end of the experiment. Growth rate (GR) as doublings day^{-1} was computed using the equation:

$$GR \equiv \frac{\log_2\left(N_t / N_0\right)}{t}$$

GR= growth rate, N_t = number of cells at time t, N_0 = initial number of cells and t = time in days.

At the termination of the experiment a portion of the *C. socialis* cells was also removed for cleaning. For experiments 2, 3 and 4, monocultures were split into two further monocultures containing what was thought to be strains of large and small cells! In experiments 2 and 3 cultures from 'large' strains were compared. In experiment 4 both the cultures with large and small strains were compared. During measurement of live chains, cells were taken from

the maximum possible number of chains, the minimum number being 5.

Cells were cleaned using a modification of Simonsen's (1974) method. Subsamples of 7ml of the culture under examination were transferred to test tubes. These were concentrated by centrifugation for 5 min. at 4000 rpm after which 6 ml of supernatant were removed. This first step was repeated as necessary in order to obtain a concentrated sample for processing. 5ml of distilled water were then added and the sample then centrifuged for 5 min at 4000 rpm. Following this 5ml of the supernatant were removed and then 5ml of potassium permanganate ($KMnO_4$) was added. The samples were left for 24h. and then centrifuged for 5 min at 4000 rpm, 5ml of supernatant was then discarded. 5ml of concentrated hydrochloric acid (HCl) was then added before heating the samples over a gas flame until there was a colour change from dark brown to colourless or light green. Following this the samples were 'rinsed' by addition of deionised water, centrifuged for 5 min. at 4000 rpm and supernatant removed. This was repeated 3 times. For observation, Light Microscope (LM) slides were prepared. These were left to dry in air for 2 days and then sealed with a cover slip using Eukit glue.

Table 2. Overview of experiments and measurements L = 'large' culture S = 'small' culture.

Experiment	Date	Measurements/Sampling
1.Growth rate	22-30.3.2006	Growth
2.June Cell size I	15.6.2006	Cleaning and measuring of cells, measuring apical and transapical axis, 50 cells at 2° C and 50 at 7° C
3. June Cell size II	22.6.2006	Cleaning and measuring of cells apical and transapical axis.100 cells measured at 2° C and 100 cells measure at 7°C, 42 cells at each of 7°C L and S and 2°C L and S
4.July live Cell size	3.7.2006	Measuring of live cell size apical and pervalvar axis. Examination of fluorescence of chloroplasts and cell colours using paint shop pro software.

Photographs of the LM slides, live culture and samples taken during field investigations were taken using a Leica DFC 320 microscope camera. During photography light setting and exposure times were kept constant where possible. Details of the pictures taken were 2078x1583 pixels with a pixel depth of 24/16 million, each photograph was 9366 k of RAM. During fluorescence photography, background light was kept to a constant minimum e.g. laboratory lights turned off and curtains closed.

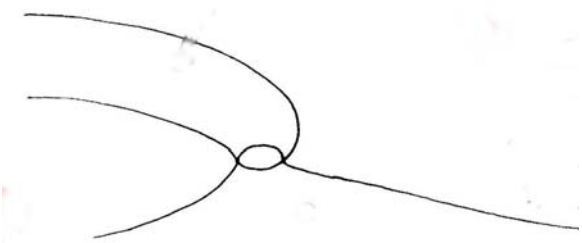


Figure 2. Valvar plane view of a cell of *C. socialis* according to Tomas (1997).

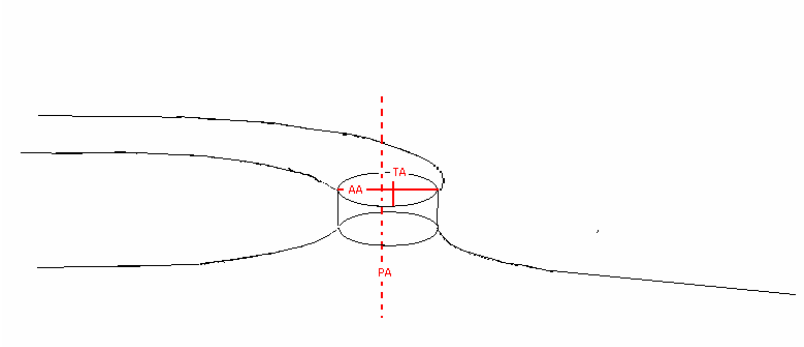


Figure 3. 3D diagram of *C. socialis*. Red lines demonstrate axis measured in this thesis-AA apical axis, TA transapical axis and PA Pervalvar axis.

2.3 Geographical distribution of *Chaetoceros socialis*

Records of observations from published articles of *C. socialis* abundance in Northern Norway and the Barents Sea were fed into a data base (Statistica 6.0). The criteria for selection of these records was all available published data. The data base included, the author(s), the date of each sampling, the depth counting samples

were taken from, the number of cells observed, positions of each individual station, salinity, temperature, density, light and pH where available. This was then mapped to demonstrate abundance through time and space.

Short-wave solar irradiance (Qs) in W m^{-2} for clear sky was computed as described in Frouin et al (1989) and modified in Eilertsen and Holm-Hansen (2000), after input of surface visibility, regression coefficients for maritime atmospheres and solar zenith angle computed at given geographical position and time according to the equations in Iqbal (1983). The modeled radiation values represents visible (PAR) light at cloud cover 0-1, i.e. approximately maximum achievable radiation level

All statistical treatments were carried out in Statistica (6.0).

3. RESULTS

3.1 Field data

Finnmark and Troms

Observations were made from the 20 - 23 February 2006. A weak stratification of the water column was observed in Altafjord and Malangen e.g. $\sigma_t = 0.1$. The temperature at 5 metres depth varied little, either within or between the different areas sampled, ranging from 3.4°C – 4.6°C. The salinity at the same depth was 33.3‰ to 34.2‰ see (Table 4). During this period the water column at stations in Ullsfjord, Porsangnes and Balsfjord was judged to be relatively homogenous. The most abundant phytoplankton observed were *Pennates s*pp.

Tromsø sound

There was poor coverage during the period March – May 2006 of the most important periods in question.

Lofoten

Observations of the physical conditions were made during field work in Lofoten April 1 - April 5 2006. The water column was homogenous at 2 of the 5 locations examined (Henningsvæstraumen and Austnesfjorden). At the other locations examined, Vestfjorden, Hadselsfjorden and Tysfjorden, the water column was judged to be weakly stratified. Water temperatures recorded were above 0°C and at 5 metres depth ranged from 4.2°C - 3°C. The salinity at the stations sampled in Lofoten at 5 metres depth ranged form 32.9‰ up to 33.5 ‰ see Table 4. The most abundant phytoplankton species observed was *Skeletonmea Costatum* together with a high abundance of *Chaetoceros spp*. An exception to the bloom situation observed in Lofoten was in Tysfjorden where high numbers of dinoflagellates were observed. All stations had Chl*a* values between

0.4-1.6. The exception to this being Tysfjorden, where the Chl*a* values at 5 metres were 4.7. see table 4

Svalbard

Observations of the physical conditions were made during field work around Svalbard from the May 10 - May 17 2006. The water temperatures were lower than those observed previously in the field work for this thesis in Finnmark, Troms and Lofoten. At the stations sampled in NE Spitzbergen and N Spitzbergen the water column was observed to be stratified. The salinity was also slightly higher at 5 metres depth than that observed previously in this field work (34-34.4‰) see Table 4. At stations sampled in NW Spitzbergen and N Spitzbergen, *Phyocystis pouchetii* dominated the counting samples. The stations taken after leaving Storfjord and heading south towards Bjornøya were dominated by *P. pouchetii* (pers. com. HC Eilertsen M Dagerlund). Chla values ranged from 0.2 – 2.3µgl^{-1}. (see Table 4)

Table 3. Summary of meteorological data collected during field work. Tromsø Sound data is omitted. Range is presented and the average of data is in brackets where appropriate/available.

	Locality	Date	Air Temperature [°C]	Air Pressure [mB]	Humidity [%]	Wind Speed [m s^{-1}]	Wind direction	Visibility [km]	Cloud Cover [1-9]
Finnmark and Troms	**Altafjord**	20.02.06	6 → 7 (6.5)	No data	No data	6-7(6.5)	NW,SW	No data	6 (6)
	Ullsfjord	20.02.06	0 → -2 (-1)			10	SW		8 (8)
	Porsangnes	21.02.06	1.6 → 4.5(3.07)			5-27 (12)	SW, NW		6-8 (7)
	Balsfjord	23.02.06	4.3 → 4.8 (4.4)			0-7 (4.2)	SE, NW		6-8 (7)
	Malangen	23.02.2006	2.8 → 3.6 (3.2)			6-12 (8.83)	NW		7-8 (9)
Lofoten	**Vestfjorden**	1-2.04.06	-0.1 → 4.2 (-2.4)	1004	67	2-6 (3.6)	NW	38	2-4 (3)
	Henningsvæstra umen	2-3.04.06	-2.7 → 3 (-0.4)	1010	91	2-11 (4)	W	30	2-4 (2)
	Austnesfjorden	3-4.04.06	-2.5 → 3 (-1.5)	1008	87	1-4 (1.9)	W, NNE	41	1-6 (4)
	Hadselsfjorden	5.04.2006	-1.7 → 0 (-0.85)	1010	91	4-6 (5)	S	50	1(1)
	Tysfjorden	5-6-7.04.06	-2-7 → 1.1(-0.86)	1010	55	3-10 (5.8)	SE	48	1-2(2)
Svalbard	**NW Spitzbergen**	10-13.05.06	-3.6 → -7.1 (-6.3)	1024-1029.8(1025)	78-99.4 (96)	8.6-10.1 (9.1)	N	95-99 (97)	1-9 (7)
	N Spitzbergen	11-12.05.06	-9.7 → -7.1 (-8.2)	1025.7-1028.6(1027)	91-98.9 (95)	9.1-7.6 (8.3)	N	96-98 (97)	6-8 (7)
	White Island	13-14.05.06	-8.6 → -7.5 (-8.1)	1019.7-1021.5 (1021)	90.1-94.5(92)	10-13.2 (11.2)	NE	94-96 (95)	8 (8)
	NE Spitzbergen	14-17.05.06	-6.4 → -5.1 (-5.1)	1013.7 – 1018.8 (1016)	81.5-95.3 (88)	8-12.4 (10.2)	NE	94-97 (95)	6-9 (8)

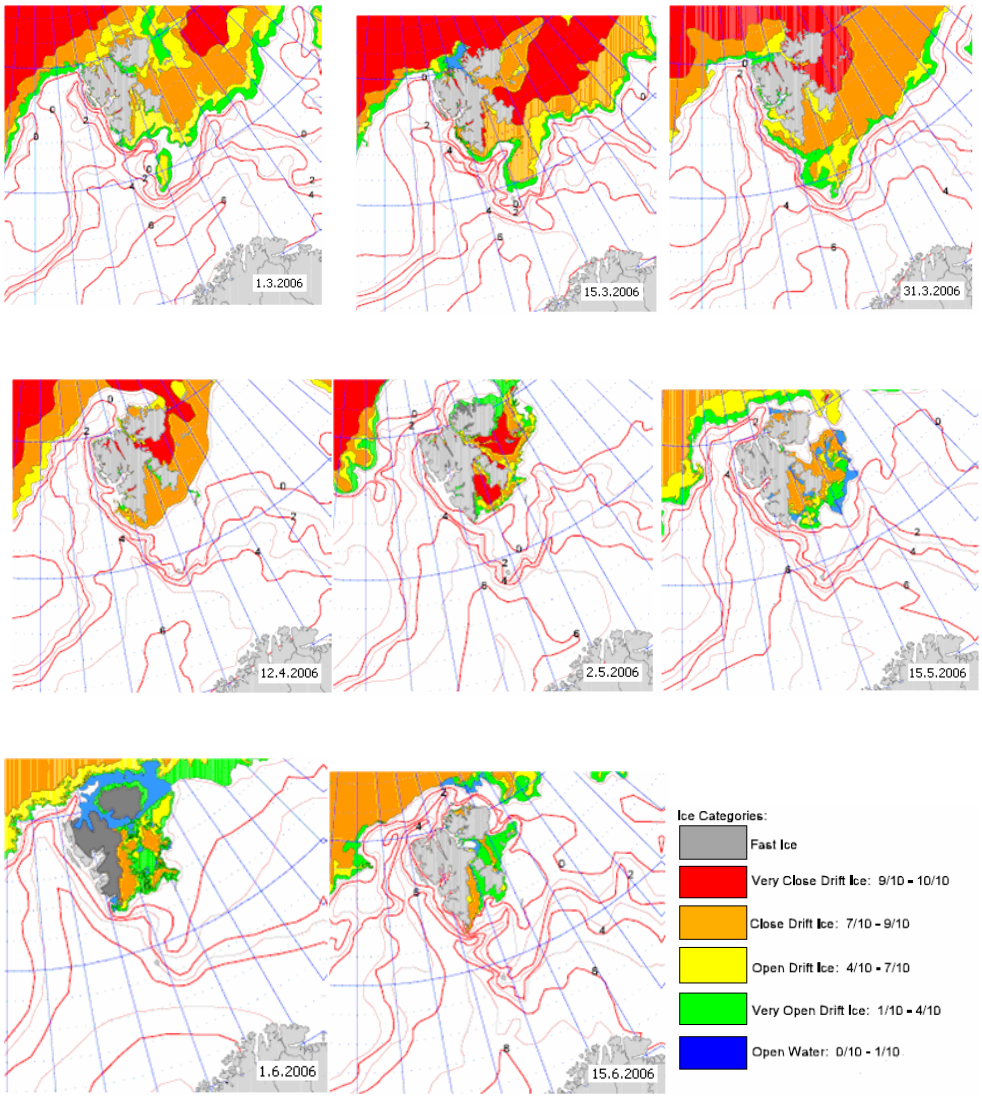


Figure 4. Maps showing the ice cover around Svalbard from the 1.3.2006 to the 15.6.2006.
Maps provided by the Norwegian Meteorological Service - Department of Sea Ice Forecasting.

Table 4. Hydrographical and biological data collected during field work and dominant phytoplankton species; $d\sigma_t$ represents difference in density anomaly from surface to pycnocline, temperature (t) and salinity (S) are taken from that measured at 5 m, Chl*a* refers to the highest observed concentration. Tromsø sound data is omitted. Abbreviations used for the most abundant Species: *C.sp=Chaetoceros sp, C.soc=Chaetoceros socialis, F.sp=Fragilariopsis sp, N.sp=Navicula sp, P.p=Phaeocystis pouchetii, Pl.sp=Pleurosigma sp, T.sp=Thalassiosira sp, T.nor=Thalassiosira nordenskioeldii, S.cos=Skeletonema costatum*

	Locality	Date	t_{5m} [°C]	S_{5m} [‰]	σ_t	Stability of the water column	Chl*a* [μgl^{-1}]	Most abundant phytoplankton
Finnmark and Troms	**Altafjord**	20.02.06	3,4	33,7	0,1	Weak stratification		Pennate unid.
	Ullsfjord	20+22.02.06	4	33,7	0	Mixed		Pennate unid., *Pl.sp*.
	Porsangnes	21.02.06	4,6	34,2	0	Mixed	No data	Pennate unid.
	Balsfjord	23.02.06	4	33,3	0	Mixed		Pennate unid.
	Malangen	23.02.2006	4,1	33,4	0,1	Weak stratification		Pennate unid., *T.sp.*
Lofoten	**Vestfjorden**	1-2.04.06	3,6	33,1	0.1-0.8	Weak stratification	0.6	*S.cos, C.sp.,T.sp.*
	Henningsvæstraumen	2-3.04.06	3,3	33,1	0	Mixed	0.4	*S.cos, C.sp..soc*
	Austnesfjorden	3-4.04.06	3,1	32,9	0	Mixed	0.9	*S.cos,C.soc,T.nor*
	Hadselsfjorden	05.04.2006	3	33,5	0	Weak stratification	1.6	*S.cos,, C.soc, N. sp.*
	Tysfjorden	05.04.2006	4,2	33,3	0,1	Weak stratification	4.7	Dinoflagellate
Svalbard	**NW Spitzbergen**	10-13.05.06	-0,3	34,4	0,2	Stratified	0.2	*P.p.*
	N Spitzbergen	11-12.05.06	-1,6	34,1	0,3	Stratified	0.1	*P.p.*
	NE Spitzbergen	14-15.05.06	-1,7	34,3	0,1	Weak stratification	1.5	*P.p., F. sp., N. sp.*
	White Island	13-14.05.06	-1,8	34	0,2	Weak stratification	2.8	*F.sp, N. sp.*
	Storfjord	16-17.05.06	-1.5	34.1	0.2	Weak stratification	2.3	*P.p., T. nor*

3.2 Observation of *C. socialis*

During the field investigations in Lofoten, Spitzbergen and Tromsø sound *C. socialis* and spores of *C. socialis* were found. Details are in Tables 5, 6, and 7. During the field investigation in Finnmark in February no *C. socialis* was found.

Tromsø sound

Sampling here was occasional and the time series is incomplete. Temperatures at which *C. socialis* were observed were 4.33°C - 4.43°C. Chains of *C. socialis* were observed at the end of March and in April. The highest cell count of *C. socialis* was 2,140 cells l^{-1}. It must be noted that the pre and spring bloom periods were poorly covered.

Vestfjorden

Sampling took place at the beginning of April. *C. socialis* were observed at temperatures between 3.32°C and 4.66°C. Salinities, at which *C. socialis* were observed, were between 32.26 ‰ and 33.5 ‰. Cell counts of *C. socialis* varied with the highest observed being 600,000 cells per litre. Weak stratification was observed and *Skeletonem costatum* and *Chaetoceros spp* dominated in the water column.

Henningsvæstraumen

Sampling took place at the beginning of April. Temperatures at which *C. socialis* were observed were between 3.04°C – 3.5°C. Salinities at which *C. socialis* were observed were between 33.06 ‰ and 33.15‰. *Skeletonema costatum* and *Chaetoceros* species dominated the phytoplankton. The highest recorded number of cells

of *C. socialis* was one third higher than that at the Vestfjorden station, at 900,000 cells l^{-1}.

Austnesfjorden

This station was sampled in early April. Temperatures at which *C. socialis* were observed were between 2.88°C - 3.26°C Salinities at which *C. socialis* were observed were between 33‰ and 33.03‰. The highest number of *C. socialis* cells was 247,275 l^{-1}.

Hadselsfjord

Sampling took place here at the beginning of April. Temperatures at which *C. socialis* were observed were between 3.03° C and 5.43°C Salinities at which *C. socialis* were observed were between 33.43‰ and 33.67‰.The highest count of *C. socialis* cells was 1,465,988 cells l^{-1}.

Tysfjorden

This station was sampled in early May. Temperatures at which *C. socialis* were observed were between 4.65°C and 5.50°C Salinities at which *C. socialis* were observed were between 33.45‰ and 33.74‰ The largest number of *C. socialis* cells observed here was 61,000 cells l^{-1}.

NW Spitzbergen

Sampling took place here in mid May. Temperatures at which *C. socialis* were observed were between 1.75°C and 1.01°C. Salinities at which *C. socialis* were observed were between 34.10‰ and 34.78‰. The highest cell count of *C. socialis* was 239,000 cells l^{-1}.

White island

Sampling took place in the mid of May. Temperatures at which *C. socialis* were observed were between -1,83°C and -1. 85°C Salinities at which *C. socialis* were observed were between 34.4‰ and 33.9‰ The maximum recorded numbers of *C. socialis* was 88,000 cells l^{-1}.

Table 5. Environmental parameters and *C. socialis* abundance from sampling undertaken from water removed from Tromsø sound in 2006.

Area	Date	°N	°E	Depth[m]	t[°C]	S[‰]	σ_t	Cells l^{-1} x 10^3
Tromsøysund	22.03.06	69 30	19 00	2-6 dependant upon the tide	4.33	No data	No data	0.3
Tromsøysund	27.03.06	69 30	19 00		4.24			2.1
Tromsøysund	18.04.06	69 30	19 00		4.43			0.3

Table 6. Environmental parameters and *C. socialis* abundance from sampling undertaken during cruises in Lofoten in 2006

Area	Date	°N	°E	Depth[m]	t[°C]	S[‰]	σ_t	Cells l^{-1} x 10^3
Vestfjorden	01.04.06	68.35	15.99	0	3.44	32.69	26.00	306
Vestfjorden	01.04.06	68.35	15.99	5	3.44	32.69	26.00	349
Vestfjorden	01.04.06	68.35	15.99	10	3.45	32.70	26.01	517
Vestfjorden	01.04.06	68.35	15.99	20	3.99	32.88	26.10	74
Vestfjorden	01.04.06	68.35	15.99	30	3.92	33.04	26.24	216
Vestfjorden	01.04.06	68.35	15.99	40	3.97	33.06	26.25	89
Vestfjorden	01.04.06	68.17	15.28	30	3.32	33.02	26.28	72
Vestfjorden	01.04.06	68.17	15.28	40	4.66	33.39	26.43	603
Vestfjorden	02.04.06	68	14.52	5	4.04	33.40	26.51	345
Vestfjorden	02.04.06	68	14.52	30	3.97	33.46	26.56	440
Vestfjorden	02.04.06	68	14.52	40	3.84	33.45	26.57	225
Vestfjorden	02.04.06	67.8	13.78	30	3.89	33.42	26.54	46
Vestfjorden	02.04.06	67.8	13.78	40	3.96	33.44	26.55	110
Vestfjorden	02.04.06	67.8	13.78	60	4.22	33.51	26.58	74
Vestfjorden	02.04.06	67.56	13.27	0	3.56	33.36	26.53	55
Vestfjorden	02.04.06	67.56	13.27	5	3.57	33.36	26.52	154
Vestfjorden	02.04.06	67.56	13.27	20	3.56	33.36	26.53	165
Vestfjorden	02.04.06	67.56	13.27	20	3.77	33.42	26.55	202
Henningsvæstraumen	02.04.06	68.15	14.33	0	3.04	33.09	26.33	621
Henningsvæstraumen	02.04.06	68.15	14.33	5	3.04	33.09	26.33	156
Henningsvæstraumen	02.04.06	68.15	14.33	10	3.04	33.10	26.33	206
Henningsvæstraumen	02.04.06	68.15	14.33	15	3.04	33.10	26.34	472
Henningsvæstraumen	02.04.06	68.15	14.33	20	3.04	33.10	26.34	388
Henningsvæstraumen	02.04.06	68.15	14.33	25	3.04	33.10	26.34	429
Henningsvæstraumen	02.04.06	68.15	14.33	30	3.04	33.12	26.35	290
Henningsvæstraumen	02.04.06	68.15	14.33	40	3.06	33.15	26.36	728
Henningsvæstraumen	02.04.06	68.14	14.33	20	3.44	33.11	26.33	387
Henningsvæstraumen	02.04.06	68.14	14.33	25	3.45	33.11	26.34	139
Henningsvæstraumen	02.04.06	68.14	14.33	30	3.46	33.11	26.34	224
Henningsvæstraumen	02.04.06	68.14	14.33	40	3.54	33.15	26.36	462
Henningsvæstraumen	02.04.06	68.14	14.33	0	3.42	33.10	26.33	116
Henningsvæstraumen	03.04.06	68.14	14.33	5	3.43	33.09	26.33	298
Henningsvæstraumen	03.04.06	68.14	14.33	10	3.44	33.10	26.33	488
Henningsvæstraumen	03.04.06	68.08	14.2	0	3.29	33.06	26.31	902
Henningsvæstraumen	03.04.06	68.08	14.2	5	3.30	33.06	26.31	231

Henningsvæstraumen	03.04.06	68.08	14.2	10	3.36	33.08	26.32	407
Henningsvæstraumen	03.04.06	68.08	14.2	15	3.37	33.08	26.32	572
Henningsvæstraumen	03.04.06	68.08	14.2	20	3.45	33.11	26.33	43
Henningsvæstraumen	03.04.06	68.08	14.2	25	3.52	33.13	26.34	22
Austnesfjorden	03.04.06	68.2	14.43	0	4.47	33.45	26.48	41
Austnesfjorden	03.04.06	68.2	14.43	5	3.03	32.93	26.22	164
Austnesfjorden	03.04.06	68.2	14.43	10	3.10	32.97	26.26	117
Austnesfjorden	03.04.06	68.2	14.43	20	3.23	33.03	26.29	70
Austnesfjorden	03.04.06	68.2	14.43	0	4.47	33.45	26.48	104
Austnesfjorden	03.04.06	68.2	14.43	15	3.23	33.01	26.27	247
Austnesfjorden	03.04.06	68.2	14.43	20	3.25	33.03	26.29	223
Austnesfjorden	04.04.06	68.2	14.43	0	3.01	32.8818	26.19	42
Austnesfjorden	04.04.06	68.2	14.43	10	3.18	32.98	26.26	56
Hadselsfjorden	05.04.06	68.3	15.03	0	3.16	33.43	26.62	495
Hadselsfjorden	05.04.06	68.3	15.03	5	3.15	33.43	26.62	140
Hadselsfjorden	05.04.06	68.3	15.03	10	3.11	33.43	26.62	223
Hadselsfjorden	05.04.06	68.3	15.03	20	3.49	33.55	26.68	1059
Hadselsfjorden	05.04.06	68.28	14.47	0	3.05	33.50	26.68	906
Hadselsfjorden	05.04.06	68.28	14.47	5	3.04	33.50	26.68	1465
Hadselsfjorden	05.04.06	68.28	14.47	10	3.06	33.50	26.68	429
Hadselsfjorden	05.04.06	68.28	14.47	20	3.19	33.54	26.70	889
Hadselsfjorden	05.04.06	68.28	14.47	30	3.42	33.60	26.73	553
Hadselsfjorden	05.04.06	68.28	14.47	40	3.73	3.67	26.76	64
Hadselsfjorden	05.04.06	68.28	14.47	120	5.43	34.15	2.96	35
Tysfjorden	05.04.06	67.53	23.26	40	5.49	33.74	26.62	8
Tysfjorden	06.04.06	67.51	16.25	0	4.65	33.45	26.48	61
Tysfjorden	06.04.06	67.53	16.26	5	4.65	33.45	26.48	12

Table 7. Environmental parameters and *C. socialis* abundance from sampling undertaken in the waters around Svalbard in 2006

Area	Date	°N	°E	Depth[m]	t[°C]	S [‰]	σ_t	Cells l^{-1} x 10^3
NW Spitzbergen	12.05.06	81.09	18.47	0	-1.66	34.10	27.45	239
NW Spitzbergen	12.05.06	81.09	18.47	1	-1.71	34.10	27.45	23
NW Spitzbergen	12.05.06	81.09	18.47	10	0.96	34.76	27.86	41
NW Spitzbergen	12.05.06	81.09	18.47	30	1.01	34.78	27.87	71
NW Spitzbergen	13.05.06	80.41	29.13	2	-1.75	34.11	27.45	11
NW Spitzbergen	13.05.06	80.41	29.13	30	-1.45	34.22	27.54	7
White Island	13.05.06	80.53	29.54	5	-1.83	34.03	27.40	49
White Island	13.05.06	80.53	29.54	30	-1.83	34.04	27.40	27
White Island	14.05.06	80.54	28.23	1	-1.85	33.99	27.37	71
White Island	14.05.06	80.54	28.23	2	-1.84	33.97	27.34	27
White Island	14.05.06	80.51	29.44	1	-1.86	34.18	27.52	88
White Island	14.05.06	80.51	29.44	2	-1.86	34.00	27.37	11
NE Spitzbergen	14.05.06	80.01	28.56	20	-1.86	34.18	27.52	170
NE Spitzbergen	14.05.06	80.01	28.56	30	-1.86	34.19	27.52	1
NE Spitzbergen	14.05.06	80.01	28.56	50	-1.86	34.19	27.52	8
NE Spitzbergen	15.05.06	79.04	33.2	30	-1.73	34.16	27.50	164
NE Spitzbergen	15.05.06	78.17	31.54	0	-1.57	34.3	2.61	176
NE Spitzbergen	15.05.06	78.17	31.54	20	-1.58	34.30	27.61	117
NE Spitzbergen	15.05.06	78.17	31.54	30	-1.55	34.21	27.53	33
NE Spitzbergen	15.05.06	78.17	31.54	50	-1.56	34.21	27.53	27
NE Spitzbergen	15.05.06	76.33	27.24	0	-1.22	34.42	27.69	253
NE Spitzbergen	15.05.06	76.33	27.24	10	-1.21	34.42	27.69	22
NE Spitzbergen	15.05.06	76.33	27.24	30	-1.21	34.41	27.69	2

3.3 Distribution of *Chaetoceros socialis* in Northern Norway and the Barents Sea (from published data).

The table below summarises the ranges at which *C. socialis* were observed in the examined literature. *C. socialis* has been observed in the area from Northern Norway to the Arctic, from March to November, at a range of temperatures from -1.86°C to +13.6°C.

Table 8. Ranges found from the literature survey of all data on C. socialis in Northern Norway, the Arctic and the Barents Sea. (Eilertsen et al 1981, Throndsen and Heimdal 1976, Heimdal 1974, Eilertsen et al 1989, Husby,2002, Evensen 1994, Lundjefelt 2001, Gaarder 1932, Ruud-Føyn 1929, Bech 1982, unknown Finnmark data 2002-2004, Donnelly 2006.)

Factor	Range
Years	1923 → 2006
Months observed	March → November
Degrees N	67.48 → 83.45
Degrees E	13.3 → 34.46
Depths [m]	0 → deepest sampling
Temperature [˚C]	-1.86 → +13.6
Salinity [‰]	22.5 → 33.5
σ_t	16.939 → 26.591
Cells l^{-1}	20 → 56907752

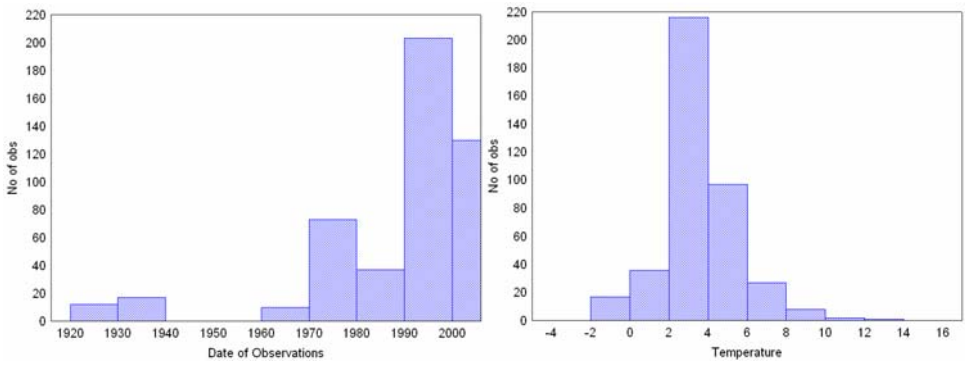


Figure 5 and 6. The distribution by year of observation of *C. socialis* and the distribution of temperatures at which *C. socialis* was observed. (Eilertsen et al 1981, Throndsen and Heimdal 1976, Heimdal 1974, Eilertsen et al 1989, Husby 2002, Evensen 1994, Lundjefelt 2001, Gaarder 1932, Ruud-Føyn 1929, Bech 1982, unknown Finnmark data 2002-2004, Donnelly 2006.)

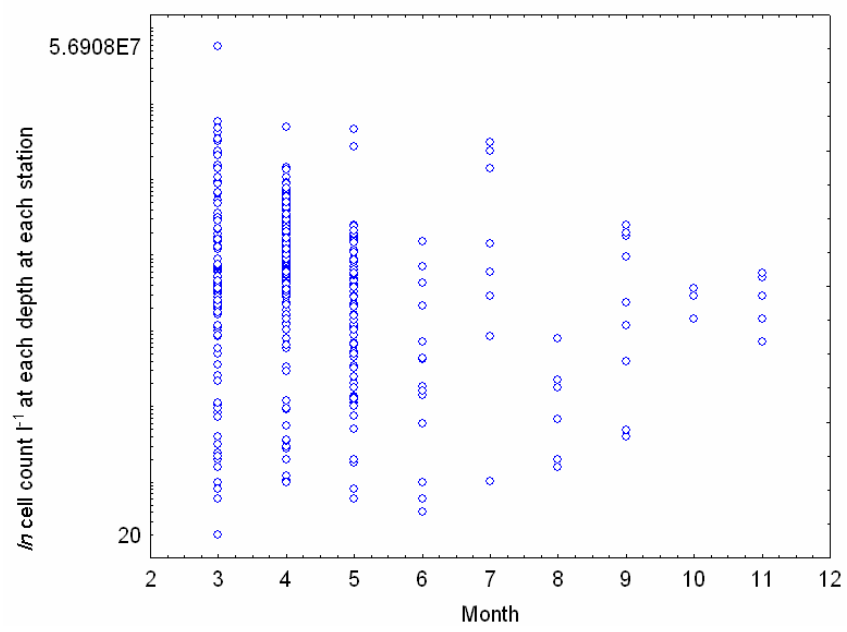


Figure 7. Natural logarithm numbers of cells observed versus month observed. (Eilertsen et al 1981, Throndsen and Heimdal 1976, Heimdal 1974, Eilertsen et al 1989, Husby 2002, Evensen 1994, Lundjefelt 2001, Gaarder 1932, Ruud-Føyn 1929, Bech 1982, unknown Finnmark data 2002-2004, Donnelly 2006.)

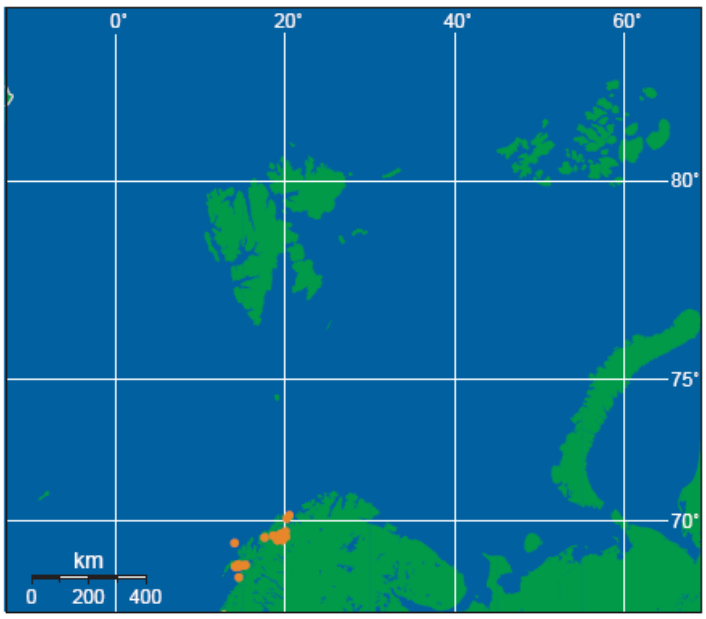


Figure 8. Observations of *C. socialis* in March. (Eilertsen et al 1981, Throndsen and Heimdal, 1976, Heimdal, 1974, Eilertsen et al 1989, Husby, 2002, Evensen 1994, Lundjefelt 2001, Gaarder 1932, Ruud-Føyn 1929, Bech 1982, unknown Finnmark data 2002-2004, Donnelly 2006.)

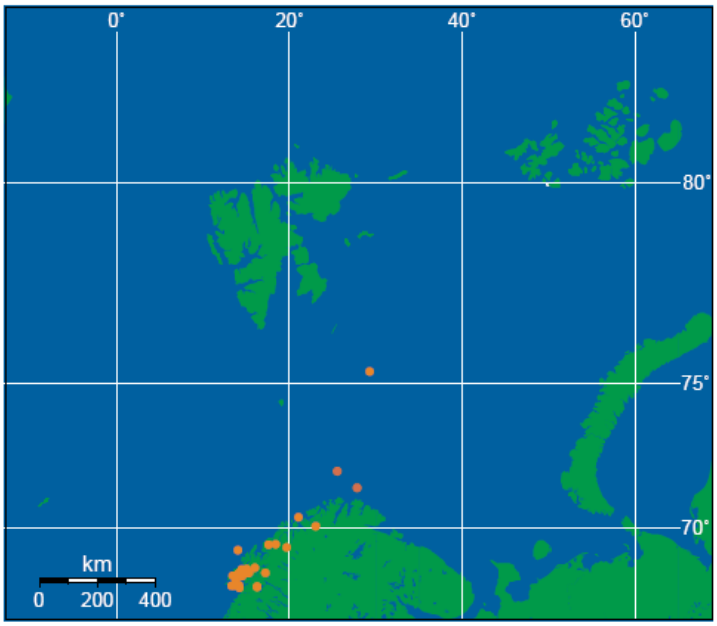


Figure 9. Observations of *C. socialis* in April. (Eilertsen et al 1981, Throndsen and Heimdal 1976, Heimdal, 1974, Eilertsen et al 1989, Husby 2002, Evensen 1994, Lundjefelt 2001, Gaarder 1932, Ruud-Føyn 1929, Bech 1982, unknown Finnmark data 2002-2004, Donnelly 2006.)

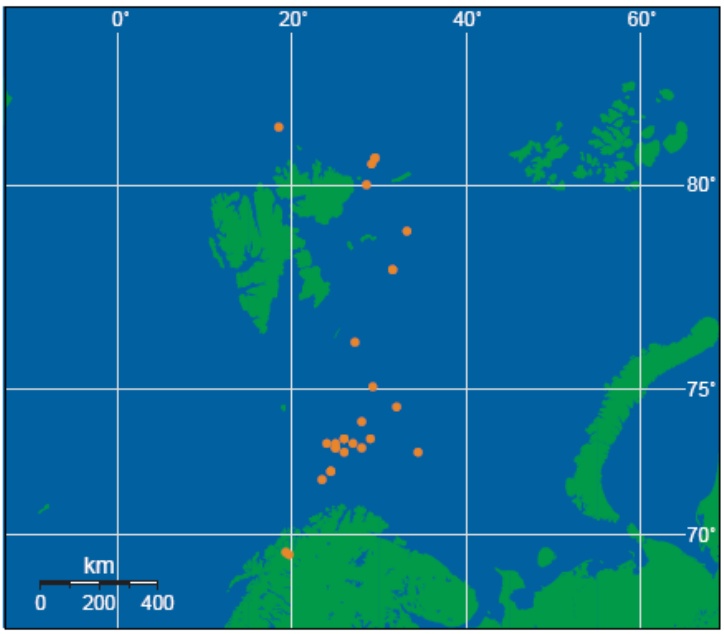


Figure 10. Observations of *C. socialis* in May. (Eilertsen et al 1981, Throndsen and Heimdal 1976, Heimdal, 1974, Eilertsen et al 1989, Husby, 2002, Evensen 1994, Lundjefelt 2001, Gaarder 1932, Ruud-Føyn 1929, Bech 1982, unknown Finnmark data 2002-2004, Donnelly 2006.)

Observations of *C. socialis* were also recorded in June, July and November. (Eilertsen et al 1981, Throndsen and Heimdal 1976, Heimdal 1974, Eilertsen et al 1989, Husby, 2002, Evensen 1994, Lundjefelt 2001, Gaarder 1932, Ruud-Føyn 1929, Bech 1982, unknown Finnmark data 2002-2004, Donnelly 2006.)

3.4 Morphology

Below, in Fig 11, is a reconstruction i.e. a scaled diagrammatic representation of the dimensions *C. socialis* cells from the sizes recorded in the experiments. It is possible to see that the cells at 2°C are differently shaped to those at 7°C. These drawings represent the average cells found in the cultures investigated. They do not represent every cell seen in the culture. It was possible to find a 'type 2°C cell' in 7°C culture and vice versa.

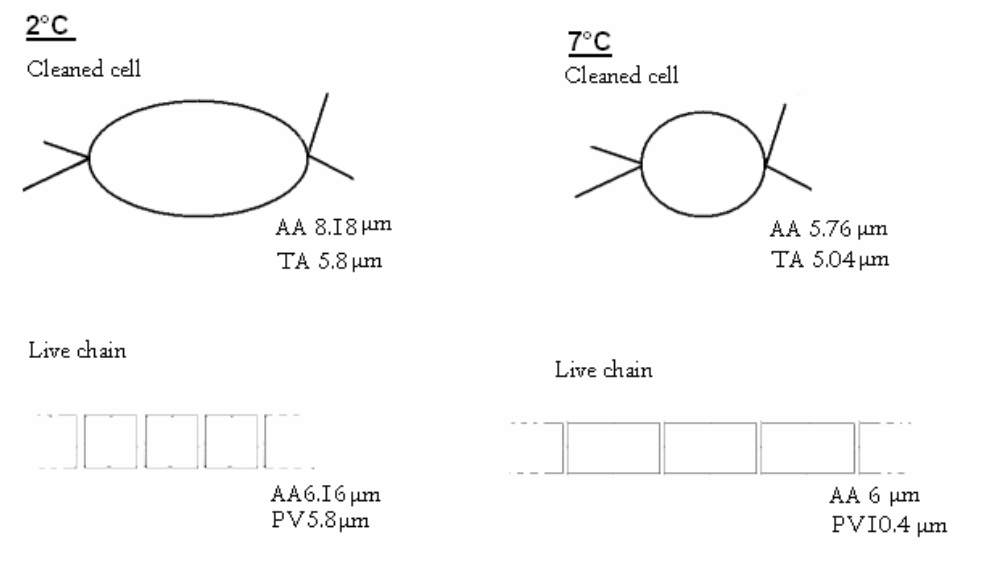


Figure 11. An average cell in scale drawings at 2°C and 7°C reconstructed from experiments 2, 3 and 4. Top figures are a valve view and below is a girdle view. AA=apical axis, TA = transapical axis and PV= Pervalvar axis.

Table 9. Volumes and surface area of the 'average' cell at 7°C and 2°C from experiments 2, 3 and 4. Volumes calculated according to Hillebrand et al (1999) using AA and TA of cleaned cells and PV of live cells (in brackets using live AA).

Temperature °C	Cell Volume µm^3	Cell surface area µm^2	Ratio V/SA
2	216 (162)	201	1.075 (0.874)
7	237 (247)	222	1.068 (1.11)

Figure 12 shows photographs of a representative selection of cleaned cells. Most of the cleaned cells demonstrated non *C. socialis* morphologies regarding setae position.

Figure 12. Photographs taken during experiment 3.

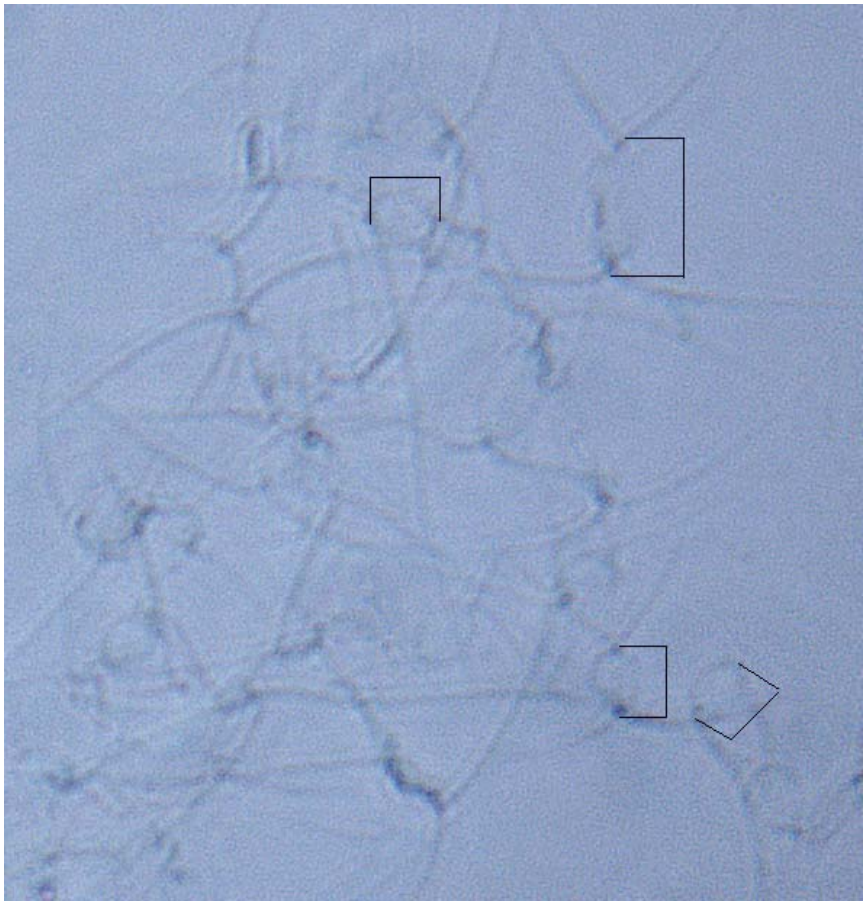


Figure 13. Photographs taken during experiment 3. The lines in this photograph indicate the apical axis of 4 cells within this one culture from 7°C

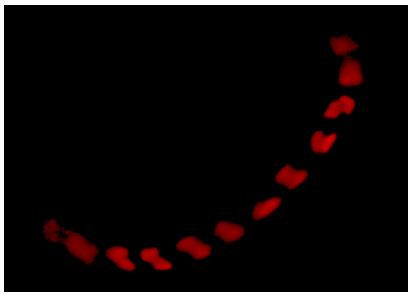


Figure 14. Fluorescence photograph taken during experiment 4 shows the chromatophores of these cells in two parts

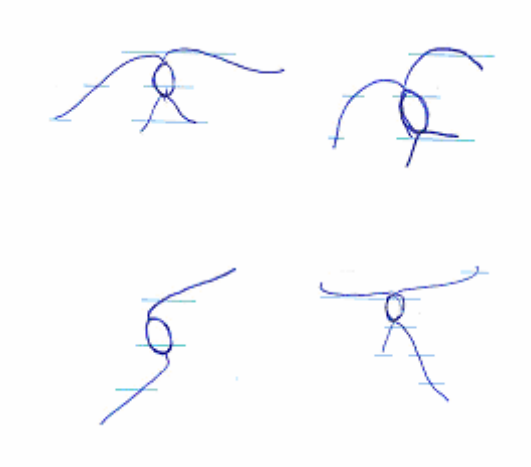


Figure 15. Observational drawings of *C. socialis* made by the author while examining the cleaned cells from experiments 2.

The photographs seen in figs 16 and 17 below were taken during experiment 4. They clearly show a similar morphology to those presented as reconstructed cells in figure 6.

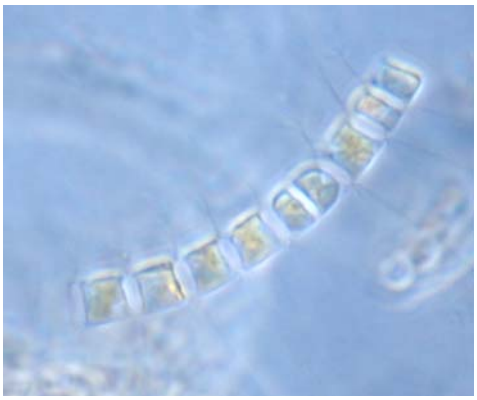


Figure 16. Large cells from exp.3 at 2°C

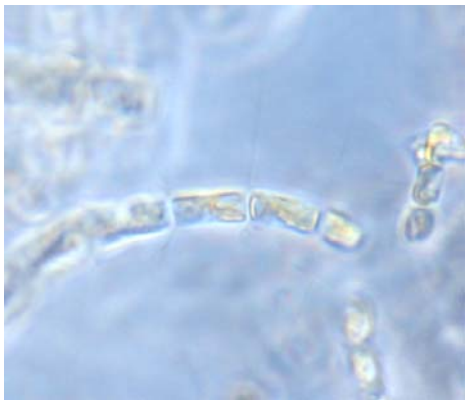


Figure 17. Small cells exp. 3 at 7°C

Figs 16 and 17 were taken at the same magnifications and same scale and are presented to demonstrate the different relative morphologies of 'small' and 'large' cells.

Figure 18. Photograph taken at station NW Svalbard st179 at 40 times magnification showing slightly more square shaped cells than in experiments undertaken at 7°C

In this section of the results the differences in morphology have been demonstrated. The cells grown at 2°C appear to be flatter and squarer than those grown at 7°C. This would also appear to be true of the cells observed in the field, with those at the lower temperatures also being flatter and squarer than those sampled at higher temperatures.

Individual observations made from the cleaned monocultures in the laboratory can be seen in fig 15. Different setae patterns to those described by Tomas 1997 fig 2 were seen. Very few appeared to have the single, longer setae which is thought to be characteristic and few were bending backwards. see fig 12 and 13. Whether or not this is just an effect of the cleaning process is unknown.

Examination of cells in the live cultures, with fluorescence, showed that the cells appear to have one chromatophore. (see fig 14)

(Gran 1879 and Cupp 1943). This chromatophore frequently appeared to be contracted in the centre.

Variation in cell size was observed during a series of experiments conducted in the laboratory to examine the size of the cells of *C. socialis.* Apical, transapical and pervalvar axis were examined. The results of these investigations are presented in table 7 and 8 and Figures 16 -19. Cells cultured from 2°C consistently showed a greater apical axis size than those at 7°C. These differences were shown to be significant according to Students t-test (see tab10.)

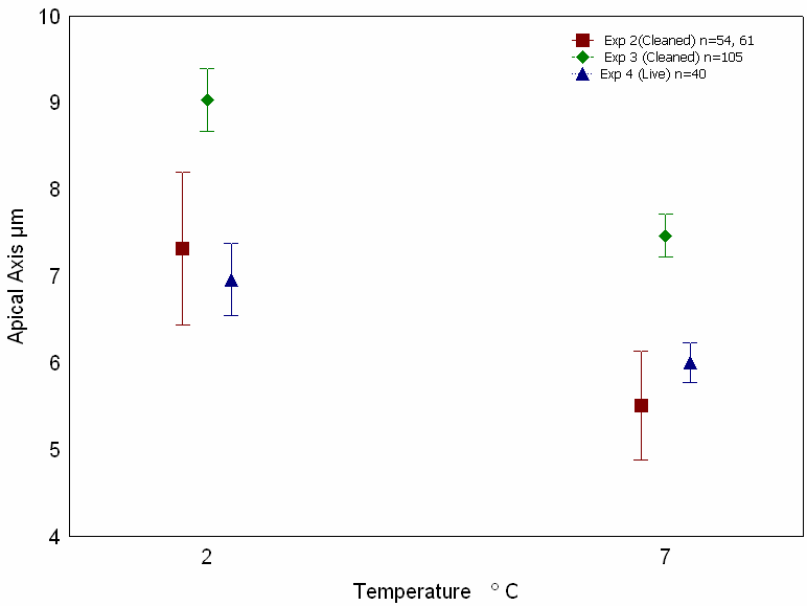


Figure 19. Apical Axis sizes.

Pervalvar axis are seen to be larger at 7°C than at 2°C however the difference is not significant. This conclusion is drawn on one set of results only. The range of transapical and apical axis is greater in the cultures grown at 2°C than at 7°C.

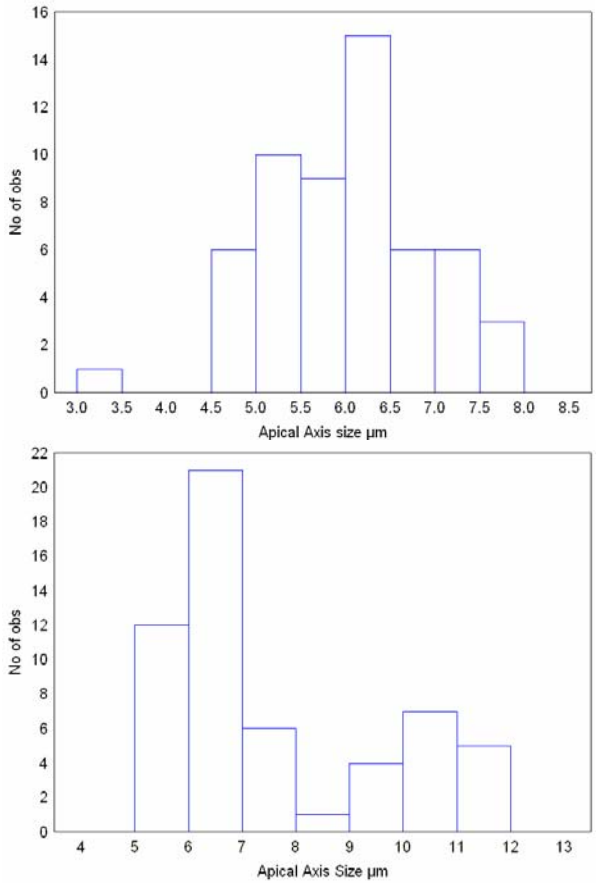
It was observed throughout experiments 2 - 4 that apical and transapical axis sizes showed a significant difference between *C.socialis* grown at 2°C and that grown at 7°C.

Table 10. Mean apical axis sizes and standard deviation. Students t-test P<0.05 is significant. All experiments were conducted using cultures which stem from 'large' cells. n= 40 (except pervalvar n= 42)

Temperature	**2°C** (+/-Sd)	**7°C** (+/-Sd)	**P value**
Experiment			**2 v's 7**
2.Cleaned apical axis size µm	7.32 +/-3.22	5.51 +/- 2.24	0.036
3. Cleaned apical axis size µm.	9.04 +/-1.89	6 +/-1.27	0.000074
3. Cleaned transapical axis size µm.	5.80 +/-1.11	5.04+/-0.90	0.039
4. Live apical axis size µm	6.96 +/-1.29	6.00 +/-0.72	0.00045
4. Live pervalvar axis size µm	8.67 +/-1.77	10.40 +/-1.63	0.13

Table 11. Mean apical and pervalvar axis sizes for examination of 'large' and 'small' cultures at both 2° C and 7°C n=40 examined during experiment 4.

	Apical Axis			**Pervalvar Axis**		
	Small	**Large**	**P value Small v's Large**	**Small**	**Large**	**P value Small v's Large**
2°C	5.58+/-0.77	6.96 +/- 1.29	0.0016	9.36 +/-1.54	8.67 +/-1.77	0.25
7°C	5.58 +/-0.66	6.00 +/- 0.72	0.57	11.04 +/- 1.61	10.40 +/- 1.63	0.55



Figures 20 and 21. Show distribution of apical axis size at stations 204 Storfjorden and 179 NW Spitzbergen respectively

There were significant differences in size between stations 204 Storfjorden and 179 NW Spitzbergen It can be seen by comparing tab. 12 and fig. 22 that the station with colder water temperature had the larger apical and pervalvar axis sizes. The size pattern shows the same trend as in the laboratory experiments.

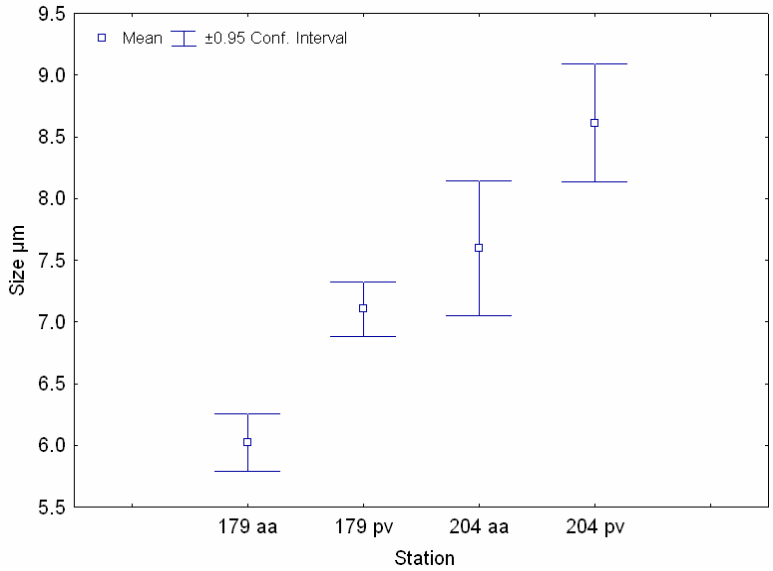


Figure 22. Comparison of apical= aa, n=56 and pervalvar=pv, n=35, 47, axis sizes from field data.

Table 12. Average temperatures in the water columns at stations 204 Storfjorden and 179 NW Spitzbergen.

Station number	**179**	**204**
Average temperature °C	0.4829	-1.4213

3.5 Physiology

3.5.1 Growth rates

The growth rates of 4 monocultures of *C. socialis* show that in experiment 1 the highest growth rate was observed at 7°C. The standard deviations suggest that there is no clear difference between the results.

Table 13. Results of growth rate experiment 1.

Temperature (°C)	Irradiance (µmol quanta $m^{-2}s^{-1}$)	Growth rate (doublings^{-d}) (SD)
2	50	0,3 +/- 0,4
2	10	-0,05 +/- 0,4
7	50	0,5 +/- 0,4
7	10	0,4 +/- 0,1

3.5.2 Fluorescence

A difference between the photographs taken at 2°C and 7°C was observed. These differences were not statistically significant. The details of the pictures are as follows; 2078x1583 pixels and pixel depth of 24/16 million each photograph was 9366 k of RAM. These pictures can be seen on figure 24.-

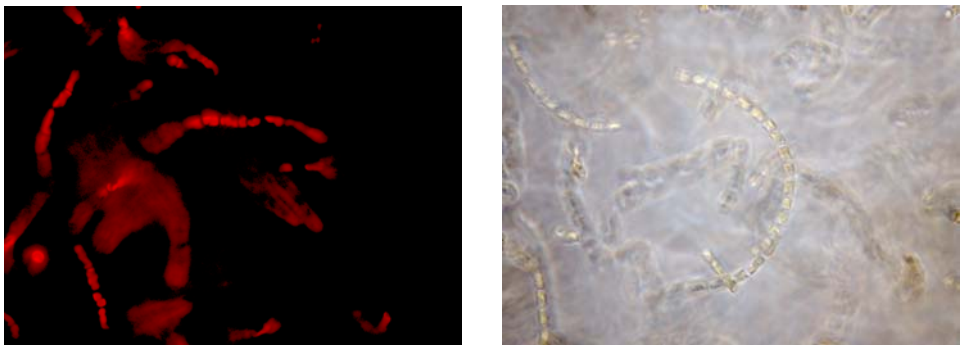


Figure 24. Examples: the photograph on the left was used to obtain the number of unique colours using fluorescence and the RGB numbers of individual cells. The photograph on the right was used for measurements of the number of unique colours in photograph 'live'.

The photographic data shows that no differences are significant. In each case, WPF (whole picture fluorescence), WPL (whole picture live) and individual cells at 7°C contain more colours than those taken at 2°C.

Table 14. Data from measurement of the number of unique colours in one whole picture as measured by paint shop-pro software. Measurements taken during experiment 4.

Number of unique colours in picture.	**Mean (+/-Sd)**	**Minimum**	**Maximum**	**P values 2°C v's 7°C**	**n=**
2°C Fluorescence	105.14 +/-24.14	62	134	0.3	7
7°C Fluorescence	106 +/-37.81	54	144		7
2°C live	130027 +/-9215.18	117984	143847		5
7°C live	160157.7+/-6337.91	141778	173031	0.3	3

Table 15. Data from the RGB number of single cells as measure by paint shop pro. Since pictures were monochromatic only red was observed. R= red G= green B= blue Measurements taken during experiment 34.

Highest values recorded for individual cells under fluorecence	**Mean R(+/-Sd)**	**G**	**B**	n=
2°C Fluorescence	184.11 +/-25.93	0	0	34
7°C Fluorescence	198.15 +/-34.12	0	0	34

4. DISCUSSION

In this thesis the centric diatom species *Chaetoceros socialis* has been examined with regard to distribution, morphology and physiology in both field and laboratory settings. The study concentrated on specimens both isolated from and sampled in Northern Norway, the Barents Sea and Arctic Regions. The focus was to find evidence of any morphological or physiological heterogeneity which may indicate adaptive strategies to the environment which may then lead to the identification of clonal difference in laboratory work. This line of investigation was carried out following formal and informal observations of large morphological variations and a broad distribution (Eilertsen and Wyatt 2000)

Phenotypic traits are characteristics which affect the way an organism looks, the way it behaves, and/or its chemical composition. The underlying mechanisms resulting in phenotypic traits are difficult to understand, this leads to difficulties in defining a species from phenotypic traits alone (Mann 1999, Furnas 1978, Wood and Leatham 1992, Lehman 1967; see also, May and Beverten 1990, Gavrilets 2003, Palumbi 1992). The traditional method of identifying species solely from morphological characteristics is now a debateable practise (e.g. Mann 1999). Identification of species by physiology alone is also difficult. An area where neither physiology nor morphology is sufficient to identify species is that of bacteria. Bacteria are now mostly defined by 'ecotypes' (Cohan 2002), i.e. populations which occur in the same ecological niche and can be identified by molecular techniques. Data from many comparative studies of algal physiology have not been able to prove any species level of difference in the physiological traits (Wood and Leatham 1992).

Identification of the phenotypic or morphological traits of a species normally takes place using only a single clonal isolate (Wood

and Leatham 1992). There are numerous examples of phytoplankton species which exhibit clonal variation in physiological and biochemical traits, for instance 34 different species can be found listed in one paper alone with each species demonstrating clonal variation (Wood and Leatham 1992) thus demonstrating that clonal variation is already a well known fact. The characteristics observed included, salinity dependant growth rate, temperature dependant growth rate, toxicity, vitamin requirement and heterotrophic capability, nitrogen metabolism, silicon metabolism, zinc dependant growth rate, pH dependant growth rate, sensitivity to pollutants, serologic affinity and chemical composition, carbon portioning and luminescence. The variation in traits within a species even seems to be detectable by copepods when choosing which phytoplankton to feed upon. Copepods have demonstrated greater variation in which food source they prefer within clones of the same species of phytoplankton than between different species (Long and Hay 2006.) *Chaetoceros socialis* has undergone very little investigation in respect of such of clonal variances.

4.1 Distribution

As Semina (1979) and Fryxell (1989) observed, the geography of diatoms is an 'urgent problem.' The distribution and therefore adaptability of individual species is relevant to many of the large scientific questions arising in recent times, not least the much discussed 'problem' of climate change.

C. socialis was, for this thesis, studied in the literature and in field observations at different localities geographically and environmentally far apart. These localities ranged from 67.48 to 83.45 degrees of latitude North and from 13.3 to 34.46 degrees of latitude East. *C. socialis* was observed during my field sampling at temperatures ranging from -1.86°C to +5.49°C (see Tab.4, 5, 6 and

8). According to the literature survey carried out the range of temperatures at which *C. socialis* has been found is between -1.86°C to +13.6°C (see Tab. 8 and Fig. 6). Fig. 6 also shows the distribution of temperatures at which *C. socialis* was found during field work. A normal bell shaped distribution of the data is displayed, with a peak between 2°C and 4°C. The temperature distribution shows that there is continuous presence of *C. socialis* between these temperature extremes. It is also necessary to note that the temperature pattern is a function of the sampling areas. Therefore it is important to take into account that observations were not made at every possible temperature. The data used in this literature investigation is taken only from Northern Norway and Norwegian Arctic Seas and from the following sources: Eilertsen et al 1981, Throndsen and Heimdal 1976, Heimdal 1974, Eilertsen et al 1989, Huseby 2002, Evensen 1994, Lundjefelt 2001, Gaarder 1932, Ruud-Føyn 1929, Bech 1982, unknown Finnmark data 2002-2004, Donnelly 2006. *C. socialis* is also reported from many other oceanic areas, including the Mediterranean (Eilertsen and Wyatt 2000). These observations suggests that the group of organisms "embraced" by the term *C. socialis* has an ability to cope with a great variety of temperatures, including those below freezing, which will influence their biochemistry with regards to enzyme function and 'antifreeze' elements.

At all locations where *C. socialis* cells have been identified all been found to have the same supramorphology with only variations in size being noted. (Pers. Comm. HC Eilertsen)

During the fieldwork carried out around Svalbard and in the Barents Sea it was possible to observe different stages of a spring bloom as sampling progressed in time (14-17 May 2006) and progressed in space (further east at the stations, NE Spitzbergen, White island and Storfjorden). At stations sampled in N Spitzbergen and NW Spitzbergen, the presence of *P pouchetii,* together with

scarce amounts of larger centric diatoms, indicated a post bloom situation. At stations along NE Spitzbergen, White Island and Storfjorden, species dominance had changed to *Flagaliriopsis sp* and *Nitschia sp* indicating an early to mid bloom stage. The phytoplankton seen in the counting samples during the cruises in Troms and Finnmark indicate a well mixed post winter situation, since pennates are characteristic of benthic algae (author's own observations). The most abundant phytoplankton species observed at NE Spitzbergen was *Skeletonmea Costatum* together with a high abundance of *Chaetoceros spp*. These are species typical of a bloom situation.

In the literature studied *C. socialis* was found at a range of salinities from 32.6917 ‰ to 34.7764 ‰. This indicates that *C. socialis* seems able to tolerate a range of salinities including the less saline water at the ice edge. In the fjords of Sweden it has been seen that halotolerant species, such as *C. socialis* and *T.minima* have a great advantage especially in areas with varying salinity. (McQuoid 2005).

Being found within these ranges of temperature and salinity suggests that *C. socialis* is phenotypically plastic with regard to temperature and salinity, both of which are thought to be influential on enzyme kinetics and other cellular processes. It must be noted that this "species" can thrive i.e. achieve large numbers across a large temperature range. Tomas (1997) refers to *C. socialis* as probably cosmopolitan and very important in the plankton close to the ice in the northern cold water region. Other authors however have noted that *C. socialis,* whilst being a neritic species typically forming resting spores which are stirred up from shallow depths into surface waters during the spring. It is also known that deepwater plankters have resting spores (Smetacek 1985) these can seed the

upper layer of the water column from the pycnoline instead of from the sediments. *C. socialis* must do both! (Booth 2002).

Through much of what is written here, there is the possibility that *C. socialis* populations were episodic and not continuous (Booth et al 2002). It may be possible to think that these episodes are made up of different groups of cells from the population.

Inspection of the data regarding distribution in time and space (see Figs. 8, 9 and 10) reveals that peak abundances *of C. socialis* during spring moves in a northerly direction from March to June, coinciding roughly with the conclusions made by Baarud & Nygaard 1978. This coincides also in the North with both the retreating ice (see Fig 4) as well as the increasing day length and corresponding increase in light intensity (that continues until summer solstice).

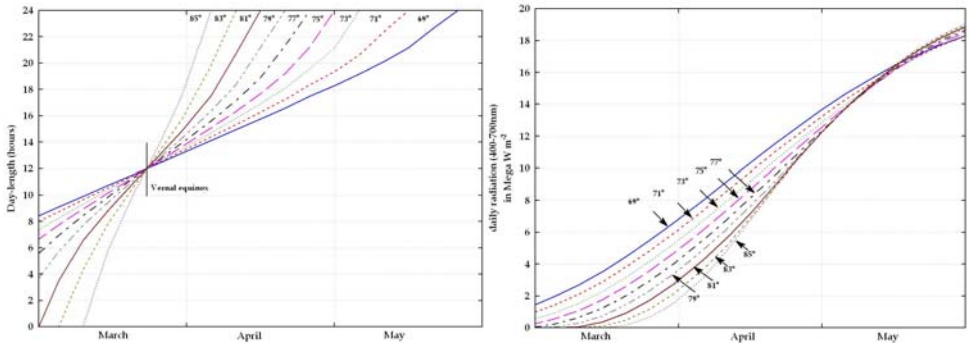


Figure 25. Length of days March – May at latitudes 69 – 85°N and longitude 20°E as computed from the algorithms referred to in Material and methods. Figure 26. Modeled daily (PAR) radiation at latitudes 69 – 85°N and longitude 20°E (see Material and Methods).

C. socialis has also, peculiarly enough, been observed during November in Finnmark at densities of 14,000 cells l^{-1}(see appendix Table1). There was negligible light during this period and sea temperatures of +7.22°C. This perhaps suggests that the cells here had exhibited a phenotypic adaptation to low light levels, or were germinating “early” due to some ‘fault or difference’ in their timing mechanism. Previous experiments carried out by Lundjefelt (2001) have shown that *C. socialis* seems to have some means of identifying the ‘time’ of year. These experiments involved subjecting

homogenous sediment to constant light and temperature regimes for a year and observing the change in species composition of phytoplankton over this time. This experiment resulted in greater abundances of *C. socialis* in spring i.e. March, April and May. This finding is partly supported by fig. 7 where it is possible to see that the greatest numbers of *C. socialis* were observed during March, April and May. During the spring bloom *Chaetoceros* species follows the smaller faster growing species such as *Skeletonema sp.* (Shevchenko et al 2004, Margalef 1967, Guillard et al 1977, Smayda 1980).

The most surprising observation in my fieldwork was the almost complete absence of *C. socialis* in the samples taken in Tromsø sound from March to May (see Tab. 5). This can possibly be explained by the lack of sampling during the pre and bloom periods of the year.

There is always a certain level of inaccuracy involved with sampling using the sedimentation method, because of the extrapolation from a very small sample. However Hasle (1954) concluded that one sample at each station or depth is satisfactory but that counting results should be treated critically, taking into account the possible uneven distribution in nature and the error in the sedimentation method (Hasle 1954).

Within one oceanographic area, abiotic conditions can vary greatly. In Altafjord the spring sea temperature may vary by as much as 4°C degrees between years (Eilertsen and Skarðhamar 2006). If species such as *C. socialis* can make physiological or morphological changes, what controls these changes? Or is it possibly a species which is capable of 'choosing' which genes to express in a specific environment? Are the changes completely random and the successful mutants making up the large majority of a bloom? Is it instant speciation?

Gallagher (1980, 1982) noted that changes in environment can lead to change in the genetic composition of a phytoplankton population. These changes in environment which affect the genetic composition will be expressed as a change in phenotypic composition of the population. The phenotypic composition was investigated here by examining morphology and physiology.

4.2 Morphology

There has been little data on the morphometrics of phytoplankton gathered on any populations (Mann 1999) and none seems to have been gathered specifically on *C. socialis*. There are few published studies of phytoplankton which involve statistical treatment of morphological data and images analysis. In the few cases I have been able to locate where morphometric measurements have been made before, there seems to be little agreement in the measurements made or the methodology used. Baumann et al (1994) and Karentz et al (1991) made measurements of *C. socialis.* Baumann finds cells to have a volume of 92μm^3 and a surface area of 113μm^2 while Karentz finds cells to have a volume of 783μm^3 and a surface area of 514 μm^2 These are very different from each other and also very different from the measurements made for this investigation. (see table 9). There are numerous explanations for this one of which is different methodologys in mathematical formulae used. For example Hillebrand (1999) notes that the formulae used to calculate the cell size in Baumann et al is strongly influenced by regions from which the samples were taken. Another explanation is that indeed the cells vary greatly in size.

Margelef (1958) concluded that the larger phytoplankton species follow the smaller phytoplankton species during a bloom scenario. Semina (1972) suggests that the mean cell size of a phytoplankton population is a result of 1) direction and velocity of

vertical water movement, 2) value of density gradient in the main pycnocline and 3) phosphate concentration. If these hydro-mechanical factors can have an effect on which species occur and affect interspecies relations perhaps they can also affect intraspecies relations, i.e. relations between cells of the same species. Much of this work on the physiological differences has been carried out in order to shed light upon the difference between species. Many of these authors overlook the fact that nutrient uptake varied considerably between clones particularly those isolated from different environments (Guillard et al 1973, Hecky and Kilham 1974).

C. socialis has already been identified as having several unique morphological features that allow it to maintain its position in the water column either 'en masse' or by seed 'en masse.' Small cells of *C.socialis* also adapt well for uptake of nutrients at low concentrations (Booth et al 2002). Furthermore it has been reported to have a long specialised setae which allows the species to form clumps in the water (Cupp 1943).

Following the measurement of the apical and transapical axis, a clear difference in the axis length can be seen in Fig. 19, tab. 10. The difference between *C. socialis* cultured at 2°C and *C. socialis* cultured at 7°C was significant (p=0.036, 0.000074, 0.039 and 0.00045). Due to the method and outcome of the cleaning process, it was only possible to measure the pervalvar axis in the final investigation in the laboratory. Table 11 shows that the pervalvar axis was longer at 7°C than at 2°C, the difference however was not significant (P = 0.13) This lack of significant difference in length in the laboratory could simply be due to the relatively small sample size. In the field data the pervalvar axis was significantly longer at station 204 than at station 179 (Fig 22).

Station 204 had colder water (-1.4213°C), than station 179 (0.4829°C , Tab.12). Pervalvar axis size also increases during the

cell division cycle which can lead to a great degree of short term variability (Furnas 1978). Therefore for the analysis of the morphometrics I will concentrate on the apical and transapical axis.

From the measurements made in experiments 2 - 4 I have constructed a diagram of the average cell which one might find in the cultures grown at 2°C and 7°C (fig. 11). It is important to note that that I have constructed a hypothetical cell using a combination of live and cleaned cell sizes which certainly has limitations; this said cells from both temperatures were treated identically when making calculations. The volumes and surface areas were calculated using formulae for cylinders on elliptical bases. Varying cell sizes of *C. socialis* can be seen in a single culture (fig 13). Variations in cell size such as those seen in figure 13 were apparent in all cultures suggesting that transition phases were observed in both cultures. The average cell, constructed by me, simply represents the dominant morphotype. It can be seen in Figure 11 that cells at 7°C create longer, rounded cells in chains, whereas those at 2°C create shorter, squarer cells in chains. The surface area to volume ratio is almost identical in both cases (Tab.9). This then raises the following questions: Why do the cells create these different shapes? What advantage, if any, is this to *C. socialis*? Is it related to the density of the culture? Is it related to some other factor in the water, not nutritional, because this was held constant, but perhaps a form of chemical stimuli which is in the water used for the experiments and which is not removed by filtering or autoclaving? Are the cells in the cultures themselves giving off chemical signals which perhaps control which cells double quickly and which do not? The diatom *C. socialis* has been demonstrated to release extracellular substances, in particular glycolic acid, this release has been judged to be passive rather than an active form of transport (Walker 1974). This

morphological feature could be related to the physiology of the individual cells.

Cultures which are started from a single cell of *C. socialis* do not maintain the same size as the initial cell. This can be seen from the experiments carried out in the laboratory with the 'large and small' cell cultures and illustrated in table 11. The longer in time these cultures are maintained the greater the mix of cell sizes (Pers comm. HC Eilertsen).

It was found by Montagnes and Franklin (2001) that there is a decrease in cell size which corresponds to an increase in temperature and which is in agreement with the results I found for *C. socialis*. The changes in cell size observed **may** also simply be an effect of the reproductive cycle. Cell size variation may also be due to auxospore formation after many asexual divisions have decreased the size of the cell (Gallagher 1983). With regard to the results obtained here I am unable to rule out that the some of the cleaned cells were in fact cleaned auxospores. This allows the cell to gain a short-term competitive advantage, by bypassing sexual reproduction. Jewson (1992) has suggested various size selective pressures, such as wider cells may decrease in diameter with each division. This decrease may be further affected by undesirable environmental conditions such as temperature changes and silicon availability. Montagnes' and Franklin's 2001 study however dealt with temperatures above 8°C, so it is possible that other effects are observed below these temperatures, such as the temperatures used in this experiment (2°C to 7°C). Furnas (1978) found that the dependent trends of division rate in individual clones changed with temperature in a complex fashion**.** The study from which this conclusion was drawn was only taken down to temperatures of 15°C.

Many species of diatoms have been shown to have a set of demes which may or may not be continuous (Mann 1999). The

observations made of the different cultures studied in this thesis may be considered demes of *C. socialis.* During the lifetime of a culture the average size of cells is reported to decrease (Cerino et al 2005, Mann 1988).The cells become smaller until they reach their lowest size limit where sexual reproduction is then reported to take place in order to restore cell size. Such events may take place at intervals of between 2 - 40 years (Cerino et al 2005). Since all cultures used in this thesis are the same age and began from a single clone the explanation of sexual reproduction, as explained here, causing these changes seems unlikely. Cells of *C. socialis* are always found in chains containing either large or small cells (Fig 16, Fig 17). This makes me wonder if in fact sexual reproduction happens more often than previously thought? Or is there something not yet investigated connected to the genes or the expression of the genes in *C. socialis* cells?

Data gathered both in the field and lab, suggests that *C. socialis* cells adapt different morphologies at lower temperatures (see Fig 11). Generally smaller celled algae are known to dominate in warmer subtropical waters (Parsons and Takahashi 1973). At lower temperatures this morphology must be advantageous to these *C. socialis* cells and therefore these cells thrive and make up a larger percentage of the population under these conditions. This could explain why both morphologies are seen together in the laboratory cultures but in each instance one of the morphologies dominated the culture. For example in some situations turbulence may favour larger cells.

C. socialis is described as having one chromatophore (Gran 1897 and Cupp 1943) Fluoromicrographs, taken for the purpose of this thesis during the growth experiments, support this conclusion for cultures grown both at 7°C and 2°C (see figure24).

The setae seen in figures 12 and 15 are different from those described by Tomas (1997) as seen in Figure 2. There are many *C. socialis* cells (Fig 12) which do not display the typical trait of one longer setae. It is possible that this is simply an effect of the cleaning process. When examining other records of cleaned cells it would appear that they maintain their characteristic setae pattern (personal observations). However, as mentioned in the introduction, there are reported cases where a change of temperature has led to the morphology of a cell changing from that of one species to that of another. For instance *Thalassiosira rotula* is reported by Syvertsen (1977) as changing morphology to *T gravida*. Therefore it is possible that *C. socialis* is also changing to another *Chaetoceros* species with the change in temperature, even though the characteristics observed for the purpose of this thesis do not sufficiently resemble another species to be able to identify it. Furthermore Fryxell (1989) observed that many Antarctic diatoms were described repeatedly as different organisms when they were merely polymorphic stages of a single organism which were not recognised as such.

The case of seasonality has not been examined during this investigation, and it is possible that some varieties/demes are associated with a specific time of year or season rather than temperature or geographic regions (Cerino et al 2005). Further investigations are needed on the effects of seasonality on the morphology of *C. socialis* and on the factors of its chemical composition (Paasche 1973 and Durbin 1977) Further investigation of *C. socialis*, by electron microscopy, would enable more accurate measurements of the morphometrics. A further question that arises from this thesis is: 'What are the morphometrics of C. *socialis* that is found further south in warmer waters?'

The morphometrics of *C. socialis* may or may not be an indicator of physiological performance. The physiological

performance of a species is important when studying the ecology of *C. socialis.* (Mann 1999).

4.3 Physiology

The data regarding growth rates may indicate something about the physiology of *C. socialis* under investigation. The doubling rate of *C. socialis* was highest in this investigation at 7°C and at an irradiance of 50 µmol quanta m^{-2} s^{-1} (see Tab.13) The standard deviations, however, suggest that it is very difficult to draw conclusions from this and previous data. Work undertaken by Brand (1981) has shown that the growth rates of genetically different strains of the same 'morphological' species, from the same water mass, can vary from 1.2 to 1.6 doublings per day. No particular or continuous growth rate is attributable to one particular temperature, light intensity or clones. This raises the question of what actually influences or controls the growth rate of *C. socialis*. Is it the time of year, time of day, the phase of life cycle the culture is in, chemical stimuli in the water or something else? From this study and previous data (Pers. comm. HC Eilertsen) it does not seem possible to link growth rates to any of these factors. It was reported by Furnas (1978) that cell size can affect the division rate of cells. When diatom cells are smaller than 6µm, temperatures of 15°C or 20°C can affect doubling rates. Much of this data is however, difficult to relate to this study as the temperatures are much higher than those under investigation in this study. Others have tried to model growth rates as functions of light – and temperature (Thebault and Rabouille 2003) and found modelling in this area is complicated.

The dates the experiments were undertaken are important. It can be seen from previous studies undertaken by Lundjefelt (1999) that there seems to be some connection between the germination time of *C. socialis* and the time of year, independent of the light

regime. Lundjefelt found that spores of *C. socialis* germinated with the most frequency in March, April and May. This finding indicates that there must be some kind of physiological mechanism which triggers the germination.

Previous works (Epply 1972) have suggested equations for calculating growth rates of phytoplankton, which are still used and quoted, viz $Log_{10} = 0.0275T - 0.070$. This equation was constructed from data collected from many different sources. Laboratory experiments carried out by the author have indicated that certain common northern Norwegian phytoplankton species may have given results which deviate from the previously published norm. These differences regard both morphology and physiology. These cultures of *C. socialis* have been observed to exhibit significantly higher growth rates than those predicted by Epply's 1972 equation. These cultures of *C. socialis* also *seem* to have distinctly variable cell sizes. This could be due to their reproductive strategy, but there are indications that this is persistent. If the difference in size is due to reproduction one might expect a continuous variation in size rather than distinct sizes being the result.

The fluorescence and full colour photograph experiments were undertaken as a pilot experiment as I needed to find out which or what type of photographs were appropriate and what types of constraints and specifications should be used (see Fig.14). The photographs taken of *C. socialis* at 7°C contain a greater range of 'unique colours' than those taken at 2°C (Tab. 14 and 15). These findings apply both to full colour and fluorescence pictures. If the number of colours observed is independent of the number of cells this could be a useful technique for assessing the physiology of a particular culture of *C. socialis* cells. Diatoms are individual organisms and stochastic events within each individual can occur. Two daughter cells resulting from a single parent cell may not

behave in an identical fashion (Brand 1981). It may therefore be important to consider phytoplankton populations as a collection of individuals which each function differently to each other. This would be important to take into account when considering ecosystem analysis. Further development of photographic techniques may also aid individual cell metabolism analysis i.e. the differences in colour between different cells may provide some indications regarding their metabolism.

4.4 Conclusion

'…is this phenotypic plasticity or genotypic variation within a single species or does it reflect the presence of cryptic species?'(Mann 1999)

In conclusion I do not believe *C. socialis* is an example of two (or more) cryptic species because it seems to be possible for small cells to be produced by the larger cells and vice versa. Demes of *C. socialis* may have been observed here or were they indeed merely cells at different stages of the natural life cycle of the cell. What is interesting is the apparent link between size and temperature observed in both field and laboratory examinations. The field data also showed that *C. socialis* is able to tolerate and thrive at a range of abiotic conditions suggesting an extreme adaptive ability. Studies of other species have suggested that the genetic variation within a population may help explain this tolerance of varying environmental conditions (Brand 1988, 89,) In a sample of *Ditylum brightwellii*, isolated from field samples, 23 of the 24 isolates studied were genetically distinct (Ryneason and Armbrust 2000).The immediate outcome of such studies is that scientists must use greater caution when interpreting the ecological significance of data obtained from single strains of particular phytoplankton (Wood and Leatham 1992).

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APPENDIX

Table 1 of Data collected for distribution of *C socialis* in Northern Norway 2006.
Tables 1 can be found online at
http://nfh.uit.no/phaeocystis/marisco/SpeciesProblem

Table 2 of Cell Size Measurements in the Field

Exp/St no	Temp°C	Apical axis size µm (Live cells)	Pervalvar axis size µm (Live cells)
St 179	0.4829°C	7.05, 6.48, 6.87, 7.02, 6.98, 6.87, 6.16 ,6.44, 6.46, 6.44, 5.68, 5.81, 5.66, 7.13, 6.72, 5.01, 5.31, 4.62,5.42 ,5.1, 5.23, 5.96, 6.72, 5.90, 6.33, 5.81, 6.59, 4.84, 6.13, 5.96, 7.57, 7.81, 6.05, 6.05, 6.33, 7.20, 4.90, 7.63, 6.35, 7.09, 7.02, 5.46, 5.75, 5.18, 5.20, 6.31, 4.92, 5.53, 4.92, 6.05, 5.46, 6.05, 4.64, 6.09, 3.47, 5.42	5.33, 6.59, 6.44, 7.37, 6.70, 6.01, 8.17, 6.70, 8.26, 6.61, 6.55, 6.42, 7.37, 6.18, 7.89, 6.72, 7.37, 7.63, 8.04, 8.65, 7.07, 7.33, 7.05, 6.66, 6.27, 6.94, 7.72 ,7., 6, 8.13, 7.15, 7.48, 6.14, 6.53, 6.53, 6.46, 7.85, 6.35, 6.76, 7.59, 8.28, 8.56, 7.76, 5.98, 7.63, 7.09, 6.44, 7.65,
St 204	-1.4213°C	6.052, 5.365, 7.826, 7.117, 6.828, 5.986, 6.607, 11.152, 11.373, 10.908, 11.129, 10.752, 10.686, 10.486, 6.695, 6.097, 6.629, ,6.873, 6.74, 6.718, 6.407, 7.649, 6.429, 8.003, 6.518, 6.762, 7.693, 6.451, 5.52,5.476, 5.698, 6.097, 6.518, 5.232, 5.609, 5.809, 6.185, 5.099, 5.875, 5.809, 5.676, 6.252, 6.141, 7.383, 7.227, 6.784, 6.008, 11.661, 11.24, 10.863, 10.708, 9.378, 10.575, 9.356 9.489, 9.755,	8.69064,9.17838, 7.62648, 6.85053, 7.80384, 7.87035, 8.38026, 12.92511, 10.26471, 8.04771, 11.3067, 9.46659, 9.66612, 9.44442, 9.24489, 7.51563, 8.46894, 7.24959, 8.02554, 7.05006, 11.48406, 10.06518, 9.55527, 7.38261, 8.29158, 8.6463, 8.57979, 8.22507, 8.49111, 8.35809, 7.60431, 8.18073, 6.14109, 7.05006, 8.31375

Table 3 Cell size measurements experiment 2.

Exp. No.	Temp°C	Apical axis size µm (cleaned cells)
2	2°C	11.30, 8.13, 4.60, 4.29, 4.83, 4.53, 4.74, 6.62, 3.88, 4.19, 4.13, 3.74, 3.65, 6.54, 3.60, 3.93, 4.44, 3.53, 3.99, 4.61, 9.32, 9.55, 12.62, 13.97, 4.85, 14.85, 7.28, 12.37, 7.60, 4.43, 8.23, 12.58, 7.89, 8.64, 7.95, 9.08, 4.36, 9.46, 7.99, 10.38, 6.78, 10.04, 9.19, 3.36, 3.35, 3.37, 6.57, 9.41, 6.71, 11.24, 8.75, 12.68, 12.44, 8.73
2	7°C	4.13, 8.47, 8.47, 8.05, 7.56, 7.39, 3.10 ,3.29, 4.09, 3.28, 3.27, 3.05, 3.57, 4.28, 4.28, 3.73, 3.16, 3.75, 3.52, 3.91, 6.55, 4.06, 3.81, 5.90, 5.83, 3.46, , 3.82, 3.77, 4.21, 3.62, 3.80, 5.51, 3.49, 3.94, 3.75, 4.21, 3.10, 3.65, 4.15, 3.88, 3.10, 3.75, 3.90, 3.12, 7.40, 8.08, 5.79, 7.99, 7.99, 6.92, 6.89, 11.58, 7.19, 11.58, 7.19, 11.81, 7.50, 7.15, 8.31, 8.84, 11.16

Table 4. Cells size measurements experiment 3

Exp. No.	Temp°C	Apical axis size µm (cleaned cells)	Transapical axis size µm (cleaned cells)
3	2°C	9.03, 10.22, 9.94, 7.41, 9.47, 8.93, 10.03, 11.44, 9.09, 9.63, 7.64, 7.50, 8.39, 7.77, 8.21, 7.76, 6.79, 8.65, 7.79, 7.21, 6.83, 9.64, 8.53, 8.39, 8.53, 7.89, 7.56, 12.26, 8.51, 8.59, 8.05, 9.22, 8.22, 6.76, 14.18, 9.35, 12.63, 9.73, 7.79, 7.00, 8.19, 7.76, 10.83, 7.77, 10.77, 11.88, 7.27, 8.11, 7.06, 7.19, 8.93, 9.32, 9.04, 11.17, 10.08, 10.22, 9.29, 7.29, 7.02, 6.79, 9.94, 8.84, 8.09, 13.87, 10.19, 9.83, 9.38, 11.25, 9.53, 8.80, 8.39, 7.29, 7.53, 6.83, 9.61, 10.31, 11.24, 13.44, 9.60, 14.31, 6.54, 7.23, 8.23, 7.60, 7.81, 8.66, 15.40, 10.00, 9.76, 9.20, 14.15, 9.68, 8.73, 8.82, 5.96, 9.98, 7.78, 5.01, 9.94, 9.72, 7.72, 8.09, 6.89, 9.55, 9.46,	5.25, 8.11, 8.03, 4.91, 6.57, 6.04, 7.01, 7.62, 5.72, 5.99, 5.95, 6.38, 6.09, 6.22, 5.39, 4.49, 6.38, 5.5, 5.9, 5.88, 5.2, 8.73, 5.58, 6.11, 6.08, 4.97, 5.4, 6.44, 4.09, 6.34, 4.82, 5.57, 5.58, 4.54, 6.06, 5.51, 7.48, 5.49, 5.03, 3.33, 5.69, 6, 4.86, 5.79, 6.57, 7.5, 5.14, 5.4, 4.83, 5.19, 5.87, 4.71, 6.75, 7.4, 6.51, 6.61, 6.11, 4.8, 4.48, 5.41, 5.51, 5.14, 5.21, 6.11,5.11, 6.16, 6.11, 6.37, 5.48, 4.87, 5.36, 5.05, 5.33, 5.18, 5.79, 5.22, 8.34, , 9.58, 6.67, 6.34, 3.59, 3.9, 4.23, 5.28, 4.51, 5.19, 7.19, 7.36, 6.16, 7.09, 8.54, 5.51, 5.11, 6.02, 3.71, 6.71, 5.62, , .66, 6.02, 6.57, 5.06, 5.11, 6.08, 5.51, 4.73
3	7°C	8.49, 11.17, 9.11, 8.02, 11.90, 8.18, 7.58, 5.49, 6.30, 11.48, 8.33, 8.36, 6.90, 6.35, 6.72, 9.12, 8.71, 8.63, 8.11, 6.82, 6.37, 6.81, 8.71, 7.57, 6.69, 7.7, 7.32, 7.07, 8.08, 9.37, 9.09, 9.24, 9.11, 8.11, 9.09, 7.76, 5.68, 8.19, 8.29, 6.64, 7.55, 7.40, 6.63, 8.94, 9.32, 8.62, 7.36, 7.21, 9.39, 5.96, 7.78, 6.49, 6.25, 7.00, 7.43, 6.09, 7.29, 7.70, 5.40, 6.74, 6.88, 5.97, 8.7, 8.91, 8.46, 5.85, 7.65, 6.2, 7.5, 5.7, 6.2, 8.26, 6.92, 6.4, 5.65, 7.09, 7.09, 5.55, 6.75, 5.06, 6.51, 6.82, 5.76, 7.12, 7.5, 6.96, 7.46, 6.61, 6.57, 9.12, 6.65, 7.43, 7.14, 5.8, 7.86, 8.47, 7.09, 7.29, 6.95, 8.01, 6.21, 6.52, 6.36, 8.04, 8.11	5.5, 6.71, 4.81, 6.2, 9.15, 4.66, 6.09, 4.7, 4.66, 7.34, 5.99, 5.62, 4.2, 5.18, 5.5, 4.07, 5.05, 6.03, 5.8, 3.98, 3.69, 4.73, 4.96, 5.01, 4.82, 5.09, 4.35, 3.73, 5.56, 5.49, 6.35, 6.39, 6.25, 6.69, 6.11, 4.5, 4.66, 5.8, 6.2, 4.96, 4.38, 6.24, 4.52, 6.34, 6.76, 5.05, 4.78, 4.99, 6.59, 4.73, 6.83, 4.23, 4.49, 4.89, 4.38, 4.66, 4.8, 3.99, 4.21, 5.01, 5.36, 5.65, 4.59, 4.82, 4.27, 4.82, 4.46, 4.35, 4.57, 4.5, 4.74, 4.55, 4.82, 3.84, 4.1, 4.86, 4.82, 4.86, 4.9, 4.21, 4.29, 4.55, 4.35, 5.22, 4.66, 5.55, 3.8, 4.04, 4.02, 4.49, 3.73, 4.38, 4.5, 4.86, 6.11, 6.13, 4.69, 4.54, 4.3, 5.1, 4.11, 4.72, 4.67, 5.8, 5

Table 5. Cell size measurements experiment 4.

Exp. No.	Temp°C	Apical axis size µm (Live cells)	Pervalvar axis size µm (Live cells)
4	2°C	6.27, 6.37, 6.49, 7.9, 6.38, 6.69, 6.15, 6.95, 6.55, 5.59, 6.09, 6.23, 7.55, 5.9, 5.75, 6.12, 6.69, 6.2, 6.27, 6.55, 6.83, 7.09, 6.49, 5.83, 6.19, 5.81, 6.68, 6.87, 6.83, 7.88, 6.44, 6.59, 6.13, 6.75, 9.96, 10.27, 9.82, 10.26, 10.02, 7.09	7.4, 6.8, 7.99, 7.09, 7.63, 6.75, 8.46, 8.53, 7.36, 6.92, 9.38, 10.85, 8.86, 9.32, 8.94, 8.53, , 7.95, 8.46, 9.16, 8.79, 9.51, 9.88, 9.03, 9.07, 8.56, 9.49, 8.11, 8.14, 7.81, 9.6, 10.49, 11.82, 11.65, 7.6, 7.79, 6.88, 7.51, 7.52, 8.78, 9.85, 11.29, 8.72
4	7°C	6.71, 6.71, 5.77, 5.18, 5.01, 4.78, 5.31, 4.64, 4.82, 4.43, 5.24, 5.62, 6.74, 6.51, 4.96, 5.85, 6.37, 5.73, 6.78, 5.81, 6.85, , 6.39, 6.09, 6.15, 6.31, 5.99, 7.09, 6.41 7.06, 6.66, 6.5, 5.68, 5.83, 6.69, 6.46, 5.22, 6.29, 6.36, 6.77, 6.37	10.85, 10.12, 9.4, 9.94, 10.78, 13.23, 12.81, 12.94, 12.84, 12.12, 10.02, 10.2, 11.03, 9.38, 11.04, 10.68, 10.59, 7.95, 9.6, 9.29, 10.61, 11.08, 10.77, 10.35, 11.03, 8.91, 10.87, 0.58, 15.75, 11.78, 7.56, 11.01, 9.65, 10.12, 8.47, 11.16, 9.75, 9.71, 8.09, 8.31, 8.54, 7.9
(Exp 4 ‘small’)	7°C	6.34, 5.8, 5.84, 6.4, 5.79, 5.5, 6.07, 6.97, 5.84, 4.82, 5.31, 5.51, 5.08, 4.92, 5.34, 4.99, 5.09, 7.01, 4.86, 4.55, 4.94, 5.45, 5.73, 6.03, 5.76, 5.82, 5.9, 5.89, 5.71, 6.49, 5.75, 4.89, 5.28, 4.55, 5.29, 5.01, 5.3, 5.09, 7.4, 5.06,	10.55, 9.79, 10.95, 11.14, 11.48, 10.92, , 1.25, 10.05, 10.7, 10.47, , 3.72, 10.73, 12.87, 10.82, 12.46, 11.21, 8.47, 10.18, 7.91, 9.53, 10.61, 11.1, 10.59, 10.14, 10.7, 11.43, 11.5, 10.56, 10.45, 11.21, 11.93, 13.18, 14.28, 9.03, 13.58, 12.73, 13.16, 13.7, 11.06, 8.02, 7.06, 12.63,
(Exp 4 ‘small’)	2°C	6, 6.78, 6.34, 6.46, 5.91, 5.83, 6.19, 5.52, 6.11, 6.26, 7.21, 7.71, 6.46, 6.52, 7.12, 6.57, 7.84, 7.24, 7.51, 8.36, 8, 6.36, 7.14, 6.81, 6.35, 6.36, 6.52, 7.23, 7.52, 7.41, 7.34, 7.45, 6.13, 6.06, 6.59, 6.64, 5.14, 5.25, 5.24, 6.21	8.75, 9.34, 8.53, 8.26, 9.91, 8.81, 8.11, 7.48, 8.99, 8.61, 8.67, 8.76, 9.9, 11.33, 10.44, 9.33, 8.44, 10.2, 8.78, 10.03, 10.47, 12.57, 11.3, 11.42, 8.71, 8.21, 7.52, 8.76, 9.02, 7.13, 7.6, 6.66, 7.4, .33, 10.61, 13.58, 11.77, 11.4, 11.03, 10.26, 8.73, 8.09

Table 6. of Cell counts.

Light µm quanta m^{-2} s^{-1}	**Temp.°C**	Cell count day1(mean 3 replicates)	Cell count day 4(mean 3 replicates)	Cell count day 6 (mean 3 replicates)
50µm	2°C	186453.3333	506325	2949637.5
10µm	2°C	20608	13333.33333	132500
50µm	7°C	607741.3333	1609250	9047500
10µm	7°C	58666.66667	159500	761750

Table 7. of fluorescence measurements

	Temp.˚C	**No. of Unique Colours**
Live Whole Picture	2°C	128572, 143847, 129006,130729, 117984
	7°C	173031, 141778, 165664
Fluorescence Whole Picture	2°C	99, 109, 134, 62, 108, 94, 130
	7°c	142, 144, 106, 54, 144, 69, 88
	Temp. °C	**'R' number**
Individual Cell Fluorescence	2°C	149, 166, 174, 214, 208, 201, 191, 184, 198, 209, 180, 192, 145, 193, 161, 215, 216, 130, 149, 172, 190, 188, 180, 197, 214, 163, 217, 237, 137, 203, 153, 157, 190, 173
	7°C	245, 219, 121, 214, 225, 191, 247, 137, 149, 198, 132, , 164, 167, 186, 218, 255, 217, 230, 211, 237, 206, 170, 201, 233, 194, 170, 203, 193, 227, 161, 175, 195, 220, 226