Seasonal variation in phytoplankton diversity with an emphasis on the seasonality and morphology of *Dinophysis* Ehrenberg (Dinophyceae) in the outer Oslo Fjord.

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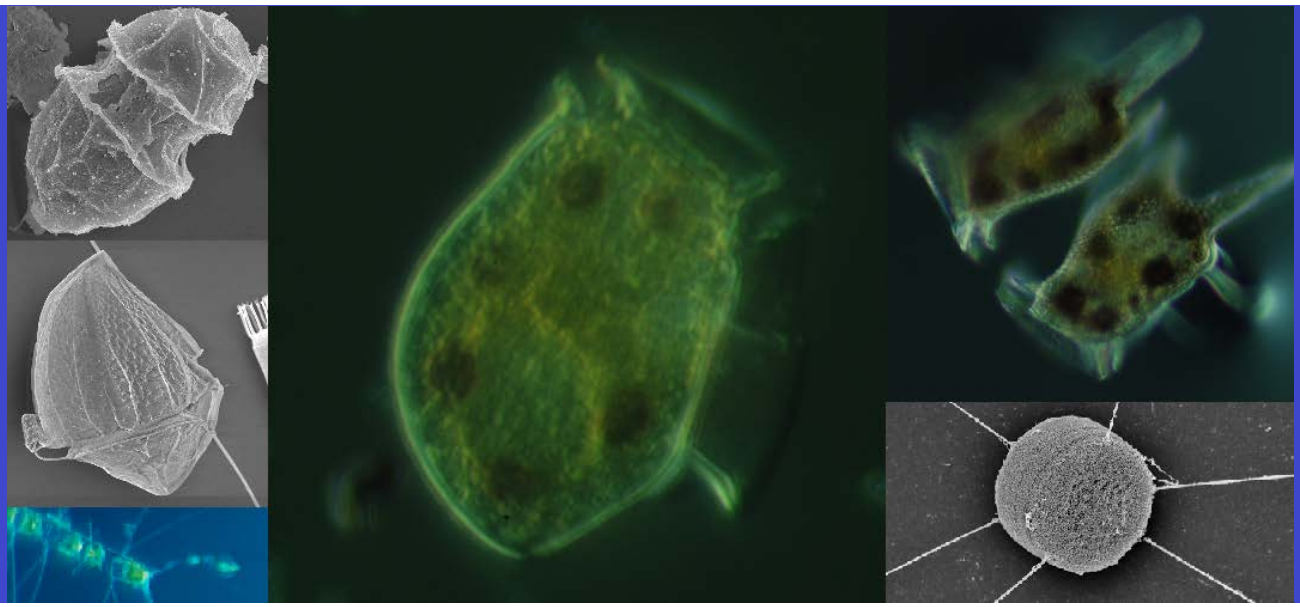

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Foreword

The work described in this thesis was performed in the period 2010-2012 at the Biological Institute at the University of Oslo, in connection with the EU projects MIDTAL (http://www.midtal.com), BioMarKs (http://www.biomarks.eu) and the NRC projects HAPTODIV and TOXALGAE. It was supervised by Wenche Eikrem and co-supervised by Bente Edvardsen and Karl Inne Ugland.

Though the period has been wrought with illness and absences of near-epic proportions, the light at the end of the tunnel was finally reached. I owe this in no small part to my supervisor, Wenche, who I may well nearly have given a heart attack towards the end of this project.
I also want to thank my co-supervisor Bente, for assisting with the groundwork of the thesis, and providing comments on the thesis as it neared completion. Also, my co-supervisor Karl Inne Ugland, for bringing much needed assistance for the final run towards the finish line.

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- My parents, for providing economical support when governmental educational funding screwed up or unforeseen expenses arrived

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Finally, I would like to dedicate this paper to my cat, Lily "Togepi" Truscott av Ochremenko (N), whose unprecedented love and kindness lit up my life until her sudden passing on the 26th of September 2011.

Abstract

This thesis examines the phytoplankton diversity in the Oslo Fjord and the seasonality of the size, shape and abundance of the genus *Dinophysis* Ehrenberg. The genus, which contains several toxin-producing species, has previously been shown to at times be highly form variable, and delimitation of some of the species has been the subject of much discussion.

Samples were collected from station Missingene (OF2) in the outer Oslo Fjord. Net hauls and natural water samples were collected for cell quantification and size measurements nearly once per month between the late summer of 2009 and the early summer of 2011.

Cell counts were performed in an inverted microscope and used to examine seasonality of diatoms and dinoflagellates, as well as to calculate the biodiversity through Shannon's diversity index and species richness. Photographs of *Dinophysis* cells in net haul samples were used to measure length and width of individuals.

Shannon's diversity index showed between 1.13 and 3.53 bits, with no clear correlation to neither temperature nor salinity, and no significant variation between the seasons. Between 16 and 53 total species were found in cell counts for any given month from this study, with an average of approximately 28 total species per month. Species richness did not correlate with salinity nor temperature, and did not appear to vary with the seasons. 90 separate species were registered between 2009 and 2010, and 82 species were found in between 2010 and 2011.

Diatoms and dinoflagellates followed a previously reported pattern in which diatom abundance was higher than that of dinoflagellates throughout the sampling period, with the exceptions of late spring/early summer in 2010 and 2011. Vernal blooms were detected in January 2010, dominated by *Skeletonema* spp. and *Pseudo-nitzschia* spp., and in February 2011, dominated by *Skeletonema* spp.

Dinophysis acuminata and *D. norvegica* were found to be the two most abundant species of their genus, and made up most of the *Dinophysis* species detected during cell counts. *Dinophysis acuminata* and *D. norvegica* both showed a short-lived abundance increase in the late spring/early summer of 2010, showing cell numbers of up to 1000 cells L^{-1} and 1600 cells L^{-1}, respectively.

Dinophysis acuminata and *D. norvegica* both had highly variable cell sizes, whereas *D. rotundata* did not show the same size variation. Most cell sizes did not conform to previously reported size ranges.

Hydrographical data showed a correlation with the sizes of *D. acuminata, D. norvegica* and *D. rotundata,* though high significance ($p < 0.0005$) was only shown with temperature against the length and salinity against the length-width ratio of *D. acuminata* cells.
Dinophysis acuta did not have a sufficient sample size to provide any statistical significance.

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1 Introduction

1.1 Seasonal cycle of phytoplankton

As can be seen on land, where various herbs grow, bloom and wither with the seasons, the microalgal plankton of temperate coastal waters undergo seasonal variations. These variations are largely attributed to light conditions and to the formation and breakdown of stratified layers of surface water, which forms a barrier against deep circulation of the waters. With such a barrier present, phytoplankton in essence gain a "false bottom" that allows them to be circulated in the euphotic zone of the water column.

The temperate coastal seas also experience four distinct seasons. In the winter, the water column is more or less identical in salinity, nutrients and temperature throughout the water column, due to surface water cooling resulting in a higher density for the top layer relative to the layer beneath, and a subsequent constant mixing of the water masses. This deep mixing of the water combined with typically low irradiance levels contribute to keeping phytoplankton abundance low in this season.

During spring, atmospheric heat increase and resulting fresh water runoff from melting ice and snow creates a layer of low-density water. In the waters of the Oslo Fjord, the first stratification of the water usually begins in February-March. Simultaneously, light levels in this time of year increases. This stratification, along with the increased irradiance and the presence of nutrients typically leads to a vernal bloom of phytoplankton, most commonly dominated by diatoms (class Bacillariophyceae). In the late spring or early summer, snow smelting causes further stratification through a decrease in surface water salinity, as well as an influx of nutrients, due to fresh water runoff from land. This, in turn, can often result in a second vernal bloom that generally occurs around May.

As summer approaches, the nutrients in the upper layer of the water column tend to be heavily assimilated by the blooming algae. In the summer, the temperature is also typically high enough to ensure a very strong stratification, effectively minimizing the ability of nutrients to penetrate into the depleted upper column. It is during this time that dinoflagellates, often being highly skilled diel migrators, experience their dominance. With the ability to cross beneath the stratified layer to absorb nutrients during the nights and subsequently return to the upper layers during the day to photosynthesize, they have a clear advantage in this season.

Finally the autumn season is typically marked by stormy weather and decreasing temperatures,

which has quite a heavy effect on the pycnocline, essentially tearing at it until it begins to break down. Combined with a lowering level of irradiance, the phytoplankton community typically starts to decline in the late autumn, until the winter finally forces a large number of the remaining phytoplankton into their resting stages. (E.g. Paasche, 2005; Throndsen and Eikrem, 2005).

1.2 *Dinophysis* Ehrenberg

The *Dinophysis* genus was first described in 1840 by Ehrenberg, and is characterized by having two large hypothecal plates and two small epithecal plates, as well as sail-like structures formed by extensions of thecal plates located near the cingulum and the sulcus (Graham et al., 2009). Typically, *Dinophysis* species have 18-19 plates in total, though its type species, *D. acuta,* only has 17 due to its missing apical pore plate (Balech, 1976; Taylor, 1987).
It is a large genus of thecate dinoflagellates, and comprises over 130 taxonomically accepted species (http://www.algaebase.org). Most of these species went poorly researched for a long time, partly due to the difficulties faced in culturing them (Scholin, 1998).
In more recent times, however, the genus *Dinophysis* has received an influx of research due to the discovery that *Dinophysis* contains species producing toxins that lead to diarrhetic shellfish poisoning (DSP) (Larsen and Moestrup, 1992), as well as more knowledge pertaining to how to culture them, for instance in regards to several *Dinophysis* species' dependence on the presence of the ciliate *Myrionecta rubra*, which they feed upon and retain their chloroplasts, despite the chloroplasts originating in cryptophytes such as *Teleaulax amphioxeia* (Janson, 2004; Park et al., 2006).
DSP is, unlike both Paralytic and Amnesic Shellfish Poisoning, thus far unassociated with human deaths, and its symptoms primarily include gastrointestinal distress with a common recovery time of three days (Hallegraeff, 2004; Yasumoto et al., 1984). However, it has been reported that some of the toxins involved may promote tumors in the stomach (Suganuma et al., 1988).
In addition to these health issues, there is also a natural economical loss associated with outbreaks of DSP-toxins. The losses experienced by shellfish industries can easily reach the millions, as was the case in Greece in 2000, where a *Dinophysis* bloom cost the industry a staggering 5 million Euros (Koukaras and Nikolaidis, 2004).
The first reported outbreak of DSP was in 1976 in Japan, and the causative organism was reported as *Dinophysis fortii* (Yasumoto et al., 1980). This was followed by the implications of *D.*

acuminata, D. acuta, D. norvegica, D. mitra and D. rotundata, as well as the benthic species *Prorocentrum lima* (Hallegraeff, 2004). In the year 2000, DSP was known to occur in such varied locations as Japan, Europe, Chile, Thailand, Canada, Australia and New Zealand (Hallegraeff, 2004).

At least eight species of *Dinophysis* have been identified as containing toxins that lead to DSP: *D. acuminata, D. acuta, D. fortii, D. mitra, D. norvegica, D. rotundata, D. sacculus and D. tripos* (Hallegraeff, 2004; Lee et al., 1989), but it has been shown that of these, *D. acuta* is the primary source of DSP in Norway (Dahl and Johannessen, 2001).

In the outer Oslo Fjord, four of these species are commonly found; these are *Dinophysis norvegica, D. acuta, D. acuminata* and *D. rotundata.* The latter is often placed in the debated genus *Phalacroma,* which has been used to describe members of *Dinophysis* that contain large convex epitheca that protrudes from the transversal sail-like extension, thus making the epitheca highly visible from a lateral view (e.g. Steidinger and Tangen, 1996; Throndsen and Eikrem, 2005). It has also been noted that members of the proposed *Phalacroma* are mainly heterotrophic, oceanic species, whereas the rest of the *Dinophysis* species are primarily auto- or mixotrophic, coastal species (Taylor et al., 2004). Molecular data also support the transfer of *D. rotundata* into the genus *Phalacroma* (Edvardsen et al., 2003). Whether they should once again be differentiated into separate genera is a subject of ongoing debate far outside the scope of this text, and the thesis will therefore lean on the side of the debate that places them in the *Dinophysis* genus for simplicity's sake.

A rarer species of *Dinophysis* in Norwegian waters, *D. tripos* was originally considered a warm temperate to tropic species, but in recent years has begun to migrate and thrive further north. It was first sighted in Norway at its west coast in mid August 2009, and detected weekly thereafter, occasionally revealing paired cells. This indicated that they were not just occurring, but also growing in Norwegian waters (Reguera et al., 2003 according to Johnsen and Lømsland, 2010). By September 2009, *D. tripos* had also spread to the Barents Sea region. In 2009, its last detection was in the beginning of November until its reoccurrence at the end of August 2010, which persisted until the end of October 2010. Also here, paired cells were frequently observed (Johnsen and Lømsland, 2010).

1.3 Microalgal blooms

Although *Dinophysis* rarely bloom, when they do, they can cause very visible effects in the form of a red tide, and with toxic species, such blooms can render nearby shellfish stocks inedible (e.g. (Shumway, 1990; Yasumoto et al., 1980). A bloom of toxin-producing *Dinophysis norvegica* in the Bedford Basin of Canada has been recorded to reach concentrations of as much as 456,000 cells L^{-1}, occurring at approximately 10m depth in the pycnocline (Subba Rao et al., 1993). High concentrations of *Myrionecta rubra* has been suggested to be a possible precursor to *Dinophysis* blooms as a result of observations made in the Gulf of Mexico (Campbell et al., 2010).

What exactly constitutes a bloom situation varies between species, and although the so-called "red tide" was one of the most common references to blooms, a bloom does not have to be red, or even visible, in order to attain bloom status (Shumway, 1990).

Not all types of algal blooms are harmful. In fact, in most cases, one can expect blooms to be beneficial to aquaculture and fisheries in that the large increase of algae provides for an increase in food and subsequent population growth in the target organisms (Hallegraeff, 1993).

However, in the case of a few species which mainly exist within the dinoflagellate division, blooms can have adverse effects, and they are then termed harmful algal blooms (HABs).

The history of recorded HABs dates a long way back, perhaps even as far back as 1000 B.C., as it has been suggested that one of the great plagues of Egypt as referenced by the Holy Bible (Exodus 7: 20-1) was, in fact, a non-toxic algal 'red tide' that created anoxic conditions and subsequent mass deaths of fish and invertebrates (Hallegraeff, 1993).

One of the first recorded human fatalities as a result of an algal bloom was when Captain George Vancouver's crew ignored the taboo of the local Indian tribes in an area of British Columbia, and proceeded to eat shellfish while the water was phosphorescent. The phosphorescence was in this case caused by a bloom of toxic algae that caused paralytic shellfish poisoning (Dale and Yentsch, 1978).

Three basic types of HABs have been established: extreme blooms that cause anoxic conditions through sheer bloom density, blooms of species that produce toxins that may eventually reach human food sources and blooms that are toxic to fish and invertebrates and thus have adverse effects on aquaculture industries (Hallegraeff, 2004).

Reports of HABs have seen an increase in the last 50 years, yet the cause of this is not certain. Several sources claim the increase to be a result of increased scientific awareness of the phenomenon, such as in 1985 when an outbreak of paralytic shellfish poisoning was detected only a

short time after a major marine laboratory moved into the area (Anderson, 1989; Hallegraeff, 2004). Another explanation could be that the eutrophication caused by aquaculture, agriculture and industry provides enough nutrients to stimulate bloom formation in certain harmful species (Anderson, 1989; Hallegraeff, 2004). Furthermore, climate changes have been implicated as a potential culprit in allowing harmful bloom species to spread to parts of the world that was previously uninhabitable for them. As an example, fossil records have shown that the dinoflagellate *Pyrodinium bahamense* existed in the Sydney Harbour region, whereas it currently only reaches as far down as Papua New Guinea (McMinn, 1989). Global warming might thus potentially allow for this species to spread as far South in modern times as well. Finally, ship transport via ballast water and importation of shellfish stocks have also been established as potential causes of the increased rate of HABs (e.g. Doblin et al., 2004; Hallegraeff and Bolch, 1992; Scarratt et al., 1993).

1.4 Microalgal species delimitation

The most visible species on our planet can, in most cases, be defined by the biological species concept. However, once you reach microscopic levels, the separation of species becomes somewhat more difficult. Many microscopic species are asexual, removing the possibility of applying the biological species concept, and in many of the remaining cases, the sexual reproduction cycle has not been sufficiently studied, making the biological species concept highly difficult to apply to these organisms as well. As a result, species delimitation in microalgal organisms has traditionally been performed through morphological separation (Hallegraeff, 2003; John and Maggs, 1997). Characteristics such as number of chloroplasts, forms and numbers of cell plating, positioning, presence or absence of various structures and even size have been used to form a very broad range of species and genera within the dinoflagellate community (Taylor et al., 2004).
Unfortunately, the morphology of many species is highly variable (Solum, 1962). A good example of this is found in the case of *D. acuminata*, which has previously been split into five separate species based on their morphologies (Paulsen, 1949), though through examination of their plate patterns, they were later found to be too similar to justify such a separation (Balech, 1976).
Lately, advances in DNA sequencing has allowed for previously ill-defined species and genera to be more readily distinguished, and has provided good tools for separating species with relatively cryptic differences in morphology (John and Maggs, 1997). One set of tools that are being developed for this is molecular probes, which allow for species detection and even in some cases

quantification of said species (e.g. Dittami et al., 2013; Edvardsen et al., 2012; Scholin, 1998).

1.5 Goals of the study

The agendas behind this study can be summed up with two points: economy and ecology. More specifically, given the previously referenced ability of *Dinophysis* to contaminate, and thus make worthless, large harvests of shellfish makes the genus a prime candidate for scientific investigations. Further, the current political and ecological focus on biodiversity provides excellent grounds for research in this field as well.

This thesis will attempt to shed light on the species richness and species diversity of the microalgal community in the outer Oslo Fjord.

It also compares the seasonal abundances of dinoflagellates and diatoms to the seasonal shifts that were reported by Paasche (2005), in which the diatoms experience their major peaks in the early spring, and dinoflagellates experience their major peaks in the late summer (Fig. 1.5.1).

Additionally, it was attempted to provide some further knowledge of the genus *Dinophysis* by examining the variation in size and shape of *Dinophysis* species within the same location, and comparing these to previous studies.

The seasonal abundance of *Dinophysis* spp. was also examined to see if any trends could be found.

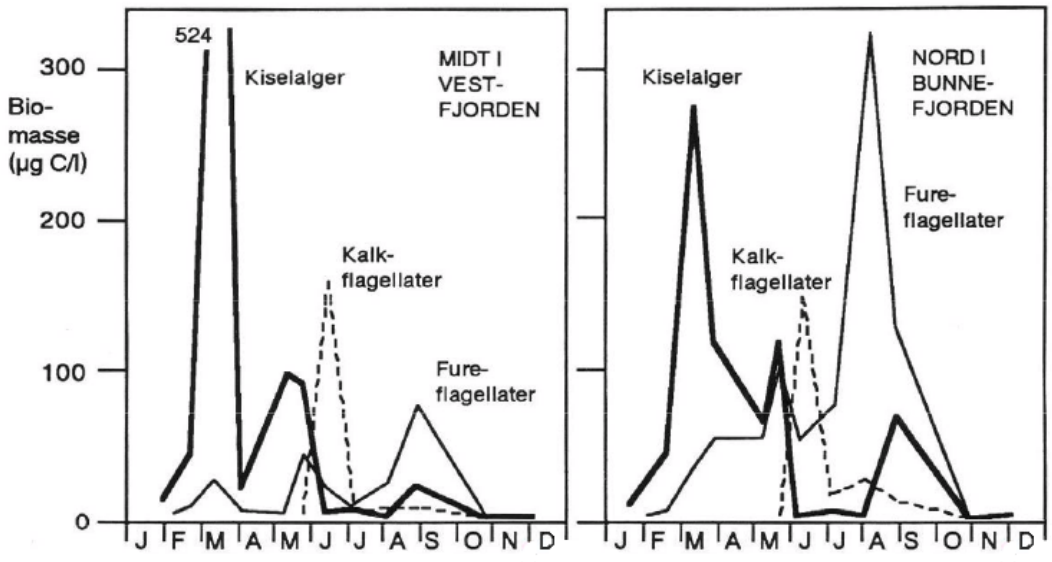

Figure 1.5.1: The seasonal cycle of phytoplankton in 1976 at two locations within the Oslo Fjord. Bold lines represent diatoms, thin lines represent dinoflagellates and dotted lines represent coccolithophores. From Paasche (2005).

2 Materials and Methods

2.1 Sampling

Samples were collected from a location in the outer Oslo Fjord, at monitoring station Missingene (OF2; 59.186668°N, 10.691667°E) (Fig. 2.1.1). This station was chosen for its hydrographical and biological conditions, which have been found to be similar to more exposed and distant stations in the coastal current (Dragsund et al., 2006 according to Hostyeva, 2011). The vessel used for the sampling was R/V "Trygve Braarud". A sampling day typically lasted from 9 AM to 4 PM. Sampling was done from June 2009 to June 2011. Dates for sampling are listed in table 2.1.

Table 2.1: List of sampling dates.

Month	2009	2010	2011
January		21.	13.
February			15.
March		11.	14.
April		12.	12.
May		11.	20.
June	22.	22.	07.
August	05.	17.	
September	22.	14.	
October	20.	20.	
November	17.	17.	
December	09.	14.	

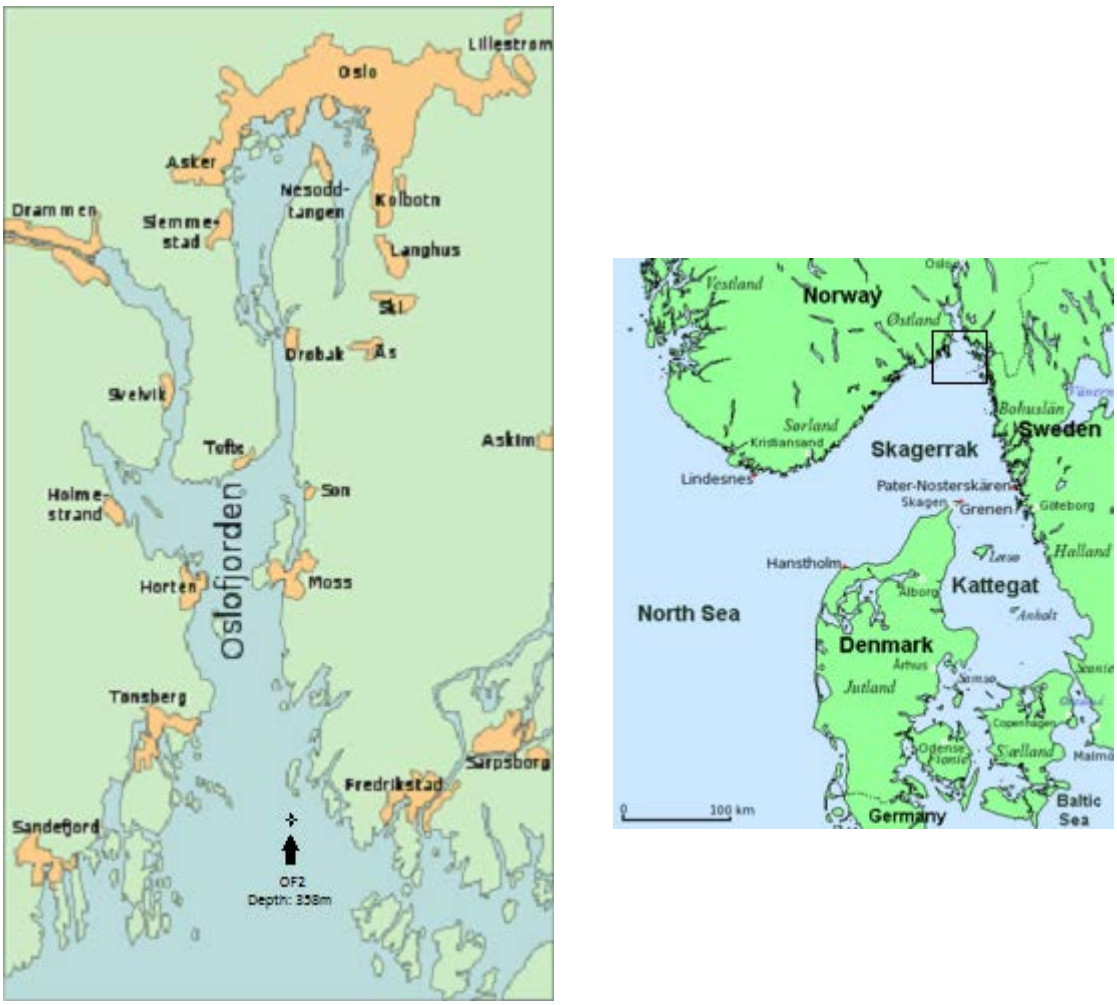

Figure 2.1.1: Maps of the outer Oslo Fjord and the Skagerrak, displaying the sampling station Missingene (OF2). (Source: http://www.thefullwiki.org)

Samples were collected in three ways. Vertical net hauls down to approximately 18 meters' depth and horizontal net hauls at low speed for 5-10 minutes were used to gather material for qualitative analyses, such as the morphological studies undertaken for this thesis. Nets for the net hauls had a mesh size of 20 µm. Natural water samples were collected with Niskin water bottles (Niskin, 1970) from 1 meter's depth for quantitative analyses, and from 1, 2, 4, 8, 12, 16, 20 and 40 meter's depth for *in vitro* chlorophyll *a* measurements.

Chlorophyll was also measured *in vivo* by a fluorometer Q300 (Dansk Havteknikk, Denmark). This fluorometer is equipped with blue light emission, which excites chlorophyll *a*. Chlorophyll excited in this way will emit red light, which is registered by the fluorometer.

This fluorometer was attached to a CTD rosette (Falmouth Scientific Inc., USA), which at the same time measured salinity in the form of conductivity, given as practical salinity units (PSU), and temperature in degrees Celsius in the water, throughout most of the water column. Density was also

automatically calculated by the CTD.
The CTD equipment did not function properly on October 2010 and May 2011, and there is therefore no hydrographical data from these sampling dates.
Irradiance was also measured during these dates, using a LI-250A light meter (Li-Cor® Biosciences, USA). However, due to several issues with proper calibration of the instrument, the readings were deemed too untrustworthy for use in this paper.

2.2 Preservation and preparation

2.2.1 Light microscopy

Net haul samples for light microscopy were preserved in four ways: neutral Lugol's solution (1%), formalin (3%), glutaraldehyde (1%) and a mix of glutaraldehyde (0.25%) and acetic Lugol's solution (1%). Concentrations listed are final concentrations. For each fixation method, 100 mL samples were used (Throndsen, 1978).
In addition, 100 mL of natural water samples collected from 1 meter's depth was preserved with 1 mL neutral Lugol's solution. All preservations were done *in situ*, and percentages and volumes listed are approximations, due to inaccurate measurements when adding water to their respective bottles as well as a general degree of inaccuracy inherent in the transfer of as viscous a fluid as glutaraldehyde (50%).
Upon return to the university, the fixated material was stored at approximately 4°C.
All flasks with water samples were marked with sampling date, station, depth and fixation method *in situ.*

2.2.2 Electron microscopy

Samples for scanning electron microscopy (SEM) were usually brought back live from the cruise, but sometimes net hauls that had been preserved onboard the ship were used instead. In these cases the samples fixated with a mix of glutaraldehyde and acetic Lugol’s solution were used.
Water samples of 4L from 1m depth were pre-filtered through a 180 µm mesh *in situ.* It was shortly thereafter concentrated *in vitro* by Tangential Flow using a VivaFlow 200 (Sartorius Stedim Biotech

GmbH, Germany), with an end volume of approximately 15 mL.
100 µL of the 1m depth concentrated sample was then pipetted onto two poly-*L*-lysine-coated glass discs mounted on aluminum stubs using double-sided carbon tape (Electron Microscopy Sciences, USA), and subjected to gas emitted by three to four drops of a 2%-dilution of osmium tetroxide (OsO_4) for two minutes.
The same volume was given direct additions of 34 µL of a 4%-dilution of OsO_4, in order to end up with concentrations of 1% OsO_4. These were also each placed on two poly-*L*-Lysine-coated glass discs. The exact same procedure was undergone for horizontal and vertical net hauls when live samples were used. Otherwise, the pre-fixed samples were pipetted directly onto the glass discs. These prepared samples were then left overnight in a humidity chamber to allow the phytoplankton to sink down to the glass without drying the samples out. Finally, the following day they were rinsed in a cacodylate buffer and increasing concentrations of ethanol until they had been thoroughly rinsed in 100% ethanol, after which time they were critical point dried with a CPD 030 Critical Point Dryer (Bal-Tec AG, Liechtenstein); a procedure in which the ethanol is first replaced by fluid carbon dioxide, then heated and kept under pressure until the critical point of carbon dioxide is passed, a point in which liquid seamlessly transforms into gas, allowing the cells to be dried out without damaging them.
Before examination, the specimens were coated with approximately 3-5 nm of platinum with a Cressington 308 UHR sputter coater (Ted Pella, Inc., USA).

2.2.3 *In vitro* chlorophyll *a*

100-500 mL (depending on phytoplankton density) of natural water samples from the 1, 2, 4, 8, 12, 16, 20 and 40m depths was filtered through Whatman glass-fibre filters (GF/F 25mm, 0.7µm mesh) *in situ* with two replicates for each depth. The filters were folded with forceps and placed in cryo vials before immediately being frozen in liquid N_2.
Upon return to the university, the samples were stored at -80°C until analysis at the Marine Biology Program, Department of Biology (UiO).
The chlorophyll *a* was extracted from the filters with 90% acetone and chlorophyll *a* concentration was determined using a Turner Designs fluorometer TD-700 (Turner Designs, USA) and calibrated for a µg L^{-1} value.
Analysis of chlorophyll *a* was performed by Rita Amundsen.

2.3 Microalgal biodiversity

The following light microscopy work was done by Vladyslava Hostyeva, and is in part also referenced in Hostyeva (2011).
Subsamples of 10 mL of the Lugol's solution-preserved natural water samples were allowed to sediment for approximately 24 hours and then examined under a Nikon Eclipse TE3000 inverted microscope in accordance with the Utermöhl sedimentation technique (Hasle, 1978; Utermöhl, 1958). Where cell densities were high, the subsample was divided into two further subsamples of 5 mL each, which were diluted with 5 mL of sterile seawater. Phase contrast and 100-400 times magnification were used. Empty cells were not included in the results. The numbers of phytoplankton cells counted in these subsamples were then multiplied in accordance with the volume analyzed, in order to provide a rough estimate of the concentration in one liter.
An attempt was made to identify the phytoplankton species to the lowest taxonomic level. The identification was primarily based on Throndsen et al. (2007), Tomas (1996;1997), Hoppenrath et al. (2009) and Cupp (1943). Electron microscopy with a Hitachi FEG S-4800 scanning electron microscope at 9-15 kV acceleration voltage and approximately 8.4 mm working distance was combined with light microscopy for precise identification of some species. Quartz PCI (Digital Imaging and Slow-Scan) software was used for digital processing of the scanning electron microscope images.

2.4 Variation in size and morphology of *Dinophysis*

Net haul samples of each month that was used for this study were examined under a Zeiss Axio Scope.A1 microscope at 200x magnification and phase contrast, and photographs were taken of *Dinophysis* cells with a Nikon D5000 digital camera. In many cases, the horizontal net haul samples were lost as a result of massive reorganization, and vertical net haul samples were used, but horizontal net haul samples were preferred in the few cases where this was possible.
An attempt was made to take photographs of at least 30 cells of each species per month, though this was abandoned where cell density was insufficiently high. The number of measurements made per species for each month are listed in table 2.2.
The photographs were later measured manually and their measurements calculated into their actual sizes by comparison to a micrometer. Lengths and widths were measured as shown in figure 2.4.1. Identification literature used for this work was Throndsen & Eikrem (2005).

Table 2.2: A list of all examined months, and how many individuals were measured for each species of *Dinophysis*. Numbers marked with a star were deemed sufficiently high to be used in statistical analyses.

	D. acuminata	D. acuta	D. norvegica	D. rotundata	D. tripos
October 2009	6	0	0	3	0
November 2009	***15****	2	***21****	***10****	1
January 2010	0	0	0	0	0
March 2010	1	0	3	1	0
April 2010	***35****	0	***66****	3	0
May 2010	***39****	0	***36****	4	0
June 2010	***13****	0	***36****	***6****	0
August 2010	***8****	0	***39****	5	0
September 2010	2	***17****	***26****	***6****	1
October 2010	***11****	***14****	***22****	***7****	1
December 2010	***11****	***30****	***44****	***11****	0
January 2011	0	3	***20****	1	0
February 2011	3	0	***34****	1	0
March 2011	5	0	***36****	0	0
April 2011	2	1	***40****	5	0
May 2011	1	0	***33****	1	0
June 2011	5	0	***42****	2	0

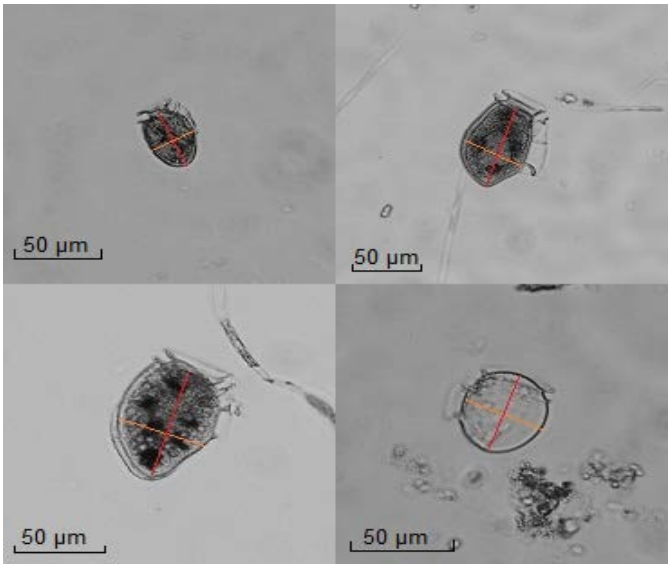

Figure 2.4.1: A representation of how the lengths and widths were measured. The orange line shows roughly what section of the cell was used for measuring width, and the red line shows roughly what section was used for measuring the length. From top left to bottom right: *D. acuminata*, *D. acuta*, *D. norvegica* and *D. rotundata.*

2.5 Statistics

The programs used for the statistical portion of this thesis were R (The R Project for Statistical Computing) and Microsoft Excel.

ANOVA tests on one-way and multiple linear regression models as well as Tukey's Honestly Significant Difference tests were used for this thesis (Dalgaard, 2008; Moore and McCabe, 2006). Visualization of the hydrographical data was created with histograms (Fig. 3.1.1) and two-dimensional scatter plots (Appendix A). They were also tested with one-way ANOVA and Tukey's HSD tests (Appendix B). *In vitro* chlorophyll *a* data by was visualized with two-dimensional scatter plots with depth along a reversed y-axis (Appendix C).

From the cell counts, Shannon's diversity index (Shannon, 2001; Zand, 1976) was calculated with a log-2 base as a measure of diversity through equitability. Further, the species richness and the abundances of diatoms and dinoflagellates were used. The resulting biodiversity data was analyzed with one-way ANOVA and Tukey's HSD tests (Appendix B), and visualized with box plots (Figs. 3.2.1, 3.2.2) and two-dimensional scatter plots (Figs. 3.2.3, 3.2.4).

The lengths of the *Dinophysis* cells and the ratio between their lengths and widths were separated by species and season and compared through one-way linear regression and Tukey's tests in order to examine their variation between the different sampling dates. Month was used in place of season for *D. acuta* and *D. rotundata* due to the low number of months where these species were present in sufficient numbers. Multiple linear regression was used to examine how the lengths and ratio varied with changes in salinity and temperature, including interaction effects. (Appendix B) and visualized with the aid of box plots and histograms (figs. 3.3.1, 3.3.3-3.3.5, 3.4.1).

3 Results

3.1 Hydrography and chlorophyll *a*

The lowest surface temperature was -1.2°C in January 2010 and the highest surface temperature was 19.0°C in August 2009, with an overall mean surface temperature of 8.6 ± 1.6°C. The temperature throughout the season followed a standard wave-like pattern (Fig. 3.1.1 A).
The depth profile is shown in detail in appendix A and showed a general pattern of stratification being broken down in around September, and reestablishing between January and February. The PSU beneath the pycnocline typically stayed at approximately 35, though did go as low as 30 in November 2009 and April 2011.
The salinity varied a bit more erratically, with a sudden plunge of 14.6 between June 2009 and August 2009, the latter having a registered surface salinity of 12.7; the lowest salinity registered in any of the sampling dates. Comparatively, the highest water surface salinity was found to be 32.7 in March 2010. Figure 3.1.1 B illustrates the variation of the salinity. The mean PSU value was 24.3 ± 1.1.
The variation in density, which is calculated as a function of salinity and temperature, is illustrated with figure 3.1.1 C, where it seems to tightly coincide with the variation in salinity. The density was calculated to be 8.1 σ_T at the lowest and 25.9 σ_T at the highest, with a mean of 18.4 ± 1.0 σ_T.
Only the surface temperature had a statistically significant variation between the seasons. There was no statistical evidence that spring temperatures differed from winter temperatures (Appendix B).
The maximum chlorophyll *a* concentrations per month, as measured *in vitro* varied from a lowest concentration of 0.4 µg L^{-1} in June 2010 and November 2010 to a highest concentration of 18.1 µg L^{-1} in August 2009 (Fig. 3.1.2).
The depths at which these chlorophyll *a in vitro* maxima were found were between 1 and 4 meters for all months except in November 2009 (16 meters, 3.2 µg L^{-1}), December 2009 (12 meters, 0.7 µg L^{-1}) and April 2011 (20 meters, 1.9 µg L^{-1}) (Fig. 3.1.3, Appendix C).
The *in vivo* and *in vitro* methods gave wildly different depths for the chlorophyll *a* depth maxima. Graphs depicting the full variation of chlorophyll *a* through the depths for each month, as measured *in vitro*, are situated in appendix C.

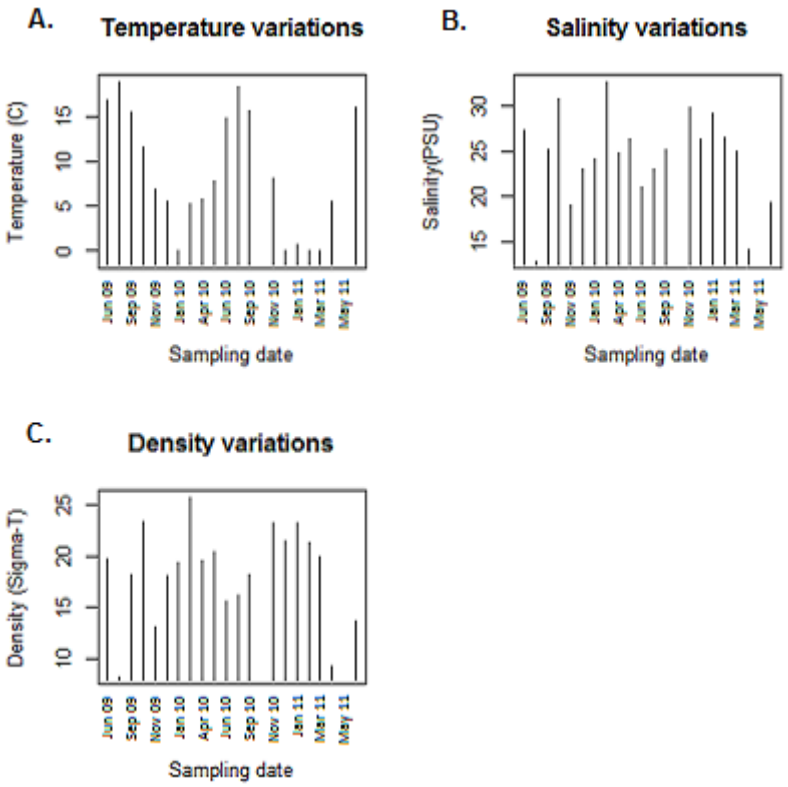

Figure 3.1.1: Bar plots displaying the hydrographical data for the sampling period. A) Temperature in degrees Celsius at 1m depth. B) Salinity in PSU at 1m depth. C) Density in σ_T.

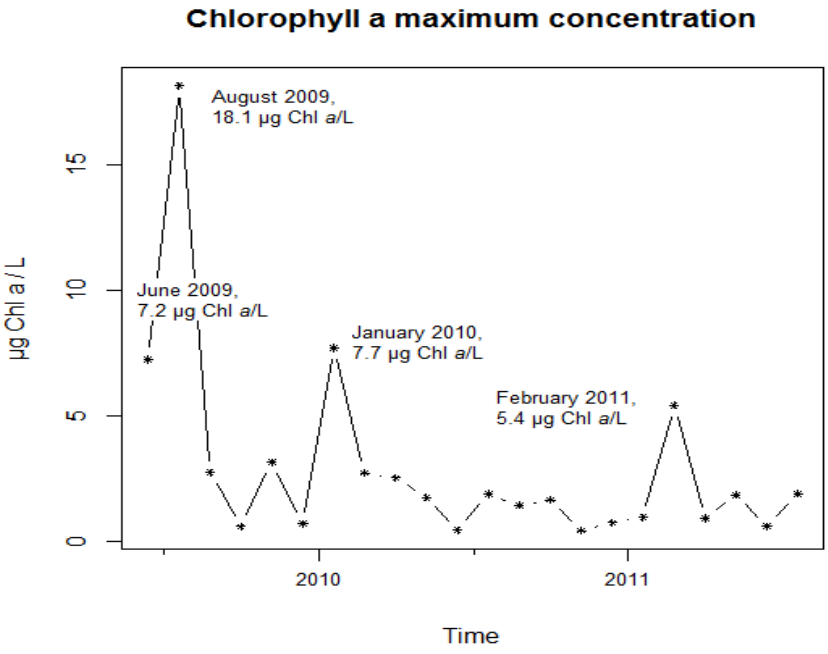

Figure 3.1.2: Graph showing the variation in maximum concentration of chlorophyll *a* as measured *in vitro*. The four highest peaks have been labelled with their respective sampling dates and chlorophyll *a* concentrations.

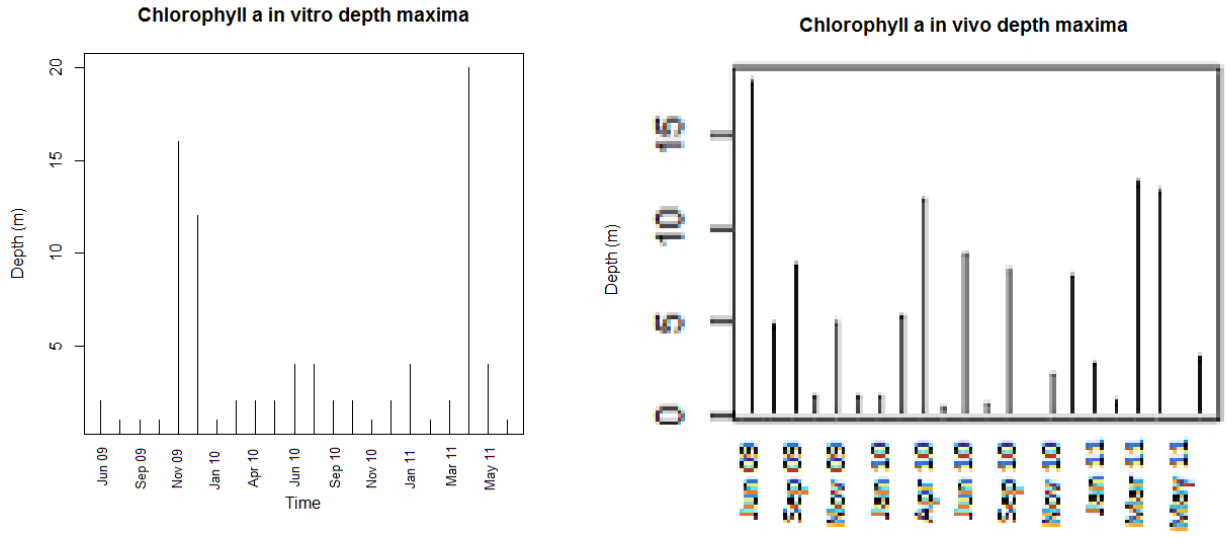

Figure 3.1.3: Bar plots showing the depth at which the chlorophyll *a* maximum was detected. To the left: *In vitro* analysis. To the right: *In vivo* analysis.

3.2 Microalgal biodiversity

Shannon's diversity index showed 1.13 bits in February 2011 to 3.53 bits in June 2010. The mean was 2.47 ± 0.14 bits.

There was no statistically significant difference between seasons nor salinity, though temperature showed a weak significance with a p-value of 0.044 (Appendix B).

The species richness registered per month varied from 16 species in May 2011 to 53 species in September 2009. The mean was 27.7 ± 1.6 species.

The species richness did not display any statistical significance for neither seasonality nor salinity and temperature in the surface (Appendix B).

Figure 3.2.1 displays these values in the form of box plots.

From June 2009 to June 2010, a total of 90 different species were registered in the cell counts. The species total for the period August 2010 to June 2011 was 82. Groups that were not determined to species level were counted as a single species for each group.

A full list of species found and their associated concentrations are listed in appendix D.

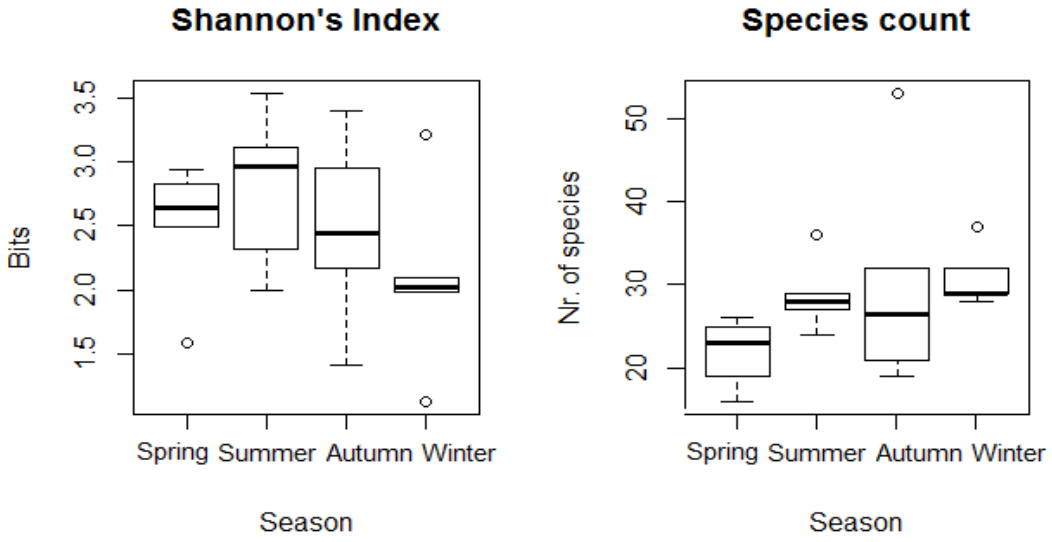

Figure 3.2.1: Box plots portraying the seasonal variation in the values provided by Shannon's diversity index (left) and the species richness (right) with associated interquartile ranges and medians. Whiskers extend to the highest and lowest values within 1.5x the interquartile range.

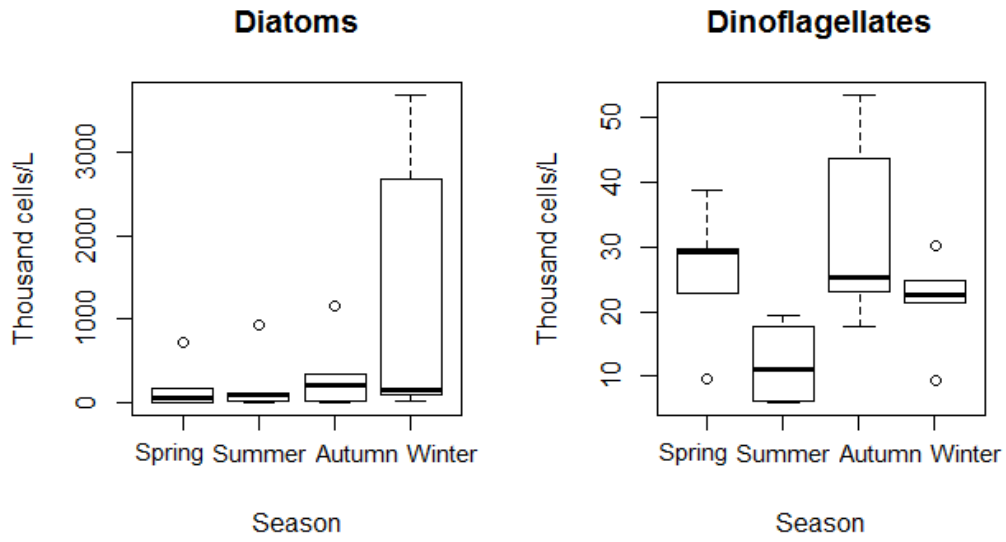

Figure 3.2.2: Box plots showing the seasonal abundance of diatoms (left) and dinoflagellates (right), with associated interquartile ranges and medians. Whiskers extend to the highest and lowest values within 1.5x the interquartile range. Dinoflagellate data from June 2011 is not represented in this figure.

The diatom concentration varied between 6400 cells L^{-1} in March 2011 to 3,681,300 cells L^{-1} in January 2010. The total mean concentration lay at 491,400 ± 199,800 cells L^{-1}. The mean for the winter months lay at 1,325,700 ± 771,900 cells L^{-1}, and the total mean for all non-winter months was 246,000 ± 86,100 cells L^{-1}, showing a much higher standard error for the winter months than the remainder.

Comparatively, the dinoflagellate concentration varied between 6000 cells L^{-1} in August 2010 to 200,700 cells L^{-1} in June 2011. The mean lay at 32,000 ± 8400 cells L^{-1}.

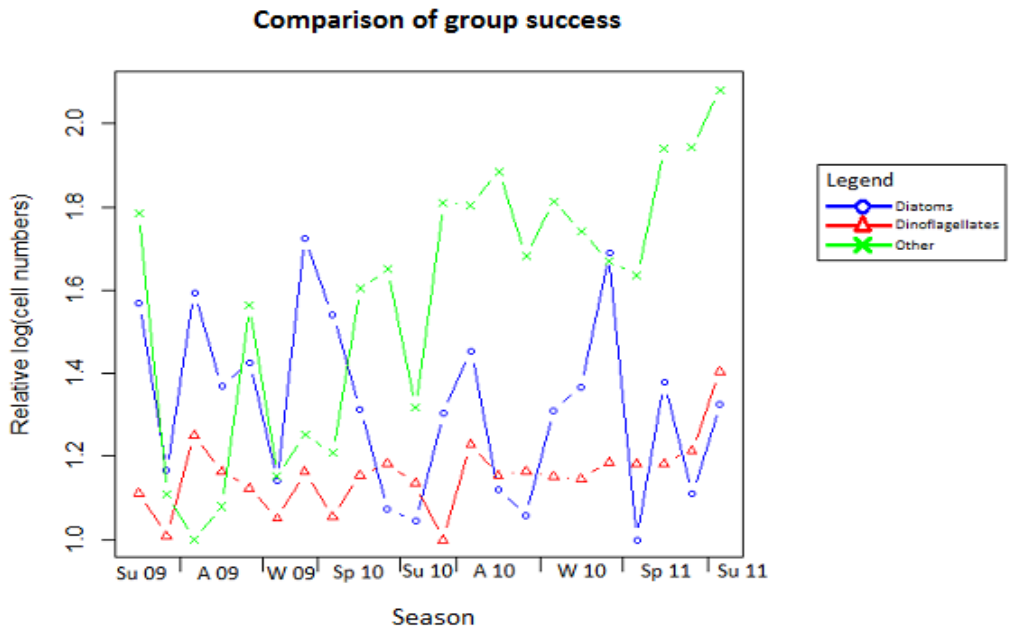

Figure 3.2.3: Graph showing the concentration of each algal group in relation to their lowest registered concentration throughout the sampling period. X-axis labels are season and year. Concentrations were log-transformed to allow for a clearer image.

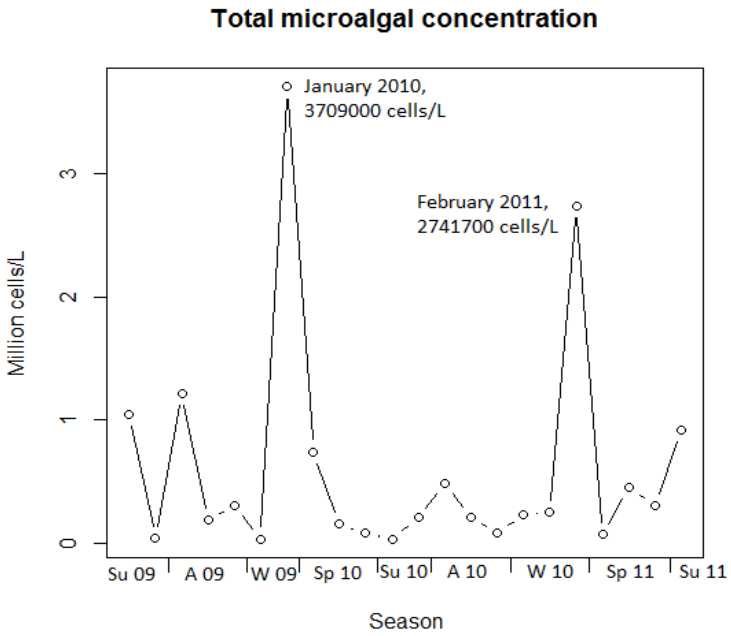

Figure 3.2.4: Graph showing the concentration of phytoplankton throughout the sampling period in millions of cells per liter. X-axis labels are season and year. The two highest peaks have been labelled with their sampling month and specific cell concentrations.

Figure 3.2.3 shows that there are two major peaks for the diatoms, both in the winter seasons, while the dinoflagellates have three major peaks. Two of these are in the beginning of the autumn seasons, whereas the third is in the beginning of the summer of 2011. All three peaks of dinoflagellates coincide with lesser peaks of diatoms. It is impossible to tell if the third peak would be higher further into the season, as it is at the end of the data set.

For the total concentration of algae, there are two clear peaks: in January 2010 and in February 2011 (Fig. 3.2.4). In January 2010, there was a bloom of several diatoms, with the vast majority of the cell numbers belonging to *Pseudo-nitzschia* spp. (1,616,000 cells L^{-1}) and *Skeletonema* spp. (1,396,900 cells L^{-1}). In February 2011 there was another diatom bloom, with the majority of the bloom being formed by cells of *Skeletonema* spp. (2,337,000 cells L^{-1}).

3.3 Variation in size and morphology of *Dinophysis*

3.3.1 *Dinophysis acuminata*

The length of *D. acuminata* was measured to be between 28.6 and 60.6 µm, with a mean length of 40.0 ± 0.6 µm. Most cells were found occupying the 35-39.9 µm interval, with 40.5% of all measured cells located here (Fig. 3.3.1 C).

The length of *D. acuminata* showed a marked difference between the seasons, with the variation being reminiscent of a wave-like pattern with a wavelength of approximately nine months, with highest mean lengths of respectively 48.1 ± 1.9 µm and 47.8 ± 1.8 µm in November 2009 and August 2010, and lowest mean lengths of respectively 34.7 ± 2.4 µm and 38.1 ± 2.2 µm in May 2010 and December 2010 (Fig. 3.3.1 A, Appendix B). There was also evidence to suggest that salinity and temperature influenced the length of the species (Appendix B).

The greatest differences in mean length were between May 2010 and November 2009 and between August 2010 and May 2010 with respective differences of -13.4 ± 4.4 µm and 13.1 ± 5.6 µm (Fig. 3.3.1 A, Appendix B).

Though the length – width ratio did seem to vary between the seasons, the highest difference was calculated to be only 0.15 ± 0.15 between winter and autumn, giving it a relatively high adjusted p-value of 0.033 (Fig. 3.3.1 B, Appendix B). Salinity also seemed to influence the ratio (Appendix B).

The appearance of *D. acuminata* deserves special mention, as it was quite variable, with at least 5 distinct morphologies being observed (Fig. 3.3.2).

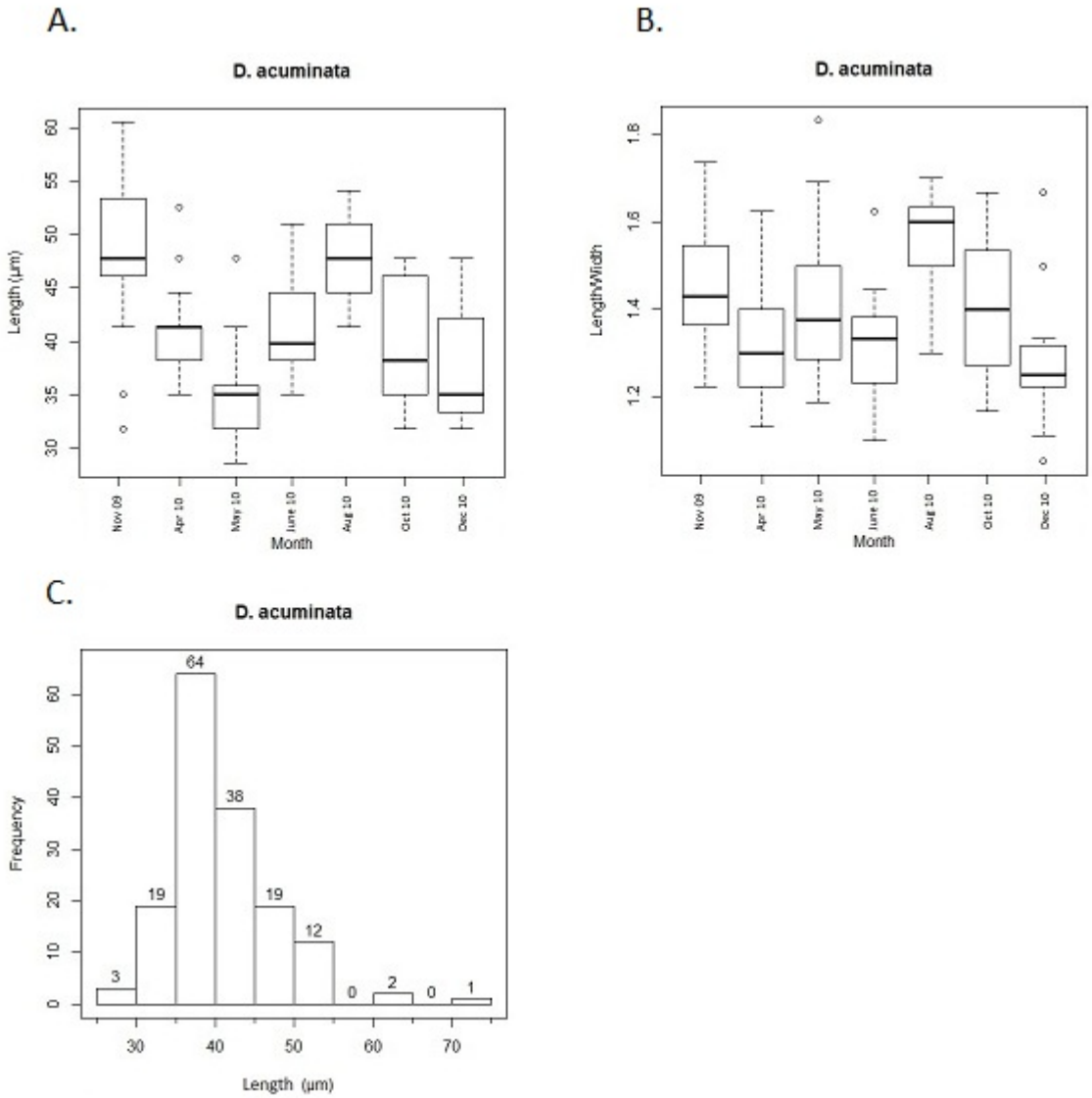

Figure 3.3.1: A) Box plot of the measured lengths of *D. acuminata* for the relevant months. B) Box plot of the ratio between the length and width of *D. acuminata* for the relevant months. C) Histogram that displays the frequency with which the lengths of *D. acuminata* cells were found within each length interval. Contains data from all measured *D. acuminata*. n=158

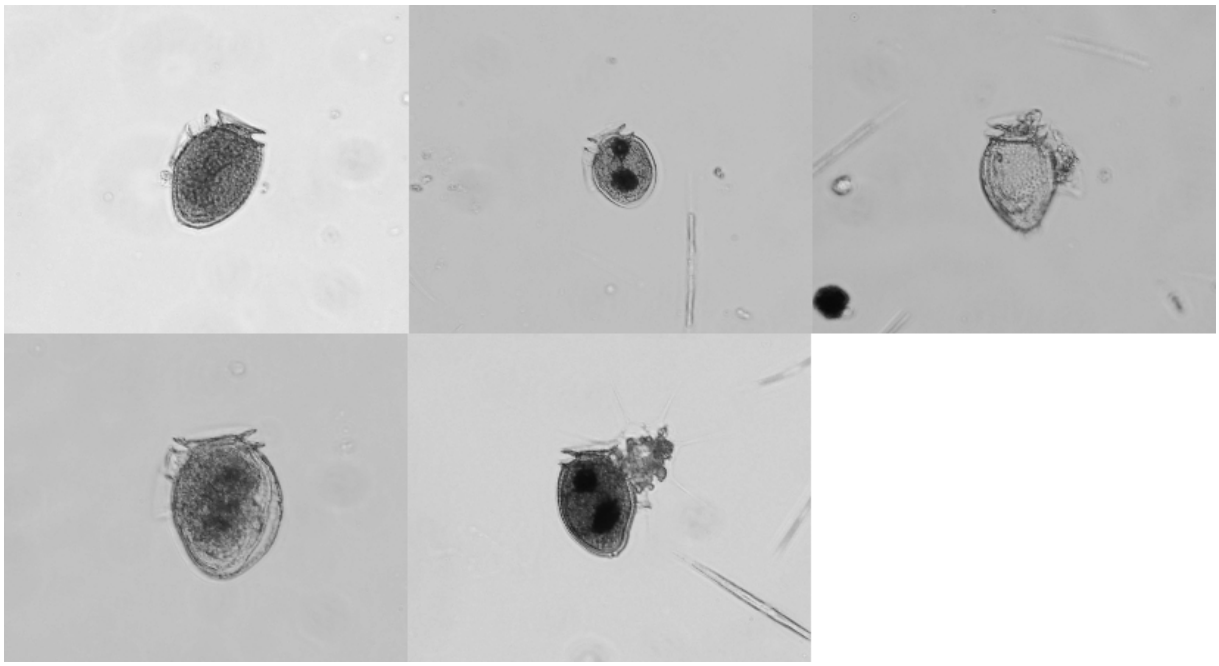

Figure 3.3.2: Different morphological appearances of *D. acuminata*. 1) April 2011. 2-3) December 2010. 4) March 2011. 5) November 2009.

3.3.2 *Dinophysis acuta*

The length of *D. acuta* was measured to be between 60.5 and 70.1 µm, with a mean length of 65.3 ± 0.3 µm. Most cells were found occupying the 60-64.9 µm interval, with 51.5% of all measured cells located here (Fig. 3.3.3 C).

The length of *D. acuta* proved to have only insignificant variation between the months, with the highest calculated difference being between December 2010 and September 2010 with 1.8 ± 1.9 µm, thus including 0 with an adjusted p-value of 0.06 (Fig. 3.3.3 A, Appendix B).

In addition, the ratio between length and width in *D. acuta* proved to be nowhere near significantly different between the relevant months (Fig. 3.3.3 B, Appendix B).

There were no immediately apparent differences in morphological appearance between the individual cells of *D. acuta*.

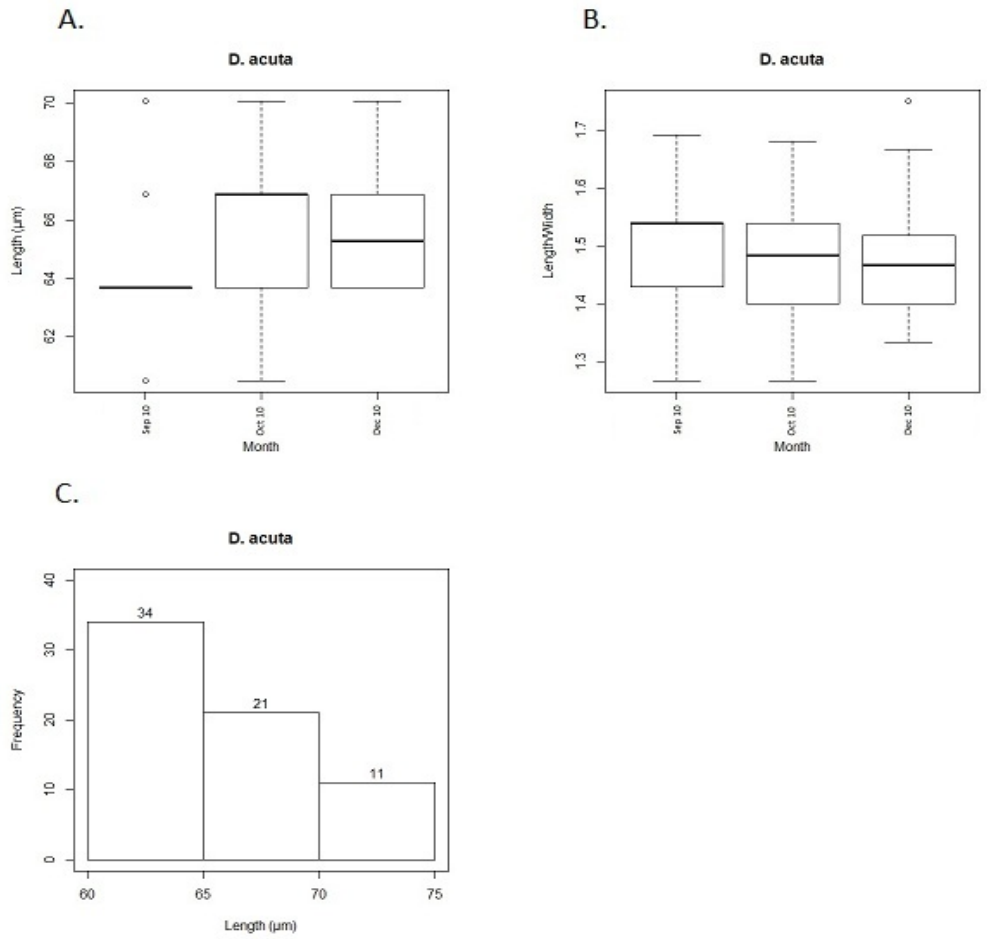

Figure 3.3.3: A) Box plot of the measured lengths of *D. acuta* for the relevant months. B) Box plot of the ratio between the length and width of *D. acuta* for the relevant months. C) Histogram that displays the frequency with which the lengths of *D. acuta* cells were found within each length interval. Contains data from all measured *D. acuta*. n=66.

3.3.3 *Dinophysis norvegica*

The length of *D. norvegica* was measured to be between 38.2 and 78.0 µm, with a mean length of 61.5 ± 0.2 µm. Most cells were found occupying the 60-64.9 µm interval, with 47.0% of all measured cells located here (Fig. 3.3.4 C).

The length of *D. norvegica* appeared to have changed significantly between the seasons, with the highest calculated mean lengths being 66.1 ± 1.2 µm in April 2010 and 66.0 ± 0.8 µm in April 2011, and the lowest calculated mean length being 55.7 ± 1.1 µm in October 2010 (Fig. 3.3.4 A, Appendix B).There was also evidence towards salinity being a factor for the length of the species (Appendix B).

The length-width ratio of *D. norvegica* did not noticeably change between the seasons, but there was evidence to suggest that salinity and temperature had an effect (Fig. 3.3.4 B, Appendix B).

There were no immediately apparent differences in morphological appearance between the individual cells of *D. norvegica*.

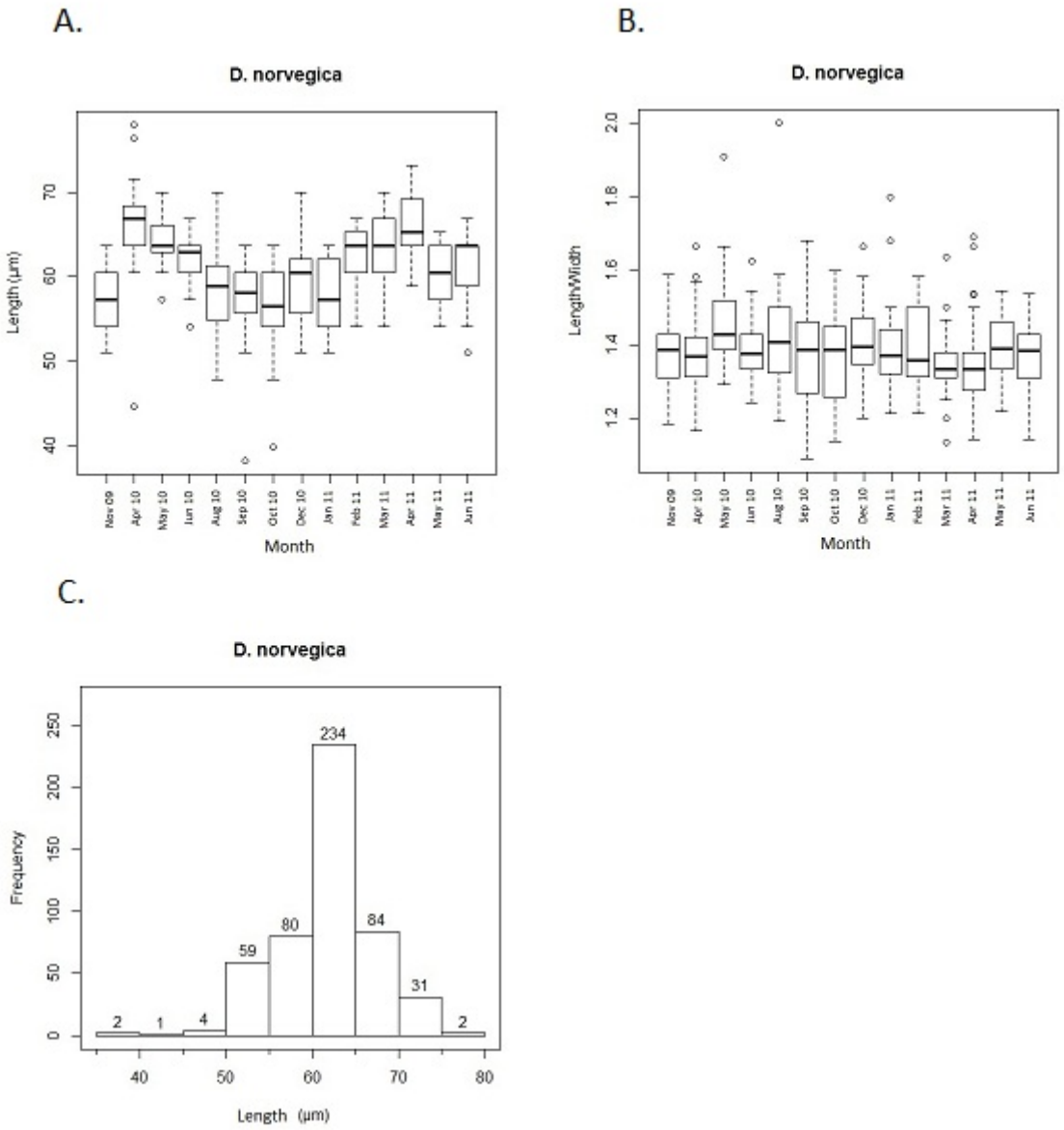

Figure 3.3.4: A) Box plot of the measured lengths of *D. norvegica* for the relevant months. B) Box plot of the ratio between the length and width of *D. norvegica* for the relevant months. C) Histogram that displays the frequency with which the lengths of *D. norvegica* cells were found within each length interval. Contains data from all measured *D. norvegica*. n = 497.

3.3.4 *Dinophysis rotundata*

The length of *D. rotundata* was measured to be between 33.4 and 54.1 µm, with a mean length of 45.3 ± 0.7 µm. Most cells were found occupying the 40-44.9 µm interval, with 42.4% of all measured cells located here (Fig. 3.3.5 C).

The length of *D. rotundata* did not show any significant changes between the months, with the highest calculated differences being 4.1 ± 6.4 µm and 4.0 ± 6.3 µm between June 2010 and November 2009 and between June 2010 and December 2010, respectively, both with an associated adjusted p-value of 0.37 (fig 3.3.5 A, Appendix B). There was evidence towards temperature having had an effect on the length of the species (Appendix B).

The length-width ratio of *D. rotundata*, likewise, did not show any significant differences between the months, and the greatest difference that could be calculated here was between September 2010 and December 2010, with 0.1 ± 0.1, and associated adjusted p-value of 0.08 (Fig. 3.3.5 B, Appendix B). There was no clear effect of salinity or temperature on the ratio of *D. rotundata* (Appendix B).

There were no immediately apparent differences in morphological appearance between the individual cells of *D. rotundata*.

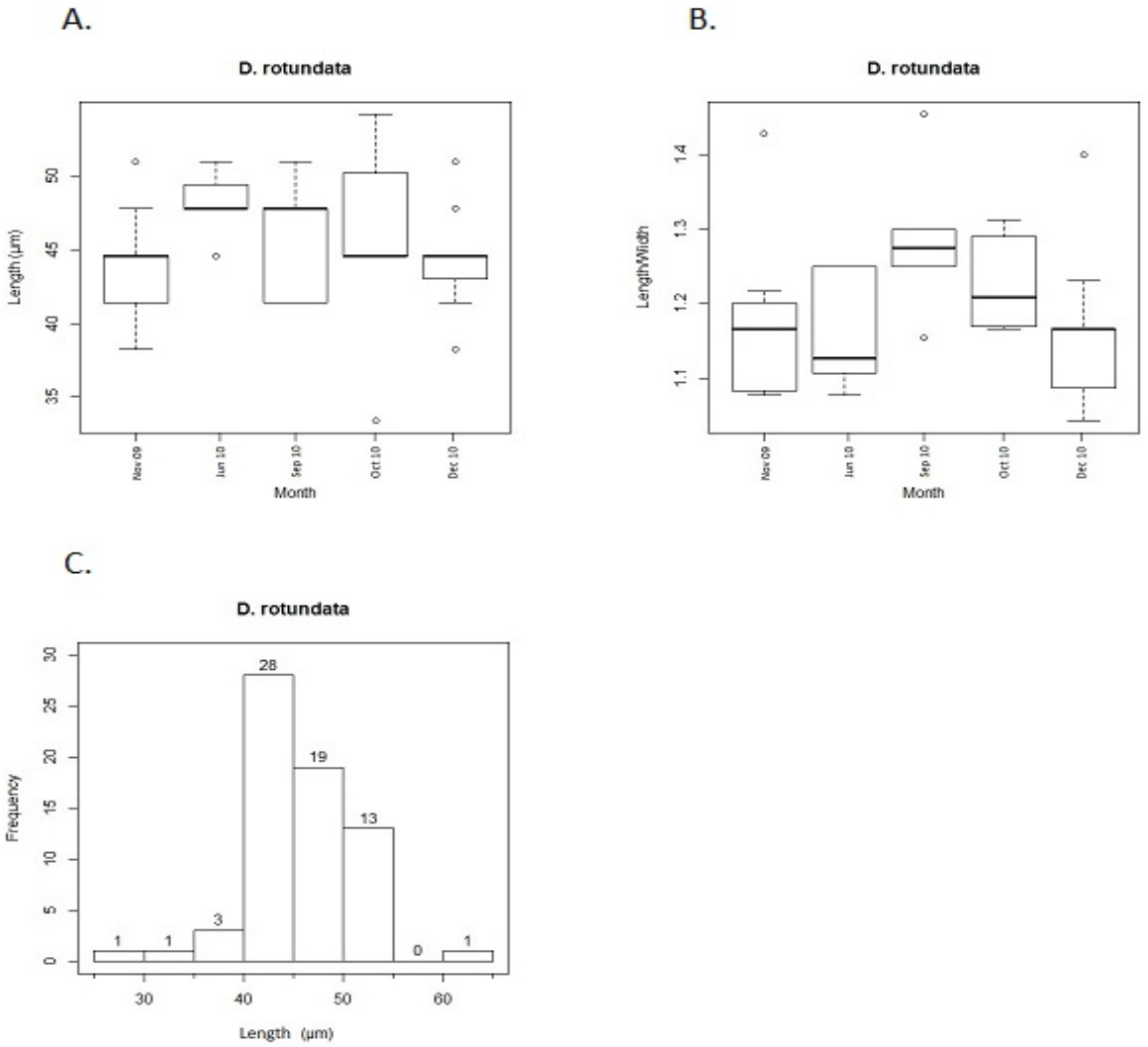

Figure 3.3.5: A) Box plot of the measured lengths of *D. rotundata* for the relevant months. B) Box plot of the ratio between the length and width of *D. rotundata* for the relevant months. C) Histogram that displays the frequency with which the lengths of *D. rotundata* cells were found within each length interval. Contains data from all measured *D. rotundata*. n = 66

3.4 Abundance variations in *Dinophysis*

The highest concentration for *Dinophysis* was found in May 2010, with an estimated 2400 cells L^{-1}. The lowest concentration different from zero was found in November 2009, December 2009 and August 2010, with an estimated concentration of 100 cells L^{-1}. *Dinophysis* was not found in August 2009, October 2009, January 2010, March 2010, September 2010, November 2010 or December 2010. *Dinophysis norvegica* was present for all months when *Dinophysis* was detected, except for September 2009 and August 2010 (Fig. 3.4.1).

Dinophysis concentration did not show to be statistically different between the seasons, nor by variations in salinity or temperature (Appendix B).

Dinophysis tripos was also registered in net haul samples from November 2009, September 2010 and October 2010, but at far too low concentrations to be of any statistical use.

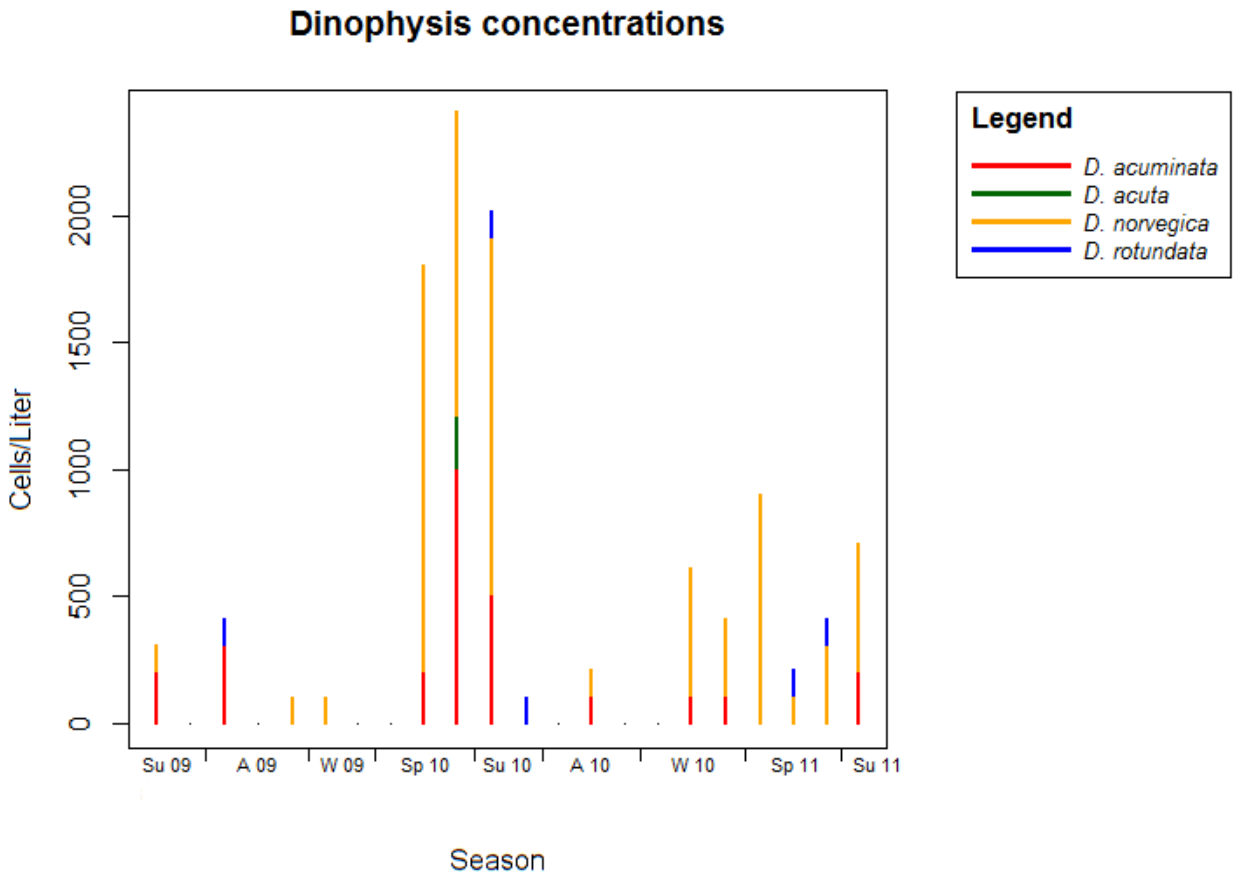

Figure 3.4.1: A bar plot depiction of the concentrations of *Dinophysis* spp. through the sampling period. X-axis labels are season and year.

4 Discussion

4.1 Analysis of methods

4.1.1 Sample collection

Although the sampling methods were about as common as they come, there are still challenges to be overcome with them. Firstly, on the subject of the net hauls, a mask width of 20 µm was used. A mask width of this size could potentially allow a few of the smaller *Dinophysis* cells to escape collection. However, as most *Dinophysis* are well above 20 µm in length, as well as the fact that the mesh size tends to, in practice, be smaller than 20 µm due to clogging by other cells and debris, this should not be considered a noteworthy problem.
As for the biodiversity samples, they were collected by taking natural water samples as described in chapter 2 – Materials and Methods. The main issue that can be seen with this method is that it is subject to patchiness. To elaborate, patchiness is a term used to describe the situation in which populations of plankton are situated in "patches" of ocean (e.g. Bainbridge, 1957). This means that when taking a sample from a very small part of the ocean, odds indicate that it is highly possible that said sample would not represent the majority of the area's total population due to hitting, or not hitting, a "patch". This is also a potential problem with vertical net hauls, but horizontal net hauls have a lower risk due to its general coverage of a larger area.
Lugol's solution is only considered to be reliable as a fixative up to one year, and many of the samples used for size measurements were stored for a longer period of time. Therefore, although most cells appeared perfectly normal, there is the possibility that the data may have been influenced by this.

4.1.2 Cell counts and identification

There are some issues related to the cell counts. For one, experience and practice in the counter is a strong factor when considering how well the species are identified and counted. Further, the cells' orientation after sedimentation is not always suitable for species identification, and may sometimes cover other cells, providing further difficulties for identification.

Another challenge in cell counts is that the identification of some species is not possible in a light microscope, nor even in an electron microscope in some further cases.
In addition, it is generally recommended to count at least 100 cells for a relatively reliable 95% confidence interval (Lund et al. 1958 according to Venrick 1978), but some species have typically low concentrations to the point where counting 100 cells is not feasible. *Dinophysis* is an example of this. There is therefore some statistical unreliability inherent in the quantitative data where the concentration is low.
Finally, some issues with the scanning electron microscopy samples prevented identification of several individuals that might otherwise have been identified. One of these issues was loss of large cells from the samples, due to lack of adhesion to the lysine-coated glasses, which could have been a result of the lysine coating method itself, or the lysine possibly having been of insufficient quality due to improper handling, long-term storage, or similar issues. In addition, in some cases the samples were completely covered in a form of organic web-like material. The most likely reason for these occurrences seemed to be a contamination in the seawater-dissolved OsO_4 that was used during preparation.

4.1.3 Measuring method

Given that the measurements were done manually, there is in itself an inherent element of human error, both in regards to inattentiveness and in regards to misreading, off-placement or even mistakes in species identification. However, given that processing by machine contains within it risks in itself, in addition to still containing some elements of human error, there does not seem to be any good reasons to choose machine computation over hand measurements, aside from the obvious time aspect.
One problem posed by manual measurements is that determining the area of each specimen is nigh impossible to do in any accurate fashion, forcing a reliance on the less accurate length-width ratio indicator.

4.1.4 Statistical analyses

Statistical analyses were done on large parts of the data set, most notably on the lengths and ratios of the *Dinophysis* cells. Here, ANOVA-tests and Tukey's Honestly Significant Difference tests were applied, as described in chapter 2 – Materials and Methods.

ANOVA tests are designed to work on independent, normally distributed material, and all lengths and ratios were relatively close to a normal distribution. The exception was the ratio measurements of *D. rotundata*. ANOVA is a very robust test towards non-normality, allowing relatively large discrepancies before it becomes unusable. In addition, one can assume independence in the material, even though the sampling location was the same for each sampling date. This is due to it being highly unlikely that removing algae from the location would impact the population one month later in an open ocean environment, where water masses and their inhabitants have relatively free and constant movement.

Another potential issue related to the statistical tests is that the sample sizes in most cases were quite a lot lower than preferred. The intention was to have at least 30 measurements per species per sampling date, but unfortunately only 44.8% of the used data complied with this. The most reliable data is therefore that of *D. norvegica*, which complied with the 30 measurement minimum for 71.4% of the used data, with the lowest number of measurements being 20, and the most unreliable is without a doubt *D. rotundata*, with no month having a higher number of measurements than 11.

4.2 Hydrography

The temperature variations followed the same pattern that had been observed in the area in recent years by the Norwegian Institute for Water Research (NIVA). Both their report and this study showed high temperatures in the summer and low temperatures in the winter, keeping below 20°C and above 0°C. The exception with this study was January 2010, which showed a surface temperature of -1.2°C (Fig. 3.1.1 A, Appendix A). Likewise, NIVA's findings in salinity were not dissimilar. They reported a surface salinity of generally <30, with salinities dropping to approximately 20°C in the late spring or early summer (Walday et al., 2010). In this study, the salinity also seemed to show such variations, with only two readings showing PSU above 30 (October 2009 and March 2010), and readings generally occupying the 20-25 interval. The two lowest readings, in August 2009 (12.7) and April 2011 (14.1), corresponded with higher surface temperatures than the previous months (Fig 3.1.1 A,B, Appendix A). The station's close proximity to the rivers Glomma and Drammenselva is also likely to noticeably impact the salinity (Fig. 2.1.1). The pycnocline was well-defined in June-August 2009, and broke down in September. It began reforming in December-January, fluctuating slightly in March 2010, before showing a clear stratification from April to November. Breakdown in 2010 occurred around December, with

stratification beginning to taking place around February 2011, after which time it stayed stratified until the end of this study. During the stratified periods, the pycnocline was only deep (>20m) in September 2010 and March 2011 (Appendix A).

4.3 Microalgal biodiversity

A Shannon's index range of 1.1-3.5 bits indicates a relatively low diversity in species when considering equitability. The fact that temperature was the only measured hydrographical factor that showed significance is noteworthy, though given the large p-value of 0.044, one must still consider the possibility of making a type I mistake in this instance (Appendix B).

Between June 2009 and June 2010, a total of 90 species were found in the cell counts. This varies only slightly from the total species count of 82 between August 2010 and June 2011 (Appendix D). Numbers from the Institute of Marine Research in Norway (IMR) at the same station show a species richness of 62 (January-September 2011) to 80 (January-November 2009) species (Lars Naustvoll, personal communication). Differences between these numbers could come as a result of differences in experience, leading to incorrect species separation in this paper's cell counts. This possibility is slightly increased in likelihood by the fact that total species found dropped by nearly 10 in the second year compared to the first. However, the numbers are not so far apart that an actual variation in the species richness can be ruled out.

This variation can be explained by a difference in detection rates of lower abundance species. Between 16 and 53 species were found at a given month in the cell counts, which is a considerable difference in species richness, yet there is no statistical evidence explaining the reason for this from this data set (Appendix B). A more solid look at which specific species made up the diversity, and how this changed over the study period correlated with hydrographical data might have revealed more information, but such an undertaking lies outside the scope of this thesis.

It should also be clarified that the data used for measuring the biodiversity was taken only from the cell counting data, in order to ensure equality in the sample sizes. It is therefore highly possible that the actual species richness would be higher than reported in this paper, since one can never be certain of how many species were not included in a sample. This is compounded by the problems with microscope identification discussed in section 4.1.2. Shannon's index is more robust in this regard, as any species not included in a sample would likely be relatively rare, and would therefore only slightly increase the value.

4.4 Phytoplankton abundance

There were two major peaks in phytoplankton abundance. These occurred in January 2010 and February 2011 and were dominated by diatoms, especially *Pseudo-nitzschia* spp. and *Skeletonema* spp. in January and *Skeletonema* spp. in February (Fig. 3.2.4). These two peaks both occur at the time of, or briefly after the year's first formation of a stratified layer, suggesting that these were typical vernal blooms.

4.4.1 Diatoms versus dinoflagellates

The two highest diatom abundance peaks were both in the month of February, while the two of the highest dinoflagellate concentrations were both found in September, and a third, higher peak was registered in June 2011. All three dinoflagellate peaks coincided with peaks of diatoms.
These findings compare well to the findings of Paasche in 1976 (Paasche, 2005), in which dinoflagellates peaked around March, May and July/August, and diatoms peaked around March/February, May and August/September. In these findings, the dinoflagellate concentration was also higher than diatom concentrations in the late summer, which also matches the findings in this paper.

4.4.2 *Dinophysis*

Dinophysis, when present, typically held concentrations of approximately 500 cells L^{-1}, but showed concentrations of around 2000 cells L^{-1} in the late spring/early summer of 2010. This high increase may be attributed to a bloom of *D. norvegica* and potentially also *D. acuminata*, which both showed much higher concentrations in this period than for most of the remaining sampling dates.
Dinophysis acuta was only found in the cell counting procedure in May 2010, and then only in the low concentration of 200 cells L^{-1}, providing little basis for which to make interpretations, apart from pointing out its comparatively low abundance. However, it should be noted that *D. acuta* has a toxicity threshold value of only 200 cells L^{-1} (Johnsen and Lømsland, 2010).
Dinophysis rotundata appeared more sporadically, making appearances in cell counts in September 2009, June 2010, August 2010, April 2011 and May 2011. Neither of these months showed a higher calculated concentration than 100 cells L^{-1}. The fact that *D. rotundata* is exclusively a heterotrophic species may account for some of the unpredictability here, as its concentrations may vary based on

the accessibility of prey. Furthermore, as shown in table 2.2, *D. rotundata* did appear in most of the net hauls, but considering the low numbers of cells found in these, the seemingly random appearances may be simply explained by the fact that such a relatively low abundance led to this species having only a low chance of appearing in the counting sample.

Dinophysis norvegica showed high concentrations in May 2010, June 2010 and April 2011, and was detected more frequently than the other species of *Dinophysis*.

All *Dinophysis* cell concentrations were low in the period October-January, which may be partly due to the breakdown of the pycnocline that happened around this time.

The presence of *Dinophysis tripos* in November 2009, September 2010 and October 2010 was in accordance with the observation months of Johnsen & Lømsland (2010). That *D. tripos*, in addition to several other southern distribution species such as *Pseudosolenia calcar-avis* and *Chattonella globosa*, have begun to spread thus far North may be possible indicators of global warming effects on the phytoplankton composition in Norway's coastal waters (Johnsen and Lømsland, 2010).

4.4.3 Chlorophyll *a*

Chlorophyll *a* was measured both *in vivo* by a fluorometer mounted on the CTD apparatus, and *in vitro* by fluorometer analysis of filtered and cryogenically preserved matter from natural water samples.

The chlorophyll *a* concentrations showed generally good consistency when compared to the cell counts (Figs. 3.1.2, 3.2.4). August 2009, however, showed an incredibly high maximum chlorophyll *a* concentration at 1m depth, compared to a very low cell concentration of <50,000 cells L^{-1}. The most likely explanation in this instance, especially given that it was more than twice as high as the second highest chlorophyll *a* concentration, is that this reading was incorrectly calibrated, which also seemed to be reflected in the rest of that month's chlorophyll *a* readings (Appendix C).

August 2009 reading aside, the average chlorophyll *a* concentration was 2.3 µg L^{-1}. This corresponds to that previously reported the same station, as previous studies in recent times have reported it to contain a median chlorophyll *a* concentration of approximately 2.6 µg L^{-1} (Dragsund et al., 2006). It is also consistent with readings by NIVA at this station, where chlorophyll *a* was measured to stay mainly within the 1-7 µg L^{-1} range (Walday et al., 2010).

The chlorophyll *a* peaks in January 2010 and February 2011 corresponded with the two highest peaks in the cell counts (7.7 µg L^{-1} and 3.7 million cells L^{-1} in January 2010; 5.4 µg L^{-1} and 2.7 million cells L^{-1} in February 2011). However, the peak in chlorophyll *a* in June 2009, at 7.2 µg L^{-1} occurred with a cell concentration of only 1 million cells L^{-1}. *Dactyliosolen fragilissimus*, 492200

cells L^{-1}, *Skeletonema* spp., 149200 cells L^{-1} and *Dinobryon* sp., 90400 cells L^{-1} made up most of the phytoplanktonic cell concentration at this date, and although *D. fragilissimus* is not a small species, and it does contain numerous chloroplasts (Throndsen et al., 2007), it is hard to imagine that this alone should bring chlorophyll *a* levels up to nearly the same point as it was with a concentration of nearly 4 million cells in the surface. One potential explanation is that there might have been a large concentration of picophytoplankton that due to their small size went undetected. The *in vitro* and *in vivo* analyses revealed highly different results (Fig. 3.1.3). As an example, *in vitro* analysis showed the highest chlorophyll *a* abundance at 2 meters in June 2009 and April 2010, whereas *in vivo* analysis placed the chlorophyll *a* peaks at approximately 18 and 12 meters, respectively. This suggests that neither of these methods can be wholly trusted to provide an accurate picture.

4.5 Variation in size and morphology of *Dinophysis*

4.5.1 *Dinophysis acuminata*

Dinophysis acuminata showed high variability in its cell length, both between months and as a response to changes in salinity. Differences in ratio between length and width were also shown, dependent on month and the combined effect of salinity and temperature. The measured lengths lay between 28.6-60.6 µm. (Appendix B). In addition, the general appearance of *D. acuminata* varied quite visibly (Fig. 3.3.2).

The shortest measured length corresponds well with that recorded by Solum (1962), who found *D. acuminata* to vary between 29 and 53 µm. The greater maximum length is also not unheard of, as Larsen (2002) recorded *D. acuminata* between 31.0 and 75.6 µm. For comparison, Hansen and Larsen (1992) postulated a length range of 40-45 µm, which is far more narrow than what has been registered in this study. Only 24.1% of the measurements in this study lay within this interval.

4.5.2 *Dinophysis acuta*

Dinophysis acuta did not show any significant variability in its cell length, which may be attributed in no small part to the fact that only three months, all located at the end of the year, had a high enough abundance for use in statistical tests (Table 2.2). Its length-width ratio was likewise not

significantly different. The measured lengths lay between 60.5-70.1 µm (Appendix B). This is within the measurements found by Larsen (2002), who recorded between 60.7 and 93.9 µm lengths. Conversely, it is clearly lower than the size range postulated for this species by Hansen & Larsen (1992), who reported a length range of 70-90 µm for this species. Only 16.7% of this study's *D. acuta* cells occupied this interval.
The data set was insufficiently large for testing the influence of salinity or temperature, and so it is unclear whether these factors had an effect on the size of this species.

4.5.3 *Dinophysis norvegica*

Dinophysis norvegica proved to be quite variable in its cell length throughout the years, both between the seasons and as a function of salinity. The length-width ratio only showed slight significance with temperature as a factor, and a somewhat stronger significance for salinity. The measured lengths lay between 38.2-78.0 µm (Appendix B). This is noticeably lower minimum size than the 48.1 µm that was reported by Larsen (2002). Conversely, her maximum length result of 89.5 µm is just as noticeably higher than this study's maximum length. Comparing this study's results to Hansen & Larsen (1992), one finds that this study's measurements far eclipses their postulated length range of 50-60 µm, as only 28.0% of the results occupy this interval.

4.5.4 *Dinophysis rotundata*

Dinophysis rotundata did not show any significant change in neither cell length nor length-width ratio over the years, and the only hydrographical factor that seemed as if it might have influenced the size ratio was temperature, which showed a weakly significant effect on the cell lengths, and was almost significant for having an effect on the length-width ratio. The measured lengths lay between 33.4 - 54.1 µm (Appendix B). This is also quite a larger range than that postulated by Hansen & Larsen (1992), who found the range 45-50 µm for this species, which translates into only 28.8% of this thesis' *D. rotundata* measurements.

4.5.5 Reasons for size variation

Separate species

It has been suggested that some species of *Dinophysis*, most notably *D. acuminata*, should be split into several other species (Paulsen, 1949). Such a situation could explain some of the variation in size.

However, for all four species the histograms of their length reveal only one peak, with a relatively steady decrease in frequency as the length interval shifts from said peak (Figs. 3.3.1 C, 3.3.3 C, 3.3.4 C and 3.3.5 C). This indicates that the recorded variations in length are simply natural size variations of one group, since in the event of separate species, one would expect there to be several peaks, each with their own normal distribution. Therefore, it does not seem likely that the varying intraspecific sizes are in themselves indications that incorrect species separation is responsible for the morphological distinctions.

Life cycle

Another possible explanation for these size variations is found within the life cycle of the genus *Dinophysis* as proposed by Reguera & González-Gil (2001). They claim that *Dinophysis* has a polymorph life cycle in which large, vegetative cells may sometimes divide into two smaller cells, which may function as gametes in an anisogamous sexual reproduction. They have also documented the ability of small cells to grow into large cells. The full cycle as suggested by Reguera & González-Gil (2001) is shown in figure 4.5.1.

There is also the possibility that the size of *Dinophysis* varies in cycles on the year-scale, but the scale of this study is not such that it has the capability of detecting it.

Phenotypical plasticity

As suggested by Solum (1962), there is a potential for phenotypical plasticity to explain some of the variation. Solum's findings were that higher salinity made cells of *D. lachmanni*, a synonym of *D. acuminata*, longer. The *D. acuminata* in this study also showed variability with salinity, though the trend here was in the opposite direction. Larsen (2002) found no correlation between salinity and cell length, and is in this supported by Zingone et al. (1998).

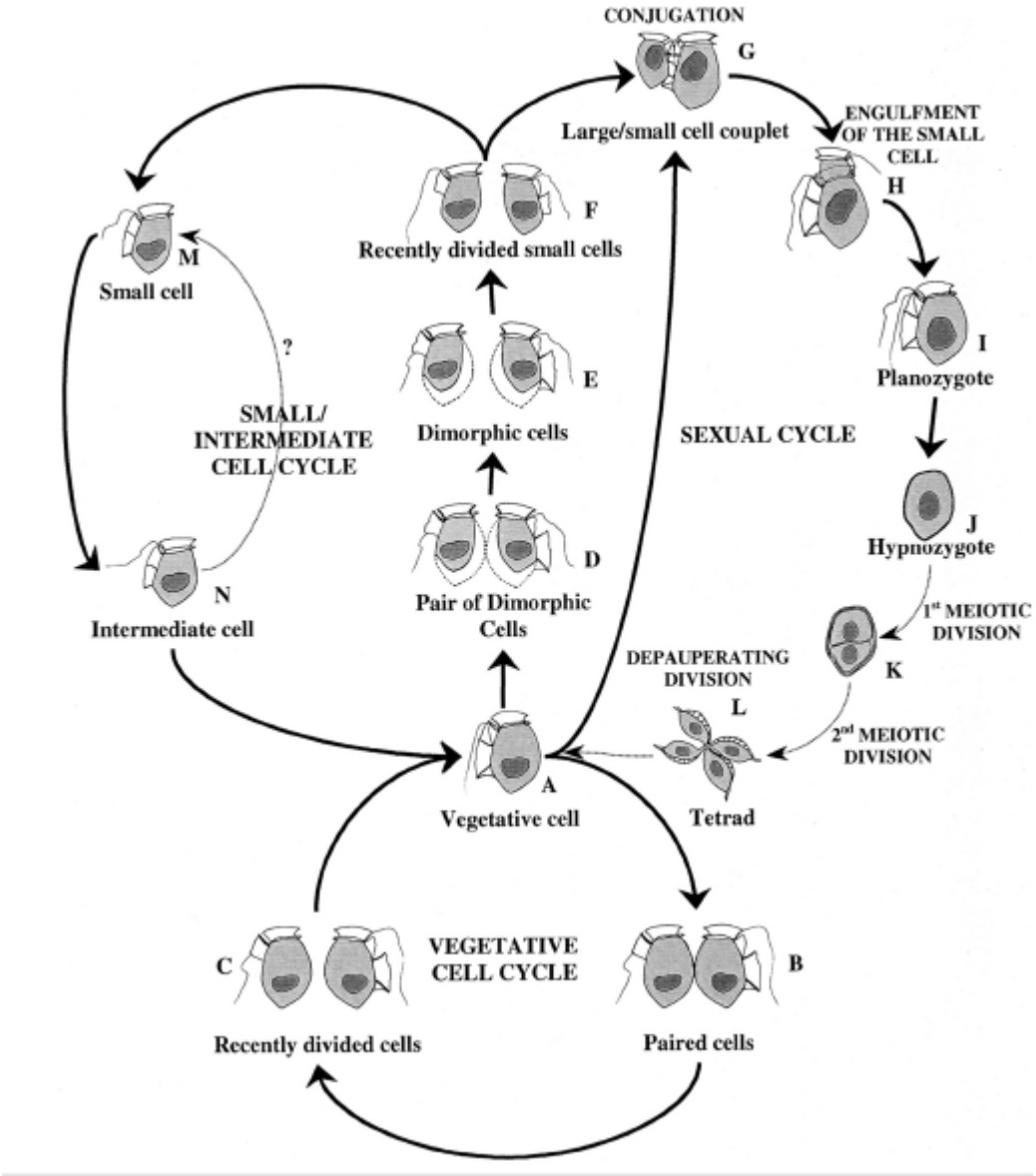

Figure 4.5.1: From Reguera & González-Gil (2001). Diagram of the confirmed (solid line) and hypothetical (dotted line) stages of the life cycle of *Dinophysis* spp. (A-C) Vegetative cycle. A) Fully developed vegetative cell. B) Paired cells. C) Recently divided cells with incompletely developed left sulcal lists. (A-L) Sexual cycle. D) Pair of dimorphic cells as a result of a depauperating division, with dotted lines representing the contour of the maternal hypothecal plates. E) Recently separated dimorphic cells. F) Recently divided small cells, still with incomplete left sulcal lists. G) Small cell acting as a (+)-anisogamous gamete and large cell acting as a (-)-anisogamous gamete. H) Engulfment of the small cell through the apical end of the sulcus. I) Planozygote with two trailing flagella. J) Suggested double-walled hypnozygote. K) Suggested first meiotic division. L) Tetrad. (M-N) Simplified small/intermediate cell cycle.

4.6 Summary and concluding remarks

Hydrographical and chlorophyll *a* readings were within previously established parameters for the area, with pycnoclines forming roughly in the spring and breaking down roughly around the late autumn. Salinity kept a generally steady PSU strength of approximately 20, though with some fluctuations, possibly owing to temperature and river runoff variations.

Diatoms showed a higher abundance than dinoflagellates throughout the study, with the exceptions of the early summer of 2010, the late autumn of 2010, March 2011 and the early summer of 2011. Vernal blooms were dominated by diatoms, and occurred in January 2010 (3.7 million cellsL^{-1}) and February 2011 (2.7 million cells L^{-1}), associated with the years' initial stabilization of the pycnocline.

Shannon's diversity index revealed a range of 1.1-3.5 bits, and species richness lay between 16 and 53 species for each month. No reliable significance was found for correlating neither species richness nor Shannon's diversity index to variations in salinity and temperature, nor were the values statistically different between the seasons. Total species found in cell counts across one year was 90 in the period 2009-2010, and 82 in the period 2010-2011.

Dinophysis species generally kept low cell numbers (approximately 300 cells L^{-1}), but showed an increase up to around 2000 cells L^{-1} in April-June 2010. *Dinophysis acuminata* and *D. norvegica* made up most of the abundance. *Dinophysis acuta* and *D. rotundata* never showed higher concentrations than 200 cells L^{-1} and mostly went undetected by the cell counts. *Dinophysis tripos* was present in the study, but in too low abundances to be registered by cell counts.

All four species showed large variations in size, and all but *D. acuta* varied outside previously established ranges.

Dinophysis norvegica displayed a much higher mean length in the spring than in the autumn, while *D. acuminata* conversely showed a greater mean length in the autumn and the summer than in the spring.

Salinity and temperature both seemed to have some correlation with the sizes of *Dinophysis*, with some variations based on species. However, these findings are in conflict with other studies, and further research is needed to see whether these correlations translate into an actual effect on the size of *Dinophysis*. Furthermore, nearly all correlations were weak, showing p-values of over 0.005, with the exceptions of temperature with length of *D. acuminata* and salinity with length-width ratio of *D. acuminata*.

Further challenges lie in obtaining a clear understanding of what impacts the sizes and shapes of

Dinophysis species, as studies demonstrate conflicting results. A good first step in this would be to obtain a solid understanding of the life cycle of the genus, for which further research is required.

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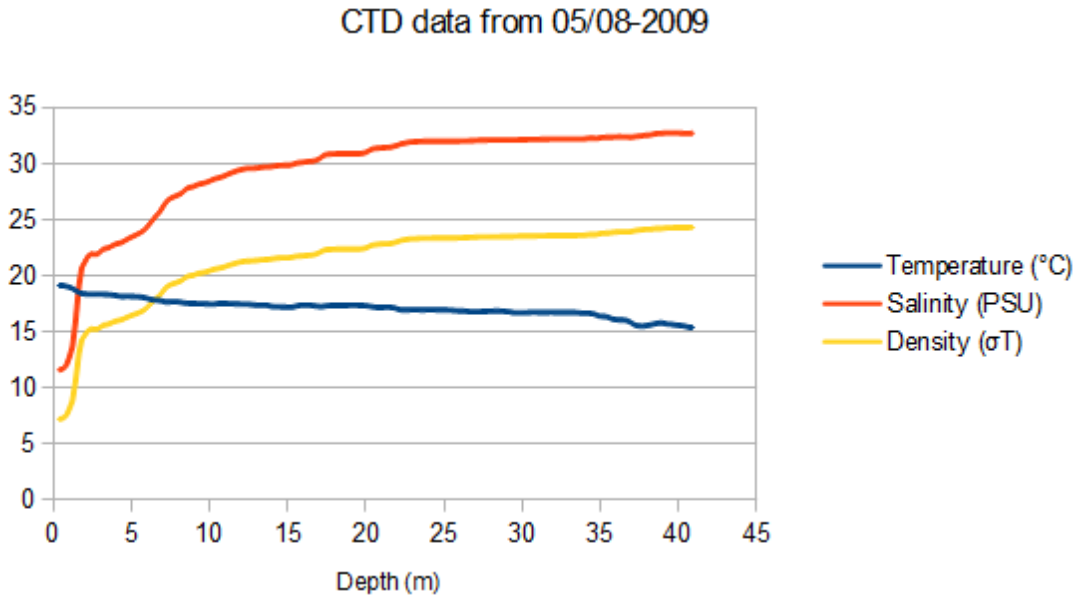
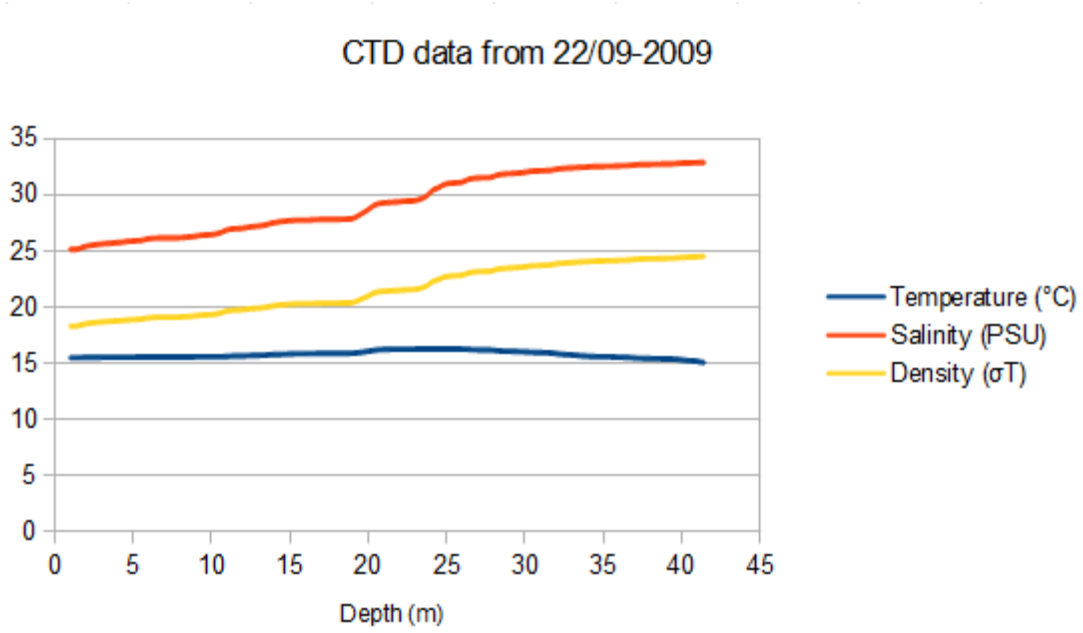
Internet websites:

http://www.midtal.com
http://www.biomarks.eu
http://www.thefullwiki.org
http://www.algaebase.org

Appendix

A. Graphs of salinity, temperature and density




CTD data from 22/09-2009
35
30
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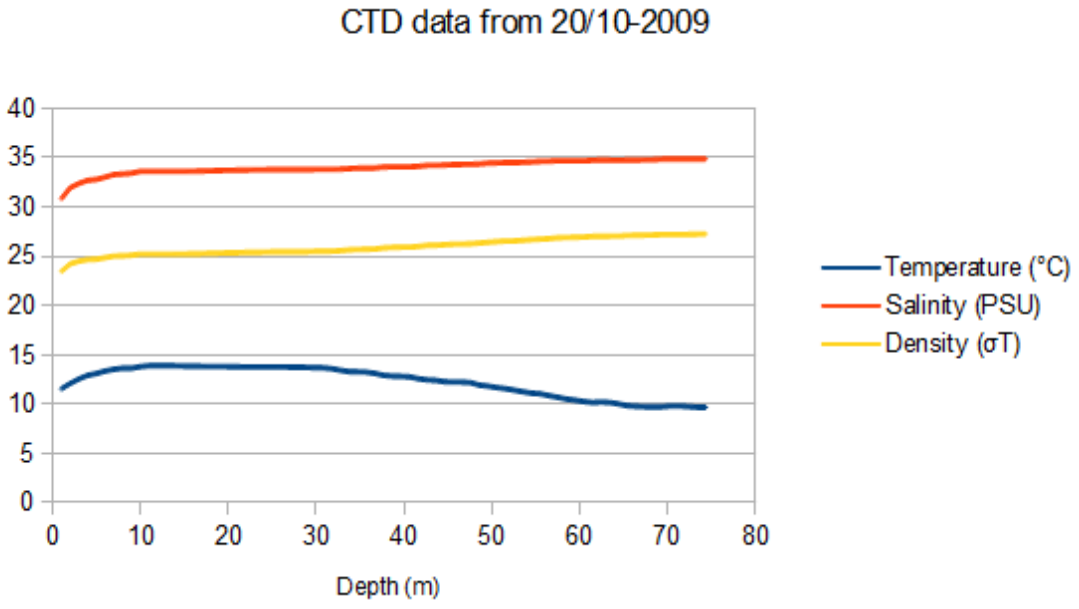
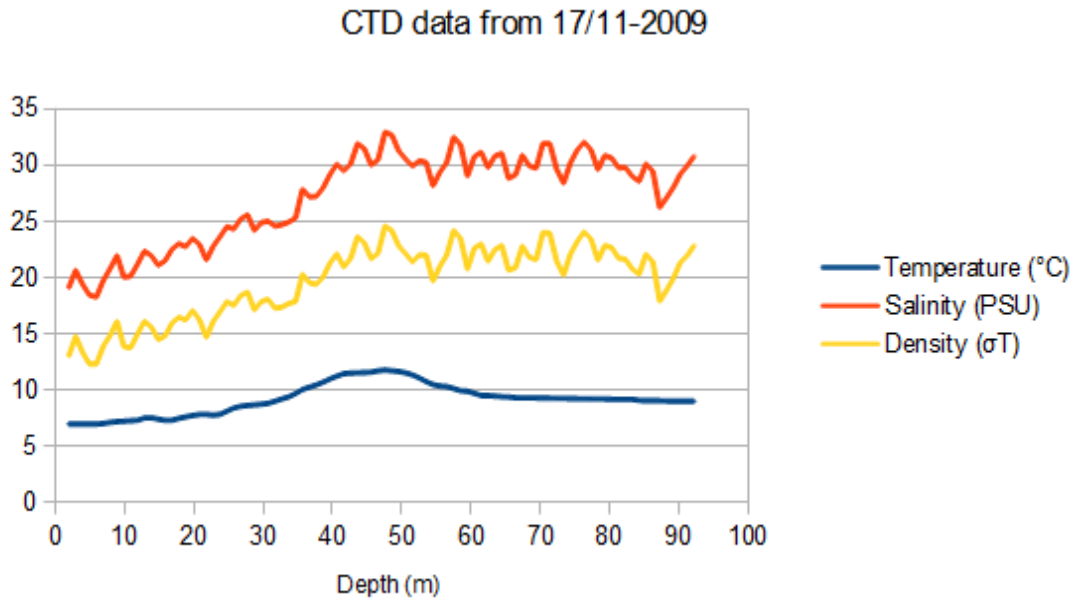
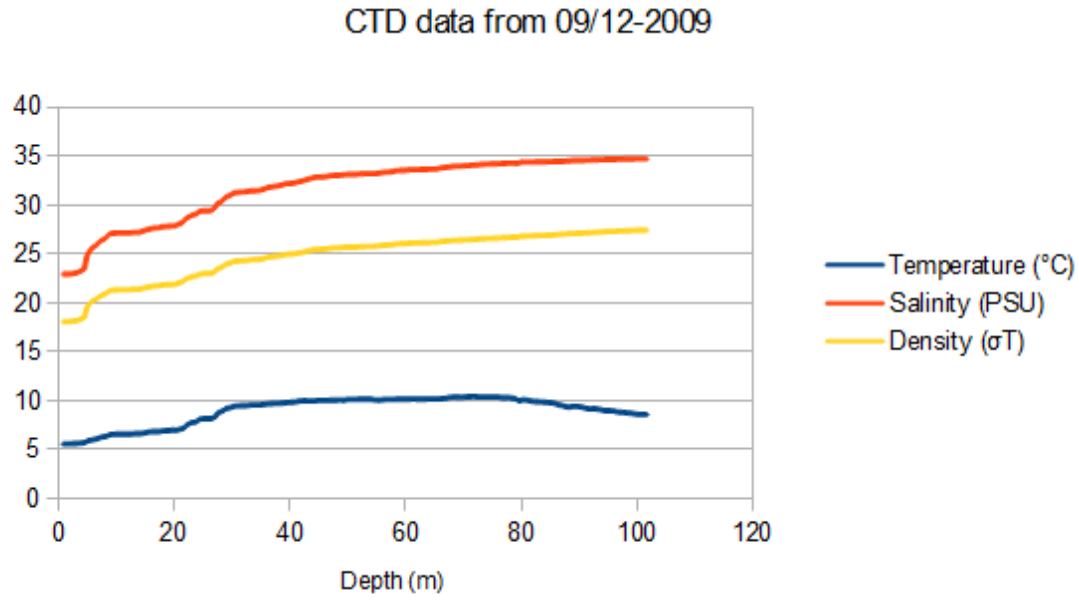
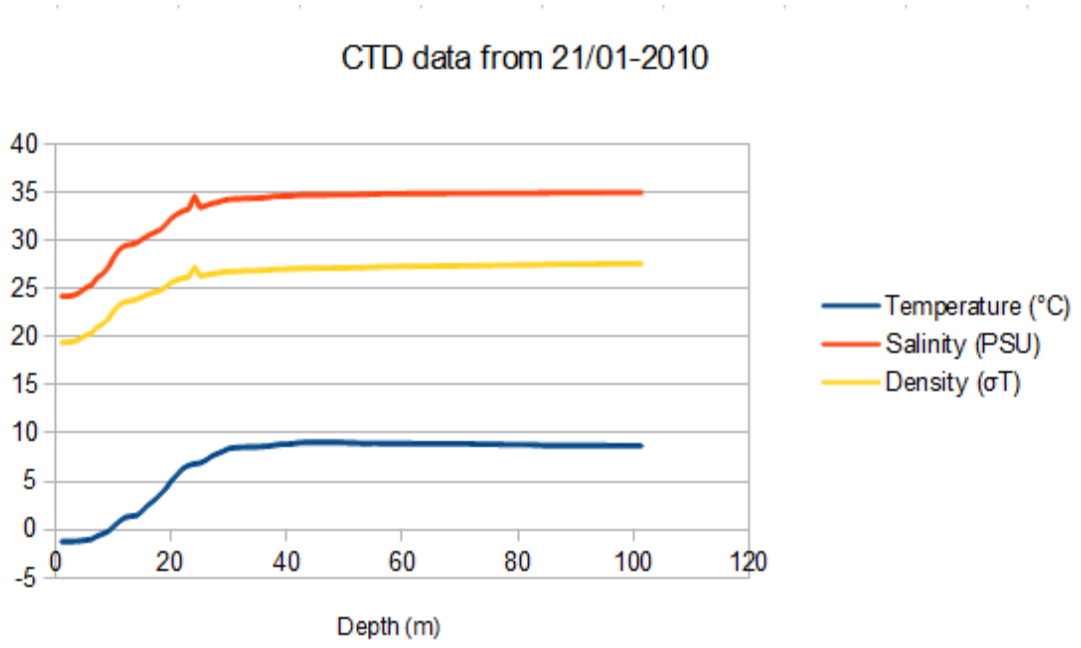
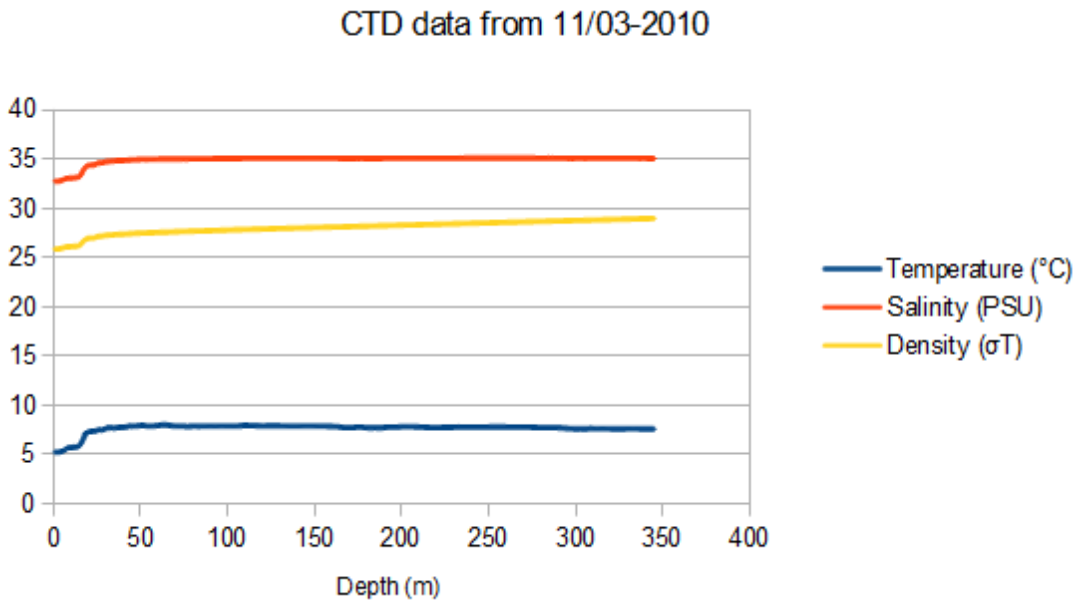
15
20
25
30
35
40
45
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

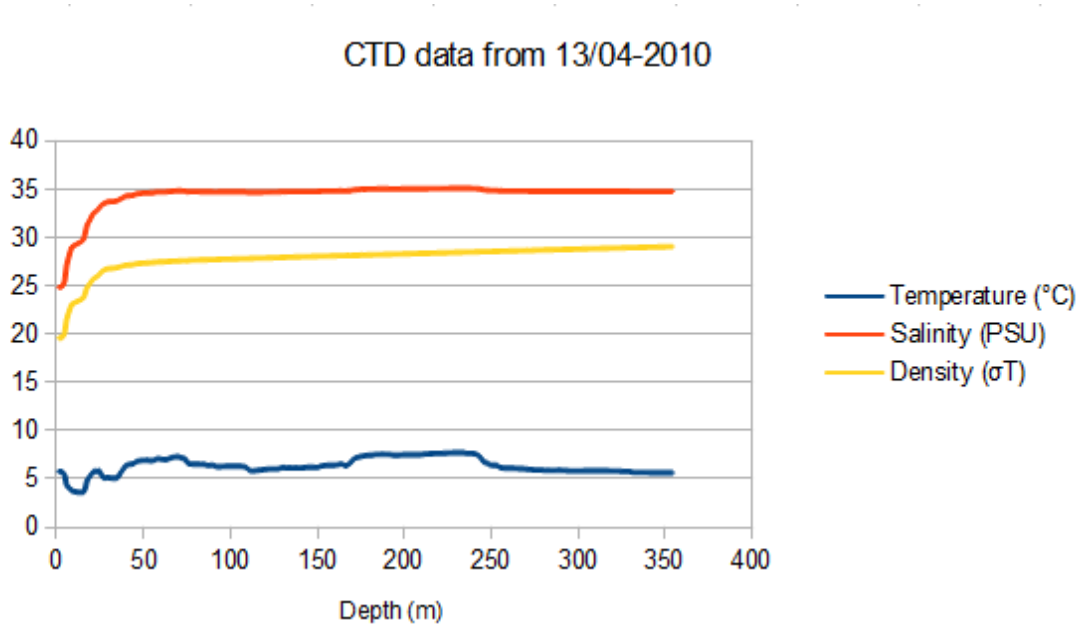

CTD data from 20/10-2009
40
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

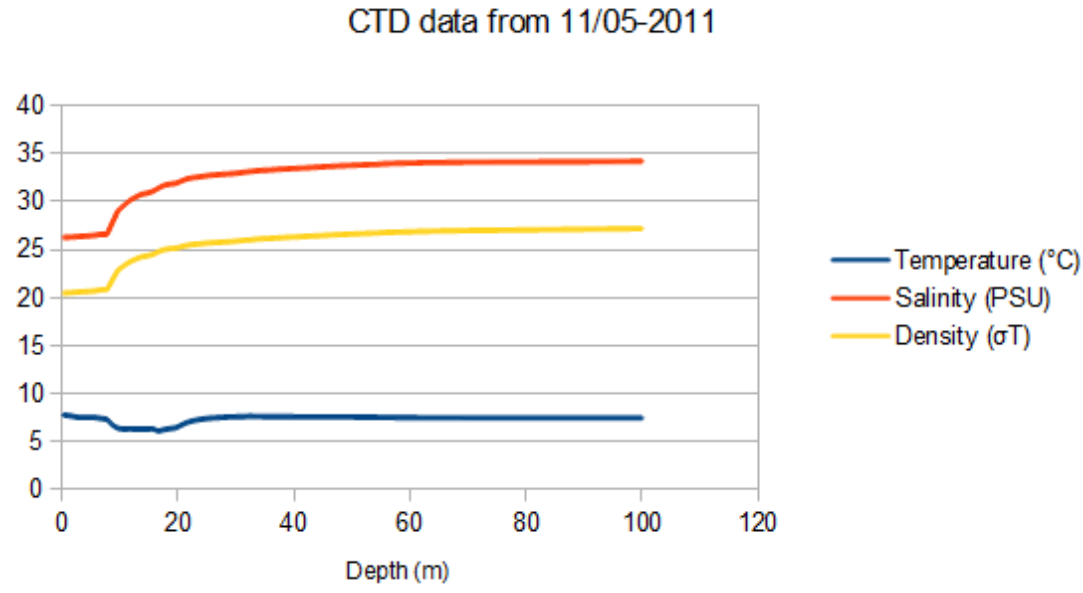

CTD data from 17/11-2009
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
100
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

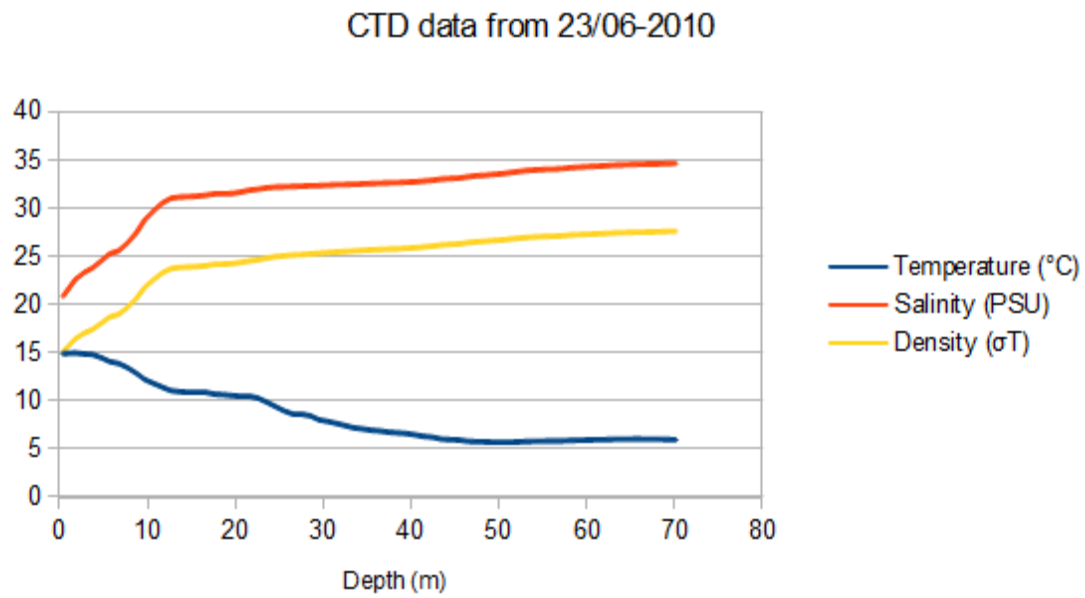

CTD data from 09/12-2009
40
35
30
25
20
15
10
5
0
0
20
40
60
80
100
120
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

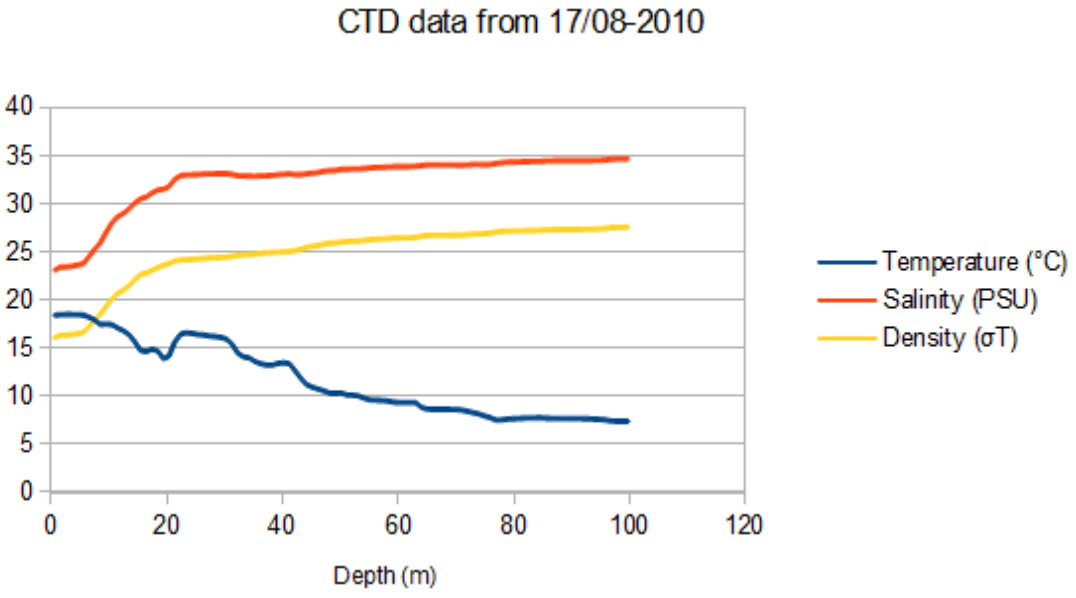

CTD data from 21/01-2010
40
35
30
25
20
15
10
5
0
-5
0
20
40
60
80
100
120
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)


CTD data from 11/03-2010
40
35
30
25
20
15
10
5
0
0
50
100
150
200
250
300
350
400
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

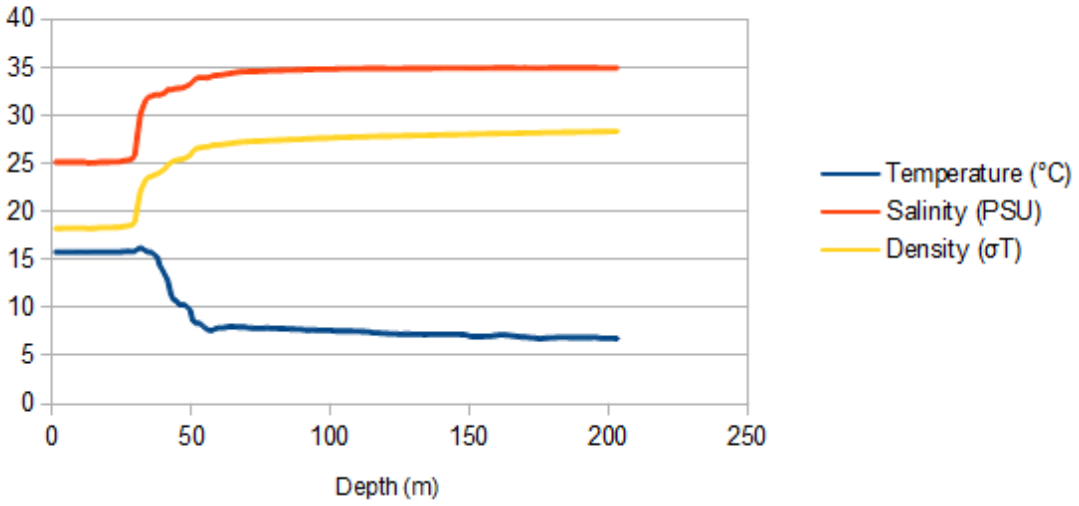

CTD data from 13/04-2010
40
35
30
25
20
15
10
5
0
0
50
100
150
200
250
300
350
400
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)


CTD data from 11/05-2011
40
35
30
25
20
15
10
5
0
0
20
40
60
80
100
120
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

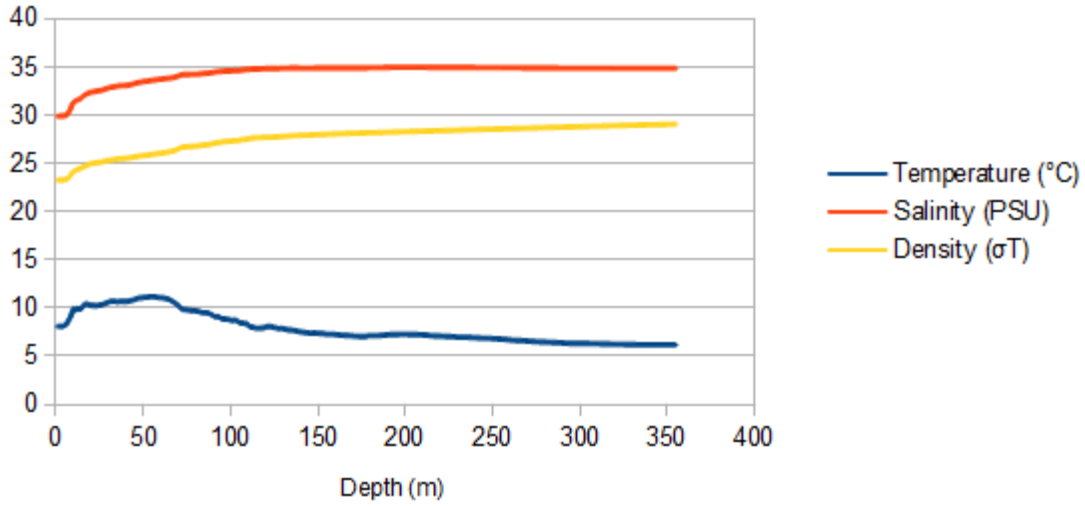

CTD data from 23/06-2010
40
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

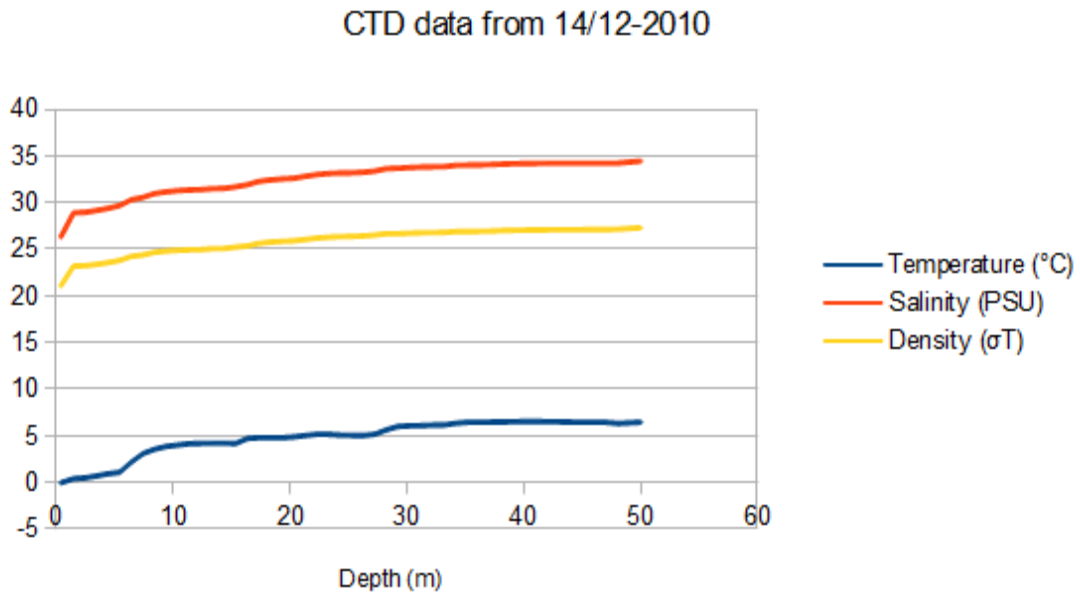

CTD data from 17/08-2010
40
35
30
25
20
15
10
5
0
0
20
40
60
80
100
120
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

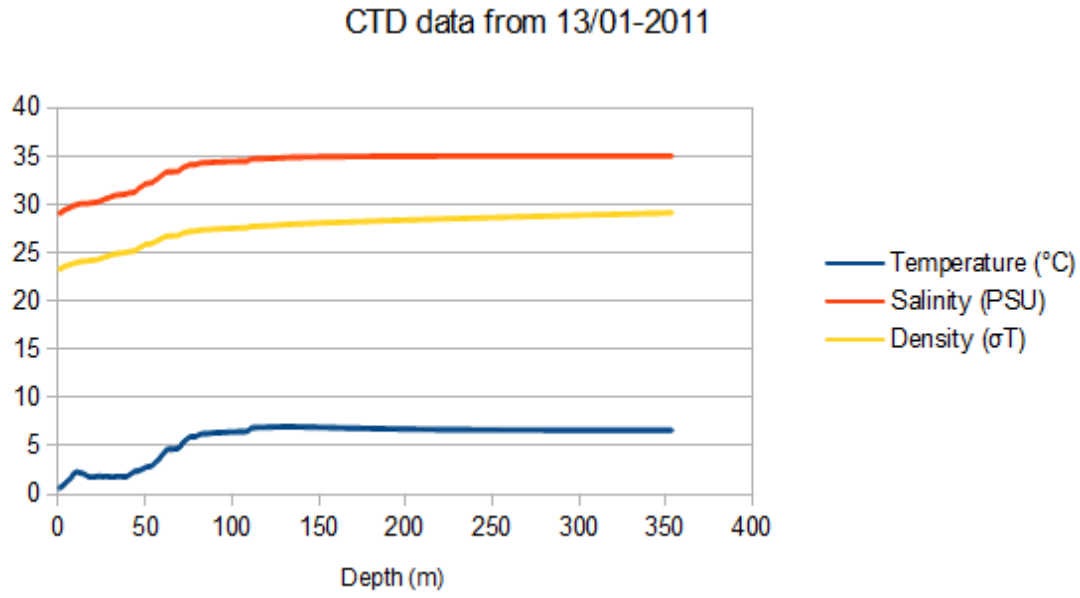
CTD data from 14/09-2010

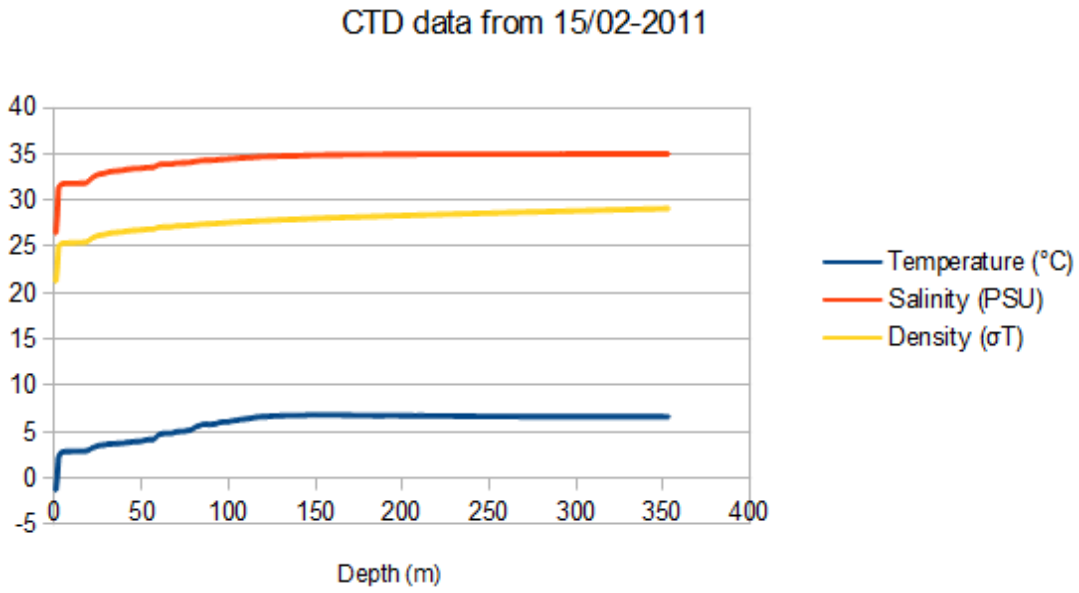


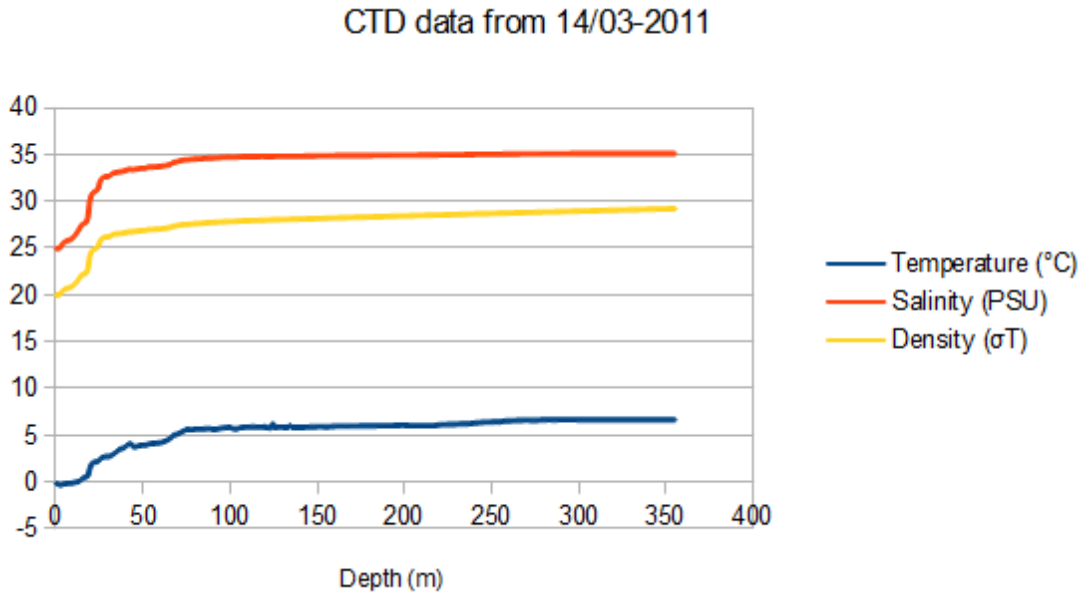
CTD data from 17/11-2010

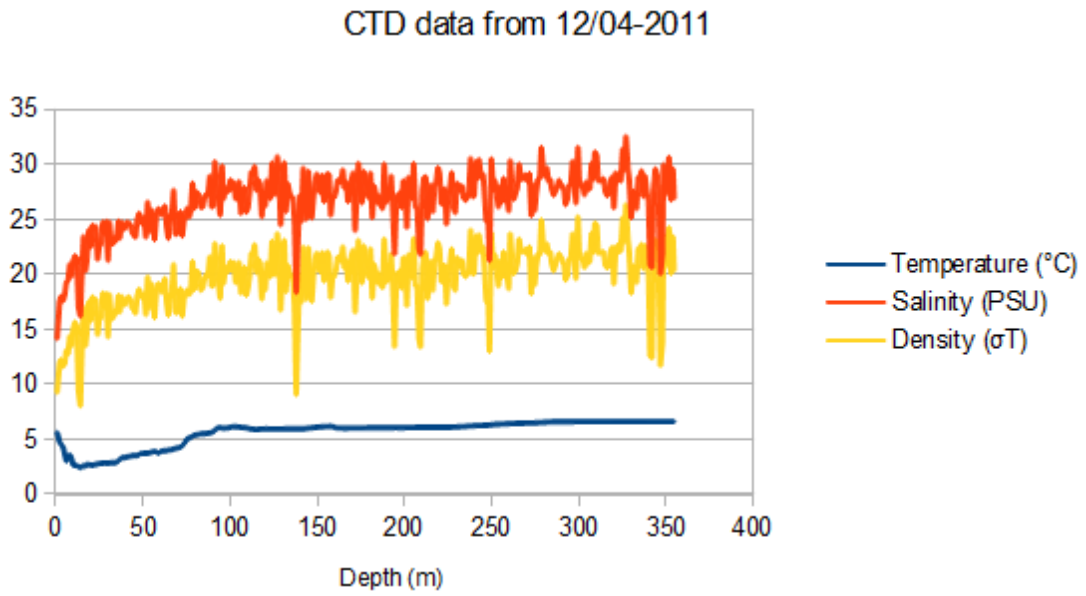


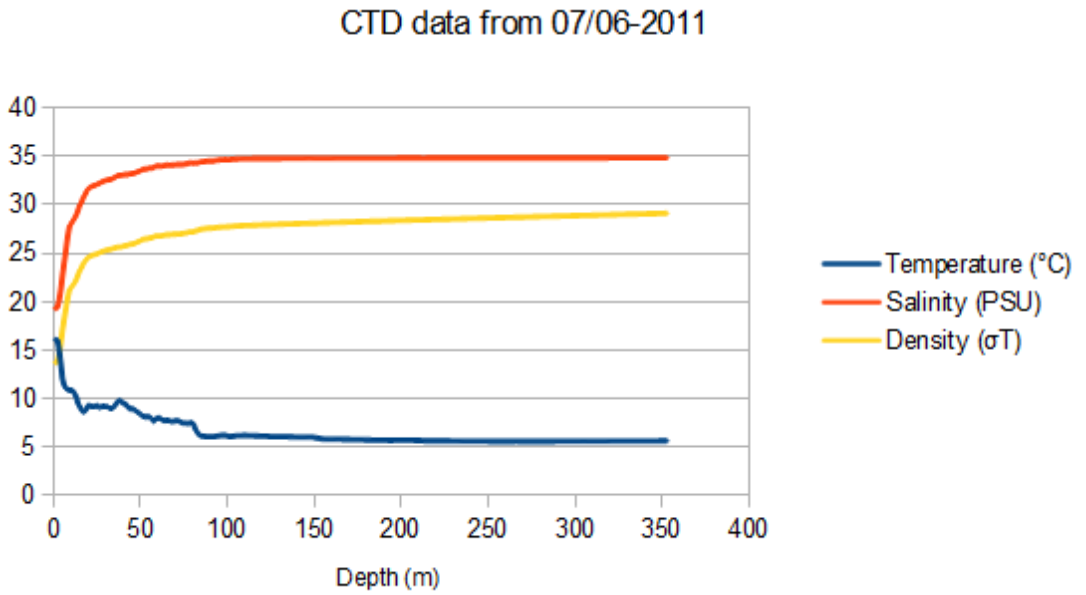

CTD data from 14/12-2010
40
35
30
25
20
15
10
5
0
-5
0
10
20
30
40
50
60
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)


CTD data from 13/01-2011
40
35
30
25
20
15
10
5
0
0
50
100
150
200
250
300
350
400
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)


CTD data from 15/02-2011
40
35
30
25
20
15
10
5
0
-5
0
50
100
150
200
250
300
350
400
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)


CTD data from 14/03-2011
40
35
30
25
20
15
10
5
0
-5
0
50
100
150
200
250
300
350
400
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)


CTD data from 12/04-2011
35
30
25
20
15
10
5
0
0
50
100
150
200
250
300
350
400
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)


CTD data from 07/06-2011
40
35
30
25
20
15
10
5
0
0
50
100
150
200
250
300
350
400
Depth (m)
Temperature (°C)
Salinity (PSU)
Density (σT)

B. Tables of results from ANOVA and Tukey's HSD tests

Hydrographical data

Salinity

	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	92.14	30.712	1.2118	0.3375	
Residuals	16	405.49	25.343			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ '	1

Temperature

	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	777.05	259.017	28.86	1.085e-06	***
Residuals	16	143.60	8.975			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ '	1

Density

	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	104.62	34.874	1.8046	0.1869	
Residuals	16	309.20	19.325			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ '	1

Salinity (PSU)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer-Spring	-3.91820	-13.02741	5.19101	0.6173312	
Autumn-Spring	1.40076	-7.70845	10.50997	0.9706116	
Winter-Spring	1.23456	-7.87465	10.34377	0.9794996	
Autumn-Summer	5.31896	-3.79025	14.42817	0.3701527	
Winter-Summer	5.15276	-3.95645	14.26197	0.3966478	
Winter-Autumn	-0.16620	-9.27541	8.94301	0.9999466	

Temperature (C)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer-Spring	12.20832	6.787456	17.6291845	0.0000438	***
Autumn-Spring	6.73982	1.318956	12.1606845	0.0126005	*
Winter-Spring	-4.05180	-9.472664	1.3690645	0.1832284	
Autumn-Summer	-5.46850	-10.889364	-0.0476355	0.0476436	*
Winter-Summer	-16.26012	-21.680984	-10.8392555	0.0000012	***
Winter-Autumn	-10.79162	-16.212484	-5.3707555	0.0001761	***

Density (σ_T)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer-Spring	-4.42238	-12.376799	3.532039	0.4111424	
Autumn-Spring	0.20432	-7.750099	8.158739	0.9998512	
Winter-Spring	1.70436	-6.250059	9.658779	0.9264428	
Autumn-Summer	4.62670	-3.327719	12.581119	0.3733762	
Winter-Summer	6.12674	-1.827679	14.081159	0.1644290	
Winter-Autumn	1.50004	-6.454379	9.454459	0.9480212	

Biodiversity data

Shannon's Diversity Index

	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	1.5448	0.51493	2.0159	0.15801	
Sal	1	0.0901	0.09013	0.3528	0.56199	
Temp	1	1.2453	1.24529	4.8752	0.04443	*
Residuals	14	3.5761	0.25543			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ ’	1

Number of species

	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	182.15	60.717	1.0118	0.4168	
Sal	1	9.02	9.015	0.1502	0.7041	
Temp	1	72.49	72.493	1.2081	0.2903	
Residuals	14	840.09	60.007			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ ’	1

Diatom cell numbers per L

	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	4.2250e+12	1.4083e+12	1.4814	0.2625	
Sal	1	4.4526e+10	4.4526e+10	0.0468	0.8318	
Temp	1	3.6291e+11	3.6291e+11	0.3817	0.5466	
Residuals	14	1.3310e+13	9.5068e+11			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ ’	1

Dinoflagellate cell numbers per L

	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	2.4151e+09	805043314	0.3792	0.7695	
Sal	1	2.6037e+08	260366663	0.1226	0.7314	
Temp	1	7.8936e+07	78936167	0.0372	0.8499	
Residuals	14	2.9723e+10	2123036332			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ ’	1

Shannon's Diversity Index					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer - Spring	0.2626560	-0.8277025	1.3530145	0.9030262	
Autumn - Spring	-0.0504065	-1.0900226	0.9892096	0.9990457	
Winter - Spring	-0.4323348	-1.5226933	0.6580237	0.6819082	
Autumn - Summer	-0.3130625	-1.4034210	0.7772960	0.8482309	
Winter - Summer	-0.6949908	-1.8338331	0.4438516	0.3403600	
Winter - Autumn	-0.3819283	-1.4722868	0.7084302	0.7568800	

Number of species					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer – Spring	6.8000000	-5.751157	19.35116	0.4405263	
Autumn – Spring	7.6666667	-4.300392	19.63373	0.3006946	
Winter – Spring	9.0000000	-3.551157	21.55116	0.2151648	
Autumn – Summer	0.8666667	-11.684491	13.41782	0.9972666	
Winter – Summer	2.2000000	-10.909256	15.30926	0.9637856	
Winter – Autumn	1.3333333	-11.217824	13.88449	0.9902690	

Dinoflagellate cell numbers per L					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer - Spring	23130.000	-47110.85	93370.85	0.7889732	
Autumn - Spring	4831.333	-62140.69	71803.36	0.9968879	
Winter - Spring	-4910.000	-75150.85	65330.85	0.9971654	
Autumn - Summer	-18298.667	-88539.52	51942.19	0.8812072	
Winter - Summer	-28040.000	-101404.18	45324.18	0.7055938	
Winter - Autumn	-9741.333	-79982.19	60499.52	0.9789320	

Diatom cell numbers per L					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer - Spring	62706.67	-1439068.6	1564482	0.9993892	
Autumn - Spring	153050.00	-1278836.5	1584937	0.9900927	
Winter - Spring	1152206.67	-349568.6	2653982	0.1699504	
Autumn - Summer	90343.33	-1411431.9	1592119	0.9981853	
Winter - Summer	1089500.00	-479053.1	2658053	0.2381951	
Winter - Autumn	999156.67	-502618.6	2500932	0.2708413	

Dinophysis

Cell size

D. acuminata (Length)						
	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	1762,35	587,45	26,8809	3,01E-013	***
Salinity	1	155,61	155,61	7,1204	0,008722	**
Temperature	1	720,18	720,18	32,9546	7,81E-008	***
Residuals	115	2513,19	21,85			

Signif. codes:	0 '***'	0,001 '**'	0,01 '*'	0,05 '.'	0,1 ' '	1

D. acuminata (Ratio)						
	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	0.22163	0.073878	3.6105	0.0157932	*
Salinity	1	0.27638	0.276378	13.5070	0.0003778	***
Temperature	1	0.05473	0.054735	2.6750	0.1049610	
Residuals	104	2.12803	0.020462			

Signif. codes:	0 '***'	0,001 '**'	0,01 '*'	0,05 '.'	0,1 ' '	1

D. acuminata (Length)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer-Spring	6.2024035	2.528553	9.8762536	0.0001344	***
Autumn-Spring	7.2202286	3.832703	10.6077543	0.0000009	***
Winter-Spring	0.5223086	-4.279252	5.3238690	0.9920452	
Autumn-Summer	1.0178251	-3.341686	5.3773357	0.9294549	
Winter-Summer	-5.6800949	-11.210464	-0.1497255	0.0416868	*
Winter-Autumn	-6.6979199	-12.042369	-1.3534704	0.0076431	**

D. acuminata (Ratio)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer-Spring	0.03888509	-0.06499615	0.142766330	0.7635835	
Autumn-Spring	0.07882581	-0.01625213	0.173903755	0.1404182	
Winter-Spring	-0.07534804	-0.20536968	0.054673610	0.4345954	
Autumn-Summer	0.03994072	-0.08279018	0.162671621	0.8312449	
Winter-Summer	-0.11423313	-0.26565534	0.037189088	0.2067705	
Winter-Autumn	-0.15417385	-0.29969769	-0.008650002	0.0333751	*

D. acuminata		
Month	Mean length (µm)	Standard Error
Nov 09	48,08917	1,942165
Apr 10	40,71884	1,444415
May 10	34,70521	2,378286
Jun 10	41,27878	1,724264
Aug 10	47,7707	1,828293
Oct 10	40,2432	2,631066
Dec 10	38,0718	2,1845
Total	**40,00193**	**0,5661726**

D. acuta (Length)						
	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Month	2	38,17	19,0827	2,893	0,06344	.
Residuals	58	382,58	6,5962			

Signif. codes:	0 '***'	0,001 '**'	0,01 '*'	0,05 '.'	0,1 ' '	1

D. acuta (Ratio)						
	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Month	2	0,01104	0,0055175	0,4453	0,6428	
Residuals	57	0,70624	0,0123902			

Signif. codes:	0 '***'	0,001 '**'	0,01 '*'	0,05 '.'	0,1 ' '	1

D. acuta (Length)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Oct 10 - Sep 10	1,6726436	-0,55686942	3,902157	0,1770956	
Dec 10 - Sep 10	1,8015486	-0,07379768	3,676895	0,0622159	
Dec 10 - Oct 10	0,1289051	-1,87058539	2,128396	0,9868339	

D. acuta (Ratio)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Oct 10 - Sep 10	-0,02530054	-0,12197313	0,071372	0,8044006	
Dec 10 - Sep 10	-0,0316372	-0,11345851	0,0501841	0,6234358	
Dec 10 - Oct 10	-0,00633666	-0,09350969	0,0808364	0,9832777	

Acuta		
Month	Mean length (µm)	Standard Error
Sep 10	64,06894	0,6623331
Oct 10	65,74158	3,694845
Dec 10	65,87049	1,821877
Total	**65,33883**	**0,3390534**

D. norvegica (Length)						
	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	3328.6	1109.54	57.3147	<2e-16	***
Salinity	1	107.0	106.98	5.5264	0.01918	*
Temperature	1	1.0	1.01	0.0524	0.81901	
Salinity:Temperature	1	27.2	27.23	1.4065	0.23628	
Residuals	432	8363.0	19.36			

Signif. codes:	0 '***'	0,001 '**'	0,01 '*'	0,05 '.'	0,1 ' '	1

D. norvegica (Ratio)						
	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Season	3	0.0459	0.015300	1.1812	0.316511	
Salinity	1	0.0921	0.092129	7.1129	0.007951	**
Temperature	1	0.0699	0.069940	5.3998	0.020619	*
Salinity:Temperature	1	0.0157	0.015665	1.2094	0.272079	
Residuals	417	5.4012	0.012952			

Signif. codes:	0 '***'	0,001 '**'	0,01 '*'	0,05 '.'	0,1 ' '	1

Dinophysis norvegica (Length)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer-Spring	-4.0831594	-5.4405756	-2.725743	0.0000000	***
Autumn-Spring	-7.2714232	-8.9045636	-5.638283	0.0000000	***
Winter-Spring	-4.4371567	-5.8817931	-2.992520	0.0000000	***
Autumn-Summer	-3.1882638	-4.9757771	-1.400750	0.0000322	***
Winter-Summer	-0.3539973	-1.9711029	1.263108	0.9425826	
Winter-Autumn	2.8342664	0.9796508	4.688882	0.0005404	***

Dinophysis norvegica (Ratio)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer-Spring	0.010277754	-0.02431188	0.04486739	0.8696907	
Autumn-Spring	-0.006025339	-0.04806602	0.03601534	0.9827554	
Winter-Spring	0.024130111	-0.01257039	0.06083061	0.3273477	
Autumn-Summer	-0.016303093	-0.06241138	0.02980520	0.7986654	
Winter-Summer	0.013852356	-0.02744513	0.05514984	0.8229956	
Winter-Autumn	0.030155450	-0.01755679	0.07786769	0.3629722	

Norvegica		
Month	Mean length (µm)	Standard Error
Nov 09	57,47649	0,7992416
Apr 10	66,17931	1,241341
May 10	63,47311	2,277447
Jun 10	61,52689	0,8191369
Aug 10	58,42724	1,244802
Sep 10	58,05977	1,363191
Oct 10	55,6601	1,127497
Dec 10	58,84313	1,250117
Jan 11	58,0414	2,489605
Feb 11	62,47658	1,106132
Mar 11	63,95966	1,074491
Apr 11	66,00318	0,7491106
May 11	60,31654	1,067841
Jun 11	61,00243	2,020602
Total	**61,53459**	**0,2372704**

D. rotundata (Length)						
	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Month	4	89,1	22,275	1,1981	0,329	
Residuals	35	650,73	18,592			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ ’	1

D. rotundata (Length)						
	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Salinity	1	0.79	0.789	0.0646	0.80121	
Temperature	1	60.69	60.688	4.9657	0.03377	*
Salinity:Temperature	1	23.60	23.604	1.9314	0.17519	
Residuals	29	354.42	12.221			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ ’	1

D. rotundata (Ratio)						
	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Month	4	0,086315	0,0215787	2,4437	0,06535	.
Residuals	34	0,300236	0,0088305			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ ’	1

D. rotundata (Ratio)						
	DF	Sum Sq	Mean Sq	F value	Pr(>F)	
Salinity	1	0.004701	0.004701	0.4808	0.49378	
Temperature	1	0.040274	0.040274	4.1192	0.05200	.
Salinity:Temperature	1	0.029726	0.029726	3.0403	0.09219	.
Residuals	28	0.273762	0.009777			

Signif. codes:	0 ‘***’	0.001 ‘**’	0.01 ‘*’	0.05 ‘.’	0.1 ‘ ’	1

Dinophysis rotundata (Length)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Jun 10 - Nov 09	4,08704883	-2,314667	10,488765	0,3702283	
Sep 10 - Nov 09	2,22929936	-4,172417	8,631015	0,8530211	
Oct 10 - Nov 09	2,00181984	-4,107424	8,111064	0,8784189	
Dec 10 - Nov 09	0,05790388	-5,358678	5,474486	0,9999998	
Sep 10 - Jun 10	-1,85774947	-9,015085	5,299587	0,9439037	
Oct 10 - Jun 10	-2,085229	-8,982211	4,811753	0,9061848	
Dec 10 - Jun 10	-4,02914495	-10,320795	2,262505	0,3671752	
Oct 10 - Sep 10	-0,22747953	-7,124461	6,669502	0,9999807	
Dec 10 - Sep 10	-2,17139548	-8,463045	4,120254	0,857022	
Dec 10 - Oct 10	-1,94391596	-7,937725	4,049893	0,8823179	

Dinophysis rotundata (Ratio)					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Jun 10 - Nov 09	-0,011989902	-0,15460487	0,13062507	0,9992008	
Sep 10 - Nov 09	0,116403001	-0,02621197	0,25901797	0,1541536	
Oct 10 - Nov 09	0,061242501	-0,07512349	0,1976085	0,6970459	
Dec 10 - Nov 09	-0,009608405	-0,13123086	0,11201405	0,9993746	
Sep 10 - Jun 10	0,128392903	-0,02783397	0,28461978	0,1493828	
Oct 10 - Jun 10	0,073232403	-0,07731158	0,22377638	0,6313727	
Dec 10 - Jun 10	0,002381497	-0,13494959	0,13971258	0,9999985	
Oct 10 - Sep 10	-0,0551605	-0,20570448	0,09538348	0,8277312	
Dec 10 - Sep 10	-0,126011406	-0,26334249	0,01131968	0,0848738	
Dec 10 - Oct 10	-0,070850906	-0,20168088	0,05997907	0,532593	

D. rotundata		
Month	Mean length (µm)	Standard Error
Nov 09	43,94904	1,143347
Jun 10	48,03609	8624245
Sep 10	46,17834	2347489
Oct 10	45,95086	1675131
Dec 10	44,00695	2,097107
Total	**45,26274**	**0,6886556**

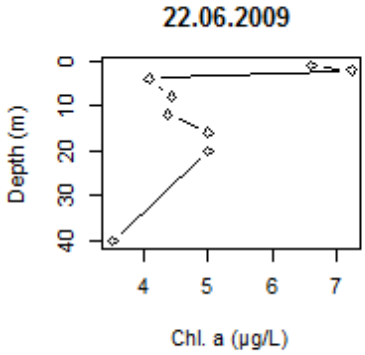
Abundance

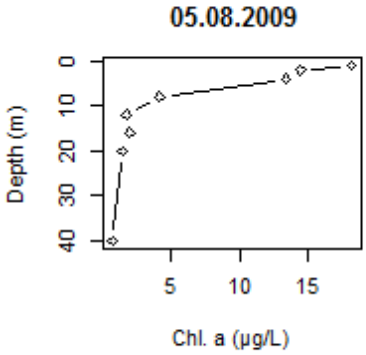
Dinophysis cell numbers per L					
	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Season	3	2832000	944000	1.8275	0.1885
Sal	1	75517	75517	0.1462	0.7079
Temp	1	599	599	0.0012	0.9733
Residuals	14	7231884	516563		

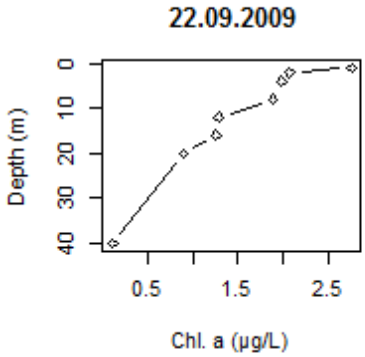
Signif. codes:	0 '***'	0.001 '**'	0.01 '*'	0.05 '.'	0.1 ' ' 1

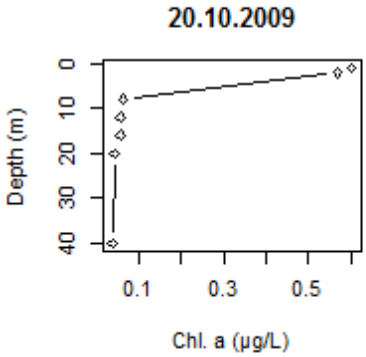
Dinophysis cell numbers per L					
Group comparison	Difference	Lower	Upper	Adjusted p-value	Significance
Summer - Spring	-330.0000	-1447.836	787.8356	0.8374794	
Autumn - Spring	-833.3333	-1899.148	232.4811	0.1582935	
Winter - Spring	-730.0000	-1847.836	387.8356	0.2854222	
Autumn - Summer	-503.3333	-1621.169	614.5023	0.5910446	
Winter - Summer	-400.0000	-1567.541	767.5412	0.7687942	
Winter - Autumn	103.3333	-1014.502	1221.1690	0.9935272	

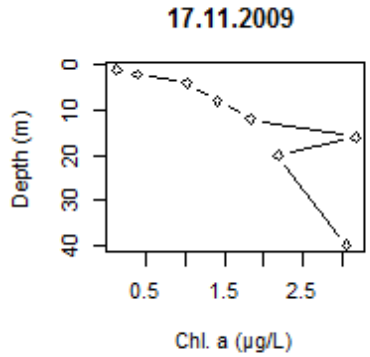
C. Chlorophyll *a in vitro* data.

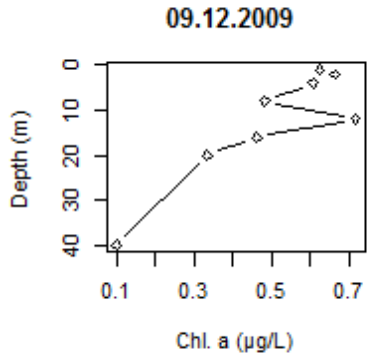


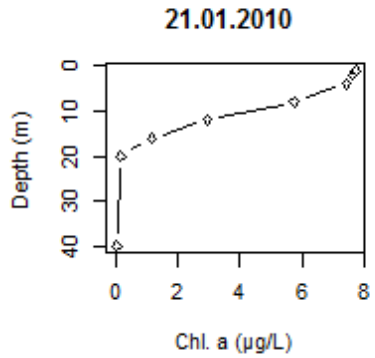


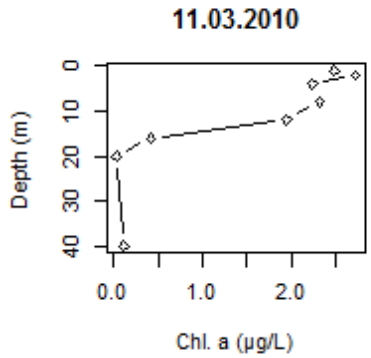


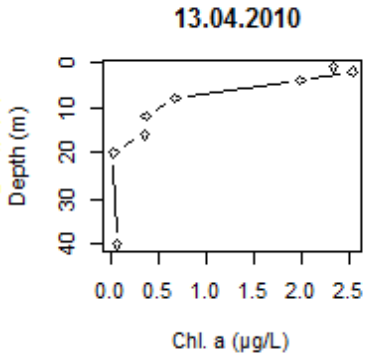











13.04.2010
Depth (m)
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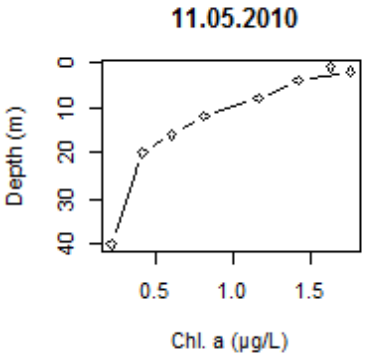
10
20
30
40
0.0
0.5
1.0
1.5
2.0
2.5
Chl. a (µg/L)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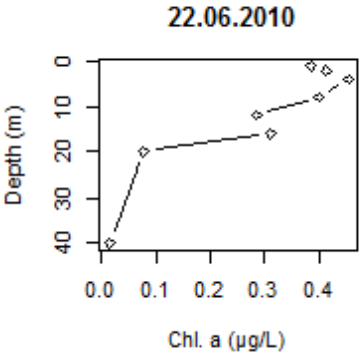
1.5
Chl. a (µg/L)


22.06.2010
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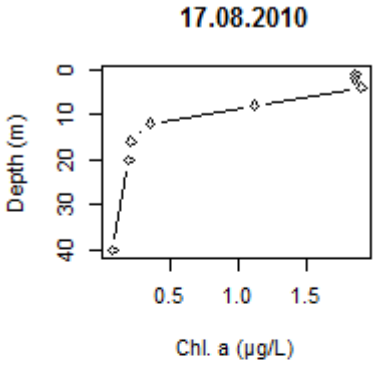
0.2
0.3
0.4
Chl. a (µg/L)


17.08.2010
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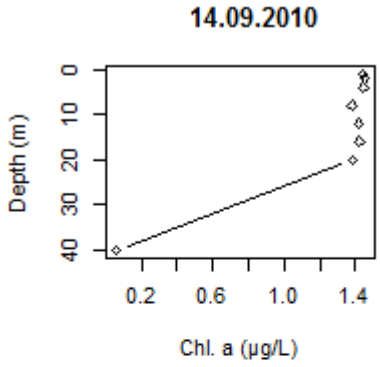
30
40
0.5
1.0
1.5
Chl. a (µg/L)


14.09.2010
Depth (m)
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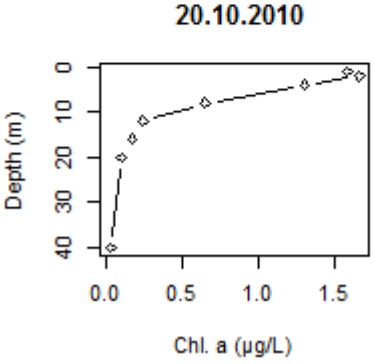
30
40
0.2
0.6
1.0
1.4
Chl. a (µg/L)


20.10.2010
Depth (m)
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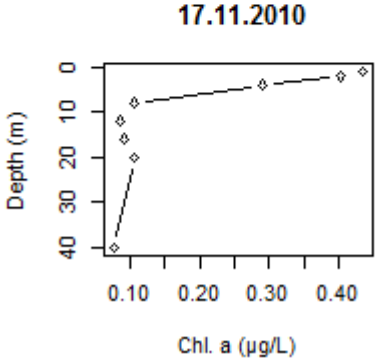
10
20
30
40
0.0
0.5
1.0
1.5
Chl. a (µg/L)


17.11.2010
Depth (m)
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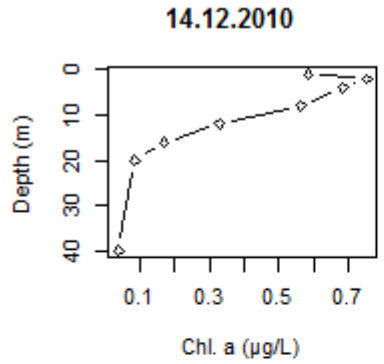
20
30
40
0.10
0.20
0.30
0.40
Chl. a (µg/L)


14.12.2010
Depth (m)
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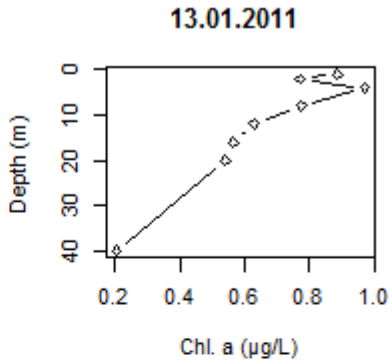
30
40
0.1
0.3
0.5
0.7
Chl. a (µg/L)


13.01.2011
Depth (m)
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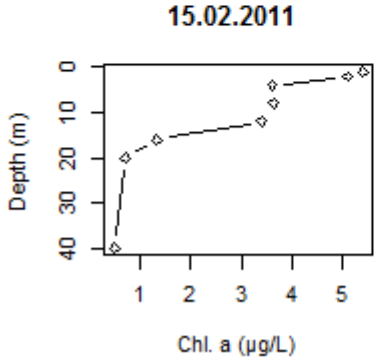
30
40
0.2
0.4
0.6
0.8
1.0
Chl. a (µg/L)


15.02.2011
Depth (m)
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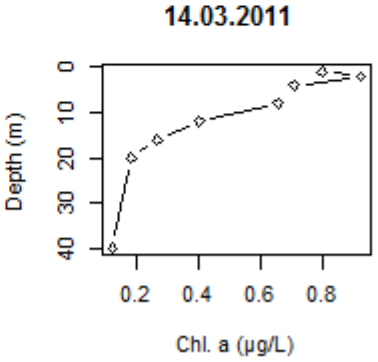
20
30
40
1
2
3
4
5
Chl. a (µg/L)


14.03.2011
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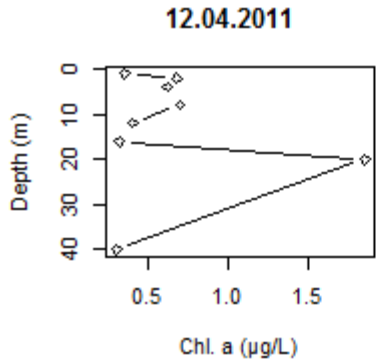
30
40
0.2
0.4
0.6
0.8
Chl. a (µg/L)


12.04.2011
Depth (m)
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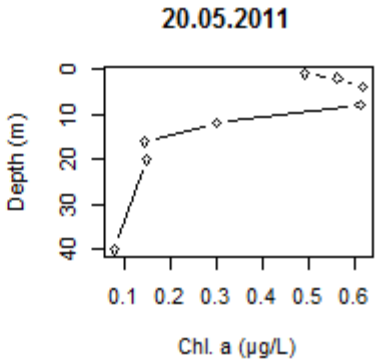
30
40
0.5
1.0
1.5
Chl. a (µg/L)


20.05.2011
Depth (m)
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40
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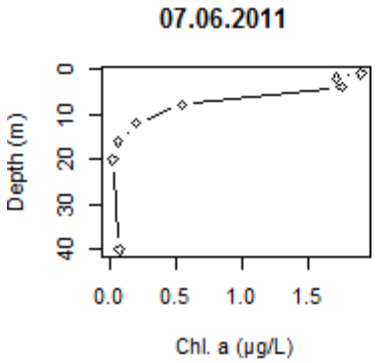
0.2
0.3
0.4
0.5
0.6
Chl. a (µg/L)


07.06.2011
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40
0.0
0.5
1.0
1.5
Chl. a (µg/L)

Date	Dateno	Depth	Chla
22.06.09	1	1	6,6125
22.06.09	1	2	7,245
22.06.09	1	4	4,0825
22.06.09	1	8	4,4275
22.06.09	1	12	4,37
22.06.09	1	16	5,0025
22.06.09	1	20	5,0025
22.06.09	1	40	3,5075
05.08.09	2	1	18,14125
05.08.09	2	2	14,40375
05.08.09	2	4	13,36875
05.08.09	2	8	4,1975
05.08.09	2	12	1,7633333333
05.08.09	2	16	2,0125
05.08.09	2	20	1,495
05.08.09	2	40	0,790625
22.09.09	3	1	2,757125
22.09.09	3	2	2,07
22.09.09	3	4	1,9856666667
22.09.09	3	8	1,8898333333
22.09.09	3	12	1,2841666667
22.09.09	3	16	1,2611666667
22.09.09	3	20	0,897
22.09.09	3	40	0,115
20.10.09	4	1	0,6026
20.10.09	4	2	0,56925
20.10.09	4	4	NA
20.10.09	4	8	0,0621
20.10.09	4	12	0,05635
20.10.09	4	16	0,05635
20.10.09	4	20	0,04255
20.10.09	4	40	0,03795
17.11.09	5	1	0,13455
17.11.09	5	2	0,39445
17.11.09	5	4	1,0281
17.11.09	5	8	1,4099
17.11.09	5	12	1,83195
17.11.09	5	16	3,1602
17.11.09	5	20	2,1781
17.11.09	5	40	3,0429
09.12.09	6	1	0,62445
09.12.09	6	2	0,66355
09.12.09	6	4	0,60835
09.12.09	6	8	0,48185
09.12.09	6	12	0,7176
09.12.09	6	16	0,4608625
09.12.09	6	20	0,3335
09.12.09	6	40	0,0989

Date	Dateno	Depth	Chla
21.01.10	7	1	7,705
21.01.10	7	2	7,5992
21.01.10	7	4	7,40485
21.01.10	7	8	5,7408
21.01.10	7	12	2,94745
21.01.10	7	16	1,16265
21.01.10	7	20	0,15525
21.01.10	7	40	0,0322
11.03.10	8	1	2,4905714286
11.03.10	8	2	2,7287857143
11.03.10	8	4	2,2375714286
11.03.10	8	8	2,3213571429
11.03.10	8	12	1,9467857143
11.03.10	8	16	0,4156428571
11.03.10	8	20	0,0306666667
11.03.10	8	40	0,1111666667
13.04.10	9	1	2,3345
13.04.10	9	2	2,53345
13.04.10	9	4	1,98375
13.04.10	9	8	0,67505
13.04.10	9	12	0,3703
13.04.10	9	16	0,35535
13.04.10	9	20	0,0306666667
13.04.10	9	40	0,0644
11.05.10	10	1	1,63
11.05.10	10	2	1,76
11.05.10	10	4	1,42
11.05.10	10	8	1,16
11.05.10	10	12	0,81
11.05.10	10	16	0,60
11.05.10	10	20	0,41
11.05.10	10	40	0,21
22.06.10	11	1	0,384675
22.06.10	11	2	0,41285
22.06.10	11	4	0,45425
22.06.10	11	8	0,399625
22.06.10	11	12	0,2852
22.06.10	11	16	0,3105
22.06.10	11	20	0,076475
22.06.10	11	40	0,0138
17.08.10	12	1	1,8515
17.08.10	12	2	1,848625
17.08.10	12	4	1,8975
17.08.10	12	8	1,112625
17.08.10	12	12	0,35075
17.08.10	12	16	0,209875
17.08.10	12	20	0,192625
17.08.10	12	40	0,077625

Date	Dateno	Depth	Chla
14.09.10	13	1	1,4389375
14.09.10	13	2	1,4504375
14.09.10	13	4	1,4418125
14.09.10	13	8	1,3814375
14.09.10	13	12	1,4188125
14.09.10	13	16	1,4216875
14.09.10	13	20	1,382875
14.09.10	13	40	0,0575
20.10.10	14	1	1,5824
20.10.10	14	2	1,6629
20.10.10	14	4	1,3018
20.10.10	14	8	0,6532
20.10.10	14	12	0,2461
20.10.10	14	16	0,1771
20.10.10	14	20	0,1035
20.10.10	14	40	0,0368
17.11.10	15	1	0,434125
17.11.10	15	2	0,4025
17.11.10	15	4	0,290375
17.11.10	15	8	0,1049375
17.11.10	15	12	0,0848125
17.11.10	15	16	0,0905625
17.11.10	15	20	0,1049375
17.11.10	15	40	0,0761875
14.12.10	16	1	0,585
14.12.10	16	2	0,755
14.12.10	16	4	0,685
14.12.10	16	8	0,565
14.12.10	16	12	0,33
14.12.10	16	16	0,17
14.12.10	16	20	0,085
14.12.10	16	40	0,04
13.01.11	17	1	0,885
13.01.11	17	2	0,77
13.01.11	17	4	0,97
13.01.11	17	8	0,775
13.01.11	17	12	0,63
13.01.11	17	16	0,565
13.01.11	17	20	0,54
13.01.11	17	40	0,205
15.02.11	18	1	5,42
15.02.11	18	2	5,105
15.02.11	18	4	3,61
15.02.11	18	8	3,64
15.02.11	18	12	3,405
15.02.11	18	16	1,315
15.02.11	18	20	0,7
15.02.11	18	40	0,485

Date	Dateno	Depth	Chla
14.03.10	19	1	0,8
14.03.10	19	2	0,925
14.03.10	19	4	0,71
14.03.10	19	8	0,66
14.03.10	19	12	0,405
14.03.10	19	16	0,27
14.03.10	19	20	0,185
14.03.10	19	40	0,125
12.04.11	20	1	0,355
12.04.11	20	2	0,68
12.04.11	20	4	0,62
12.04.11	20	8	0,7
12.04.11	20	12	0,405
12.04.11	20	16	0,32
12.04.11	20	20	1,855
12.04.11	20	40	0,305
20.05.11	21	1	0,49
20.05.11	21	2	0,56
20.05.11	21	4	0,615
20.05.11	21	8	0,61
20.05.11	21	12	0,3
20.05.11	21	16	0,145
20.05.11	21	20	0,15
20.05.11	21	40	0,08
07.06.11	22	1	1,9
07.06.11	22	2	1,71
07.06.11	22	4	1,75
07.06.11	22	8	0,545
07.06.11	22	12	0,195
07.06.11	22	16	0,06
07.06.11	22	20	0,02
07.06.11	22	40	0,07

D. Cell counts

	22Jun09	05Aug09	22Sep09	20Oct09	17Nov09	09Dec09	21Jan10	11Mar10	13Apr10	11May10	22Jun10
Class Bacillariophyceae											
Asterionellopsis glacialis			4400						400	800	800
Attheya septentrionalis					400	1000	9400	3500			
Cerataulina pelagica	1000	1000	500								
Chaetoceros contortus			600								
C. cf constrictus		1100					1300				
C. curvisetus			44200	1500	3700						
C. danicus		200	400	200	5100	100	7800				
C. debilis				500	4200						
C. decipiens			8000	800						1900	
C. diadema									30800		
C. didymus							700				
C. laciniosus		500			1600			8300			
C. minimus	36500		17600								
C. cf atlanticus		200	8000		5100	100					
C. similis					700		1500				
C. simplex			600						50100		
C. socialis			212000		700			53000			
C. subtilis			1000				500				
C. tenuissimus	7000	100	12400				4200				
C. teres			15600								
C. throndsenii	57400										
C. wighamii	3800		25200								
Chaetoceros spp.	68500	300	138000	5800	5900	500	98000	134800	9000	1500	1500
Coscinodiscus spp.		100	100		200	300	200	500			
Cylindrotheca closterium	55500	200	116500	3000	400	100	3200	300	200	700	200
Dactyliosolen fragilissimus	429200	800	3600	2100	1200	200	1000				
Ditylum brightwellii			100	500	300	100	3000				
Guinardia flaccida			100							500	200
G. delicatula	1000		3600	1300		100	2500	300			
Leptocylindrus danicus	35900	1700	61600	900	5300	500	96900	30900			
L. minimus	10500		5400		4000						
Naviculoids		200	1000	300	1700		2800	3300	2500	3600	4800
Pleurosigma normanii				200							100
Proboscia alata	4700	600	300		2300	1200	11900	1500	600	300	400
Pseudo-nitzschia spp.	69100	15000	208700	91500	150100	11400	1616000	141200	1400	800	500
Pseudosolenia calcar-avis							100				
Rhizosolenia cf borealis/styliformis	100									100	
R. hebetata f semispina	300						1500				
R. pungens		400	300	200							
Rhizosolenia sp.	300		400		1700		3500	7800	100		
Skeletonema spp.	149200	4600	270500	47200	64300	5800	1396900	28000	1400	1600	1000
Thalassionema nitzschioides	8900		300				86400	128000	3400	400	
Thalassiosira spp.			1600	1800	8300		325500	178600			
Unidentified centric diatoms	1000	600		5000		1000	6500	9800	300		
Actiniscus pentasterias											100
Class Dinophyceae											
Akashiwo sanguinea			100			200			100		
Amphidinium cf longum			300								
Amphidinium sp.		100									
Ceratium furca		100		100							
C. fusus					300	100		100			300
C. horridum		300				100				200	
C. lineatum	100	600			1000	1100					100
C. longipes	200	100				200					
C. tripos	200	200	100		700	400					
Dinophysis acuminata	200		300						200	1000	500
D. acuta										200	
D. norvegica	100				100	100			1600	1200	1400
D. rotundata			100								100
Diplopsalisoids									200		
Gonyaulax digitale			100								
Gymnodinium sp.	1900					100	900			600	2000
Gyrodinium cf spirale			100								
Gyrodinium sp.			100	100	400			700	200	1200	200
Heterocapsa cf triquetra	3600	100	8100			300				1200	
Katodinium sp.										700	
Microacanthodinium cf claytoni	900										100
Oxytoxum sp.			2600		700	100					300
Prorocentrum cf glaciale			2400								
P. micans			5900								
Prorocentrum spp.			8300								
Protoceratium reticulatum											100
Protoperidinium bipes	100	100	1500		300		300	300		100	300
P. brevipes	600							200			
P. conicum	100										
P. depressum									100		
P. pallidum						200	400	700	600	100	
P. pellucidum	200		100								
P. steinii	400		200							1100	100
Protoperidinium spp.					400						1000
Scrippsiellaoids	5600	200	11200		700	700	100		2500	900	1500
Unidentified thecate							9100				
Unidentified small gymnoid	1500	4700	8800	25000	13100	5700	13900	4800	13400	16300	9800
Unidentified medium gymnoid			1888					2800	4000	4300	1600
Unidentified large gymnoid			1200								
Class Euglenophyceae											
Eutreptiella spp.	1100		500	1000			300	400			
Class Chrysophyceae											
Dinobryon sp.	90400							1900	28600	38500	4600
Class Dictyochophyceae											
Dictyocha fibula		100				200					
Dictyocha speculum		1100	100		22200	1400	2700				

	17Aug10	14Sep10	20Oct10	17Nov10	14Dec10	13Jan11	15Feb11	14Mar11	12Apr11	20May11	07Jun11
Class Bacillariophyceae											
Cylindrotheca closterium /Nitzschia longissima	700	3900	600	1000	400	300	2100	0	100	0	900
Proboscia alata	100	0	0	100	0	0	500	0	0	0	0
Skeletonema sp.	0	1200	1700	1100	12100	144000	2337000	1300	14900	8300	83000
Ditylum brightwellii	0	0	0	0	0	0	0	0	0	0	0
Dactyliosolen fragilissimus	700	7500	0	0	1200	0	800	0	0	0	1500
Cerataulina pelagica	46300	56400	0	0	0	0	0	0	0	0	0
Thalassionema nitzschioides	0	0	0	0	0	0	0	0	400	0	0
Thalassiothrix longissima	0	0	0		0		0	0	0	0	0
Leptocylindrus minimus	0	4100	1600	0	0	1900	900	0	0	0	0
Leptocylindrus danicus	600	10100	0	0	0	2600	36800	1000	0	0	0
Guinardia flaccida	0	0	0	0	0	0	0	0	0	0	0
Guinardia delicatula	0	2500	500	0	1900	2500	1500	0	0	0	0
Naviculoids	0	0	500	700	0	500	53700	500	6200	7800	1500
Pleurosigma normanii	0	0	0	0	0	0	100	0	0	0	0
Eucampia sp	0	0	0	0	0	0	0	0	0	0	0
Paralia sp.	0	0	0	0	0	0	0	0	0	0	0
Pseudo-nitzschia delicatissima gr.	10700	108900	2300	2500	0	0	400	100	0	400	0
calliantha		0	0	0	0	0	0	0	0	0	0
Pseudonitzschia seriata gr.	1200	0	0	0	0	0	0	0	0	0	0
pungens		0	0	200	0	0	0	0	0	0	0
cf. faudulenta				0	0	0	0	0	0	0	0
Pseudo-nitzschia spp.	11900	108900	2300	2700	79800	3900	400	100	200	400	0
Rhizosolenia hebetata f. semispina		100	0	0	0	100	0	0	0	0	0
Rhizosolenia cf. pungens		1400	0	0	0	0	0	0	0	0	0
Rhizosolenia setigera		0	0	0	300	0	0	0	0	0	0
Rhizosolenia cf.borealis/styliformis		0	0	0	0	0	0	0	0	0	0
Rhizosolenia sp.		0	0	0	0	300	17400	2700	0	0	0
Pseudosolenia calcar avis		0	100	0	1900	0	0	0	0	0	0
Melosira sp.			0	0	0	0	0	0	0	0	0
Licmophora							0	0	0	0	0
Unindentified small centr.diatoms	7500	6700	500	900	0	0	8100	0	0	0	9300
Attheya septentrionalis		0	0	0	0	300	2500	0	1400	0	0
Chaetoceros simplex		0	0	0	0	0	0	0	0	0	0
Chaetoceros subtilis		0	0	0	0	0	0	0	0	0	400
Chaetoseros minimus		0	0	0	0	0	700	0	0	0	1800
Chaetoseros throndsenii		0	0	0	0	0	0	0	0	0	2400
Chaetoseros tenuissimus		0	700	900	600	0	10400	700	39300	0	0
Chaetoceros wighamii		0	0	0	0	0	0	0	0	0	0
Chaetoceros affinis		0	0	0	0	0	0	0	0	0	0
Chaetoceros curvisetus			0	0	0	0	0	0	0	0	0
Chaetoceros didymus		0	0	0	0	0	0	0	0	0	0
Chaetoceros cf. pendulus or cf. peruvianus		0	0	0	0	0	0	0	0	0	0
Chaetoceros socialis		2100	5800	0	0	0	92000	0	100800	0	10500
Chaetoceros teres			0	0	0	0	0	0	0	0	0
Chaetoceros cf. brevis		0	0	0	0	0	0	0	0	0	0
Chaetoceros cf. constrictus		0	0	0	0	0	0	0	0	0	0
Chaetoceros laciniosus			0	0	0	0	0	0	0	0	0
Chaetoceros danicus		0	0	0	0	0	0	0	0	0	0
Chaetoceros debilis		0	0	0	0	0	2900	0	0	0	0
Chaetoceros decipiens	400		0	0	0	0	0	0	0	0	0
Chaetoceros contortus	3200		0	0	0	0	0	0	5400	0	0
Chaetoceros similis	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros concavicornis f.volans f.criophilum	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros spp.	9500	20300	0	0	0	1900	64100	0	3900	0	0
Asterionellopsis glacialis		3800	0	0	0	0	0	0	0	0	0
Striatella unipunctata		0	0	0	0	0	0	0	0	0	0
Coscinodiscus spp.		100	0	0	0	0	0	0	0	0	0
Thalassiosira cf. hyalina		0	0	0	0	0	0	0	0	0	0
Thalassiosira cf. rotula		0	300	0	0	0	0	0	0	0	0
Thalassiosira anguste-lineata		0	0	0	0	0	500	0	0	0	0
Thalassiosira gravida		0	0	0	0	0	0	0	0	0	0
Thalassiosira nordenskioeldii		0	0	0	0	700	2500	0	0	0	0
Thalassiosira cf. pacifica-angulata		0	0	0	0	0	0	0	0	0	0
Thalassiosira spp.		0	1400	500	0	0	32500	0	0	0	0
Licmophora sp.	100	0	0	0	0	0	0	0	0	0	0

Class Dinophyceae		0	0	0	0	0	0	0	0	0	0	0
	Akashiwo sanguinea	0	0	200	0	700	0	300	0	0	0	0
	Ceratium horridum	0	100	0	0	0	0	0	0	0	0	0
	Ceratium lineatum	0	0	1900	0	700	100	0	0	0	0	0
	Ceratium fusus	0	0	0	0	0	0	0	0	0	0	0
	Ceratium longipes	0	0	0	0	0	0	0	0	0	0	0
	Ceratium tripos	100	200	200	100	100	0	0	0	0	0	3500
	Ceratium macroceros	0	0	100	0	0	0	0	0	0	0	0
	Ceratium furca	0	0	0	100	100	0	0	0	0	0	0
	Dinophysis norvegica	0	0	100	0	0	500	300	900	100	300	500
	Dinophysis acuminata	0	0	100	0	0	100	100	0	0	0	200
	Dinophysis dens	0	0	0	0	0	0	0	0	0	0	0
	Dinophysis rotundata	100	0	0	0	0	0	0	0	100	100	0
	Dinophysis acuta	0	0	0	0	0	0	0	0	0	0	0
	Dinophysis tripos	0	0	0	0	0	0	0	0	0	0	0
	Dinophysis odiosa	0	0	0	0	0	0	0	0	0	0	0
	Actiniscus pentasterias	0	0	0	0	0	0	0	0	0	0	0
	Micracanthodinium cf.claytoni	0	0	0	0	0	0	0	0	0	0	0
	Prorocentrum cf. minimum	400	0	0	0	200	0	0	0	0	0	1200
	Prorocentrum micans	900	700	1400	0	0	0	0	0	0	0	0
	Prorocentrum cf. glacile	100	100	200	0	0	0	0	0	0	0	0
	Protoperidinium divergens	0	0	0	0	0	0	0	0	0	0	0
	Protoperidinium depressum	0	0	0	0	0	0	0	0	0	0	0
	Protoperidinium conicum	0	0	300	0	100	0	0	100	0	0	0
	Protoperidinium steinii	0	0	0	0	100	0	0	100	200	0	800
	Protoperidinium granii	0	0	0	0	0	0	0	0	0	0	0
	Protoperidinium pallidum	0	0	0	0	0	0	400	0	0	0	0
	Protoperidinium pellucidum	0	0	0	0	300	300	700	900	0	0	0
	Protoperidinium oblongum	0	0	0	0	0	0	0	0	0	0	0
	Protoperidinium ovatum	0	0	0	0	0	0	0	0	0	0	0
	Protoperedinium leoins	0	0	0	0	0	0	0	0	0	0	0
	Protoperedinium brevipes	0	0	0	0	300	0	0	0	0	0	0
	Protoperidinium spp.	0	0	0	0	100	0	0	0	0	0	0
	Gonyaulax digitale	0	0	0	0	0	0	0	0	0	0	0
	Protoceratium reticulatum	0	0	0	0	0	0	0	0	0	0	500
	Protoperidinium /Minuscula bipes	0	0	0	0	0	0	0	0	0	1200	400
	Diplopsalis-group	0	0	0	0	0	0	0	0	0	0	0
	Alexandrium sp.	0	0	0	0	0	700	0	0	100	0	700
	Heterocapsa sp.	0	0	0	0	0	0	1100	0	14900	0	900
	Scrippsiella gr./trochoidea	300	0	0	0	1800	4000	4200	1500	4500	600	4800
	Unidentified thekat dinoflag. (8-8,5µm)	0	0	0	0	1700	1900	0	0	0	0	0
	Unidentified thekat dinoflag.(15-17µm)	0	0	0	0	0	0	2000	400	0	3000	20100
	Unidentified thekat dinoflag.(19-21,6 µm)											29100
	Polykrikos cf. schwartzii	0	0	0	0	0	0	0	0	0	0	0
	cf. Azadinium spinosum	0		0	0	0	0		0		0	
	cf. Enciculifera sp.	0	0	0	0	0	100	0	0	0	0	0
	cf. Gymnodinium lohmanii	0	0		0	200	100	0	0	0	0	0
	cf. Karlodinium veneficum	0	0	0	0	0	0	0	0	0	0	0
	cf. Gyrodinium fusiforme	0	0	0	100	800	100	0	0	0	0	0
	cf. Gyrodinium spirale	0	0	0	0	0	0	0	0	0	0	0
	cf. Oxytoxum complex	0	0	0	0	0	0	0	0	0	0	0
	cf. Amphidinium sphenoides	0	0	0	0	400	100	200	500	0	0	0
	cf. Amphidinium longum	0	0	0	0	0	0	0	0	0	0	16100
	Amphidinium sp.	1600	400	1100	500	200	0	0	0	0	0	0
	cf. Katodinium glauc. /Gymnodinium vestif.						700	0	2400	0	0	1000
	cf. Katodinium sp.	0	0	0	0	0	0	0	0	0	0	0
	Unidentified naked dinoflag.(8-24 µm)	1800	40700	16500	18500	10400	10000	15600	13200	8700	2500	110400
	Unidentified naked dinoflag.(25-40 µm)	700	0	0	5900	4400	2700	3900	8100	900	17600	10500
	Unidentified naked dinoflag.(50-110 µm)	0	1500	1000	0	0	0	1400	1300	0	0	0
Unidentified flagellates	(ca. 5-10 µm)	0	0	0	0	0	0	0	0	0	0	9600
Class Dictyochophyceae		0	0	0	0	0	0	0	0	0	0	0
	Dictyocha speculum	0	0	600	1200	1100	700	600	0	0	0	0
	Dictyocha fibula	0	0	0	0	0	0	0	0	0	0	0
Class Chrysophyceae												
	Dinobryon sp.	0	0	0	0	0	0	0	0	48900	10500	0
Cryptomonads/Pyramimonads		106100	102900	171000	45500	108500	63400	27100	35200	197700	230200	594200
Class Euglenophyceae												
	Eutreptiella cf. braarudii	800	100	1000	200	0	4700	16000	0	600	9100	2700