

**FROM THE ICE TO THE OPEN OCEAN**  
~THREATS TO PHYTOPLANKTON PRODUCTIVITY  
IN THE ANTARCTIC MARINE ECOSYSTEM FROM A  
CHANGING CLIMATE~



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*Submitted in fulfilment of the  
requirements for the degree of Doctor of  
Philosophy, Department of  
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# CERTIFICATE OF AUTHORSHIP/ORIGINALITY

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I certify that the work presented in this thesis and the research to which it pertains, are the product of my own work and to the best of my knowledge, original. Any quotations, ideas or work conducted by others, published or otherwise, are fully acknowledged in accordance with the standard referencing practices of the discipline. Co-authors of published, submitted papers or articles in preparation have been acknowledged for their contributions and for each publication herein my personal contribution and role clearly described. Furthermore, I certify that this thesis has not previously been submitted, in whole or in part, for a degree at this or any other university.

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Signed \_\_\_\_\_

Katherina Petrou (PhD Candidate)



# ACKNOWLEDGEMENTS

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This thesis is dedicated to my beautiful husband Javier. His unwavering love has been the essential ingredient for my happiness during the evolution of this work. I would like to also thank those who have been there for me throughout my life. My family, who have always been supportive and encouraging of the choices I've made both personally and professionally and whose unconditional love has guided me through life on steady feet and with strong resolve. They have taught me to never underestimate the value of love and the importance of laughter.

My formative years are filled with people who've inspired me, instilled me with a passion for discovery and an unabating thirst for knowledge. From my earliest memories I am aware of my debt to teachers and friends who have shaped my interest in the natural world. What a marvel to behold! This unique and beautiful planet we call home. I have always drawn inspiration from Nature and have been intrigued and captivated by the complexity and perfect chaos that surrounds us. I cannot overstate the role that Nature herself has played in consolidating my inquisitive personality.

In the preparation of this thesis and the work that it represents, special thanks must be given to my supervisors. To my principle supervisor Professor Peter Ralph (UTS) for believing in me, for all the amazing opportunities and expressing continual enthusiasm for my research, to Dr Martina Doblin (UTS) for her continual motivation and guidance, and to Dr Christel Hassler (CSIRO) for her enthusiasm and for introducing me to the intricacies of iron chemistry. Each has contributed to the successful completion of this work, graciously imparting their expert knowledge freely and without reservation, for this I am eternally grateful. Professor Douglas Campbell (Mt Alison University) was instrumental in the success of part of this thesis for which I am sincerely appreciative.

Thank you to Dr Björn Rost and the Phytochange group for making my research at the Alfred Wegener Institute for Polar and Marine Research interesting and thoroughly enjoyable. Special thanks to Sven Kranz and Christiane Uhlig for their friendship and kindness during my stay in Bremerhaven and openly inviting me into their circle of friends.

Heartfelt thanks are extended to all members of the Aquatic Processes Group for all the laughs, support and pearls of wisdom. In particular, thanks to Olivia Sackett and Dr Ross Hill for the successful and enjoyable collaborations. I wish to acknowledge the late Neil Ralph and his ingenious talents for making dreamed-up laboratory and field equipment into a reality. To Dr Ross Hill, thanks for being a great expedition partner in Antarctica, your tireless coring efforts and sled racing skills will be cherished always. Gratitude must also be extended to the crew and fellow expeditioners on the *Aurora Australis* who helped make the Antarctic experience truly memorable. To Dr Isabel Jimenez-Denness, I extend my warmest thanks for her friendship, patience and guidance not to mention her generosity in sharing her afternoon chocolate cake...mmm yummm!

Finally, thanks to the University of Technology, Sydney, in particular the Science Faculty and Department of Environmental Sciences for their financial and logistical contributions to my research, with special thanks to the staff for their assistance and support.

*And now there came both mist and snow,  
And it grew wondrous cold:  
And ice, mast-high, came floating by,  
As green as emerald.*

*And through the drifts the snowy clifts  
Did send a dismal sheen:  
Nor shapes of men nor beasts we ken –  
The ice was all between.*

*The ice was here, the ice was there,  
The ice was all around:  
It cracked and growled, and roared and howled,  
Like noises in a swound!*

*Samuel Taylor Coleridge  
The Rime of the Ancient Mariner*

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*“The sea, once it casts its spell, holds one  
in its net of wonder forever.”*

*Jacque Cousteau*



# 1 SUMMARY

# 1 Summary

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The Antarctic marine ecosystem is unique and dynamic, changing seasonally and forming specialised niche habitats including open ocean, sea ice and meltwater environments. Phytoplankton are key species in the structure and function of the Antarctic ecosystem, instrumental in the regions biogeochemistry, fundamental to the food web and strong contributors to global primary production and carbon sequestration. Understanding the photosynthetic plasticity of Antarctic phytoplankton is essential to understanding the effects global change is likely to have on primary production in the region. Through a series of experiments, this thesis explores the processes of light acclimation, photoprotection and photoinhibition in Antarctic microalgae under different environmental stressors, comparing photophysiological responses of species known to inhabit the sea-ice, meltwater and pelagic regions of Antarctic waters.

The photosynthetic properties of three Antarctic diatoms (*Fragilariopsis cylindrus*, *Pseudo-nitzschia subcurvata* and *Chaetoceros* sp.) to changes in salinity, temperature and light were compared. Large heterogeneities in the photoprotective capacity of the three species and several distinct physiological strategies in response to the rapid changes in the ambient environment were observed (Publication I). Similarly, photosynthesis and net primary productivity was species-specific with large differences between environmental conditions (Publication II). Fast induction kinetics and pulse amplitude modulated fluorometry were used to demonstrate high levels of flexibility in light acclimation capabilities of sea ice algae from the east Antarctic. Inhibitors and pigment analyses identified xanthophyll cycling as the critical mechanism for photoprotection and preferred means by which sea ice diatoms regulated energy flow to PSI (Publication III). While immunoblot analyses of natural communities measured minimal D1 protein breakdown in algae exposed to irradiances up to  $200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . These data showed that sea ice diatoms had low intrinsic susceptibility to PSII photoinactivation and strong irradiance-dependent induction of non-photochemical quenching that was independent of protein re-synthesis (Publication IV).

The remaining chapters investigated photoprotective strategies and photosynthetic plasticity of phytoplankton under nutrient limitation. Nitrogen

## SUMMARY

depletion in *F. cylindrus* had a strong influence on non-photochemical quenching capacity and resulted in the impairment of photosynthetic electron transport resulting in the formation of Q<sub>B</sub> non-reducing PSII centres within the photosystem (Publication V). The influence of iron-limitation and high light stress on the growth and physiology of Southern Ocean phytoplankton revealed a community-based response of measurable changes in pigment ratios, photosynthetic capacity and community composition (Publication VI). Iron-limited phytoplankton altered the allocation of photosynthetically derived energy, increasing photoprotective pigment pools and down-regulating photochemistry, at the expense of photosynthetic plasticity.

# 2 GENERAL INTRODUCTION

## 2 GENERAL INTRODUCTION

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### 2.0 THE BLUE PLANET: OCEANS, PHYTOPLANKTON & PRIMARY PRODUCTION

*"Life originated in the sea, and about 80% of it is still there" Isaac Asimov*

Oceans cover more than 70 % of the Earth's surface; therefore it is no surprise they harbour many undiscovered secrets about the life-forms and complex interactions contained within. In addition to boasting great biodiversity, the world's oceans have a significant influence over global processes, providing half of the planet's oxygen, regulating climate, absorbing anthropogenic CO<sub>2</sub> and feeding 70% of the world's human population. The socio-economic value of marine biota is estimated at ~US\$21 trillion annually (Costanza et al 1997), with the calculations based on the combined contributions from recreation, food and ecosystem services, highlighting the importance of oceans to human existence.

Phytoplankton are the biological link that couples atmospheric and oceanic processes (Fig 2.1). They are a highly diverse group of microscopic marine protists that inhabit the sunlit surface waters of the ocean, the euphotic zone. Phytoplankton are generally unicellular although some form chains or colonies, and are key to the health and productivity of the marine ecosystem, influencing nutrient cycling, food web dynamics and global biogeochemical cycling (Buesseler 1998; Garibotti et al 2003). Global phytoplankton carbon biomass equates to approximately 2% of all photoautotrophic biomass on the planet, yet accounts for 40-50% of global carbon fixation (Field et al 1998). More than 100 million tonnes of inorganic carbon is fixed by phytoplankton on a daily basis (Behrenfeld et al 2006). This organic carbon is then transferred through the food web, re-released to the atmosphere and sequestered to ocean depths (Fig. 2.1).

Diatoms are an ecologically important group of phytoplankton in the global ocean, contributing up to 50% of all marine primary production (Nelson et al 1995).

They play a significant role in the export of material from the surface waters to depth and are major players in the export of carbon and silicate from the surface to the deep ocean (Smetacek 1999). In particular, diatoms are the dominant phytoplankton group in polar ecosystems (Armbrust 2009). Unlike anywhere else in the world, Antarctica has large silicate deposits covering the ocean floor, a result of diatom frustules that have settled over geological time (Treguer et al 1995). This region has been identified as one of the most important in supporting silicate and carbon export (Coale et al 2004) and thus a major participant in global biogeochemical fluxes (Fig. 2.1).

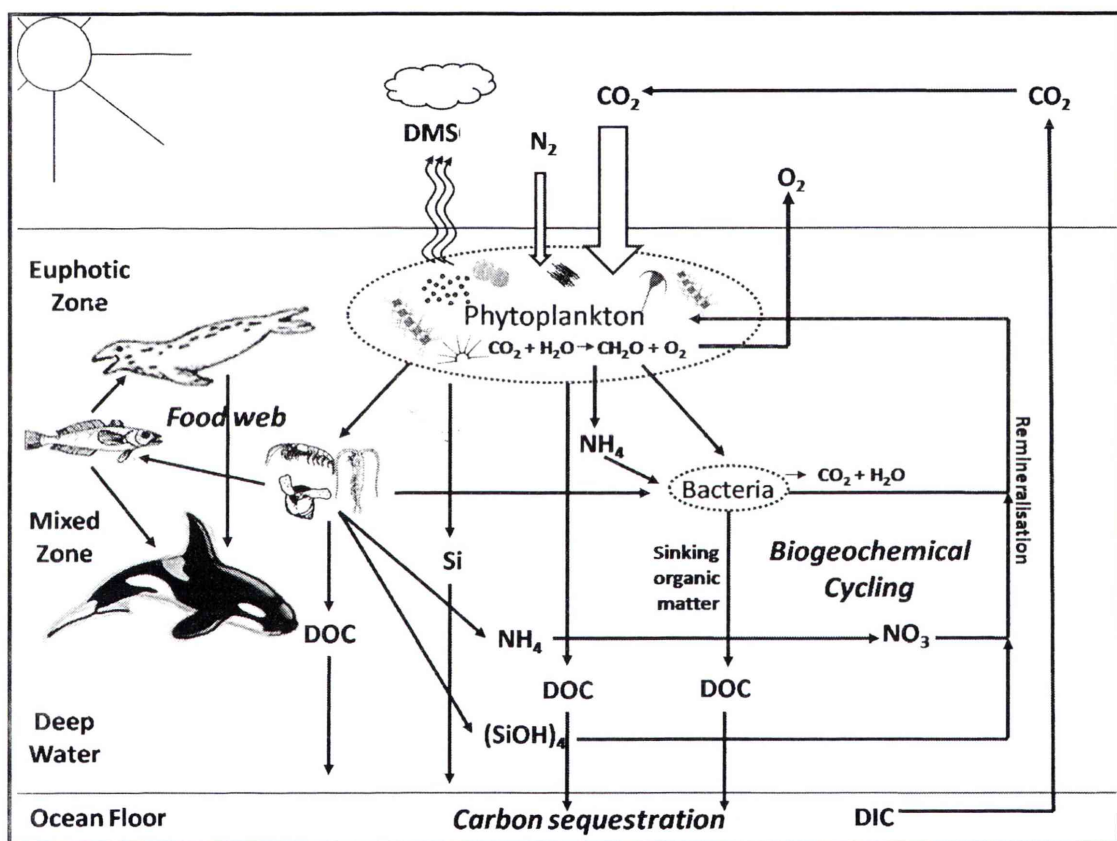


Fig. 2.1 Simplified model of phytoplankton-driven ocean-atmosphere gaseous exchange, trophic interactions, and biogeochemical cycles in the marine environment. Biogeochemical conversion of  $\text{CO}_2$  into dissolved organic carbon (DOC) via photosynthesis and waste products is shown. Re-mineralisation pathways of silica, nitrogen,  $\text{CO}_2$  and organic carbon stores into dissolved inorganic carbon (DIC) are also depicted.

Photosynthesis is the process by which inorganic carbon enters the living biosphere, connecting biogeochemical cycling with ocean productivity, and linking cellular processes (biochemical and physiological) with environmental condition (Fig. 2.1). Due to its pivotal role in atmospheric, oceanic and trophic processes, knowledge of phytoplankton photosynthesis and photosynthetic processes are vital to understanding variability in marine primary production (Falkowski 1994).

Measuring primary productivity using photosynthesis requires an understanding of light harvesting capacity, electron transport, carbon fixation, and the sensitivity of each of these processes to environmental perturbation. Chlorophyll *a* fluorescence provides a direct measurement of photosynthetic pigment excitation and reflects the photosynthetic activity of organisms' *in vivo*, providing information on the efficiency of energy conversion for primary production (Schreiber 2004). The advantage to using chlorophyll *a* fluorescence is that it is a rapid, non-destructive, non-invasive yet highly sensitive technique for ascertaining information on photosynthetic condition (Falkowski and Kolber 1995). It is particularly powerful when used in combination with other physiological measures such as photosynthetic pigments, gas exchange, protein and molecular changes, as well as cellular nutrient stoichiometry. The broad applicability of chlorophyll *a* fluorescence has led to greater understanding in plant stress physiology and rapid advancements in the interpretation of fluorescence signals. Pulse Amplitude Modulated (PAM) fluorometry has been extensively used in microalgal research, due to its ability to assess photosynthetic stress non-invasively. It allows for a precise interpretation of fluorescence signals, as it is able to discriminate between photochemistry, fluorescence quenching and heat dissipation (Schreiber 2004). It is based on the constrained relationship between the yields of photochemical energy conversion and non-photochemical quenching. Additional information can be obtained from fluorometers that are able to measure light-induced kinetic changes in chlorophyll *a* at microsecond resolution. Fast induction kinetics can determine effective cross sectional area of PSII, proportion of inactive reaction centres and measure the polyphasic rise in fluorescence, the OJIP transient. The OJIP transient reflects changes in electron transport from microseconds to seconds, enabling the evaluation of PSII characteristics including heat dissipation (Strasser et al 2004). Both fluorescence techniques are widely utilised in this thesis.

## 2.1 FROM THE ICE TO THE OPEN OCEAN: SEA ICE, MELTWATER AND PELAGIC ECOSYSTEMS

The Antarctic marine ecosystem is a unique and dynamic environment, extending from the ice-edged continent to the open ocean. Phytoplankton are key species in the structure and function of this ecosystem, instrumental in biogeochemical cycling, fundamental to the Antarctic food web and strong contributors to global primary production and carbon export.

Antarctic sea ice covers more than 40% of the Southern Ocean in winter (Lizotte 2001) and is a defining structural feature of the Antarctic marine ecosystem (Fig. 2.2). The seasonal formation and decay of sea ice is a major driver of thermohaline circulation (Fig. 2.2) and due to its high albedo, the sea ice also plays an essential role in the global energy balance (Eicken 1992). The sea ice is well recognised for its role as an important habitat (Legendre et al 1992; Arrigo and Thomas 2004), as well as for its critical contribution to primary production over winter (Arrigo et al 1998). The frozen habitat is perforated by a complex network of hyper-saline brine channels and pockets, which are home to microorganisms, including microalgae (Fig. 2.2). These tiny life-containing brine channels are characterised by low light and reduced supply of nutrients from the bottom water (Lizotte and Sullivan 1992a; Robinson et al 1998).

Few sea ice species are endemic to the ice environment alone. Instead, as the surface waters freeze, it is the entire pelagic community that is incorporated into the newly-formed ice, however, only those species able to acclimate to the new conditions survive to form the sea ice assemblage (Mock and Thomas 2008). Dominant species in the annual sea ice (pack ice) include *Fragilariopsis cylindrus*, *Fragilariopsis curta*, *Cylindrotheca closterium*, *Entomeneis kjellmannii*, *Navicula* sp. and *Nitzschia frigida* (Mock and Kroon 2002; McMinn and Hatton 2006; McMinn et al 2007). In particular, *F. cylindrus* has been recognised as an indicator sea ice species (Roberts et al 2007), dominating the sea ice zone (Kopczynska et al 2007), yet also known to bloom in the stratified waters of the meltwater zone (Beans et al 2008).

As the ice-edge retreats, phytoplankton blooms can persist for several weeks and extend for hundreds of kilometres. The melting of the sea ice leads to the formation of stable surface waters characterised by shallow mixed layers and low salinities



(Lizotte 2001), an ideal environment for phytoplankton bloom development. Over 70% of blooms occur when surface salinity drops below 33 psu (Dierssen et al 2002). Blooms tend to start with the release of meltwater, followed by increases in temperature which contribute to the stratification of surface waters, and aid in maintaining the shallow mixed layer (Strass and Nöthig 1996). Antarctic spring blooms can make a significant contribution to annual primary productivity, influencing the persistence of growth season, and the synchronisation between life cycles of the phytoplankton and grazers, such as krill (Strass and Nöthig 1996). Typical bloom forming species in the meltwater zone are diatoms from the genus *Fragilariopsis* (Beans et al 2008), *Pseudo-nitzschia* and *Chaetoceros* sp. (Kopczynska et al 2007; Tortell et al 2008). However, the prymnesiophyte *Phaeocystis antarctica* also blooms frequently in Antarctic waters often dominating coastal environments (DiTullio and Smith 1996; Tortell et al 2010) and is a major contributor to carbon fixation (Smith et al 1996) and carbon export (Dunbar et al 1998).

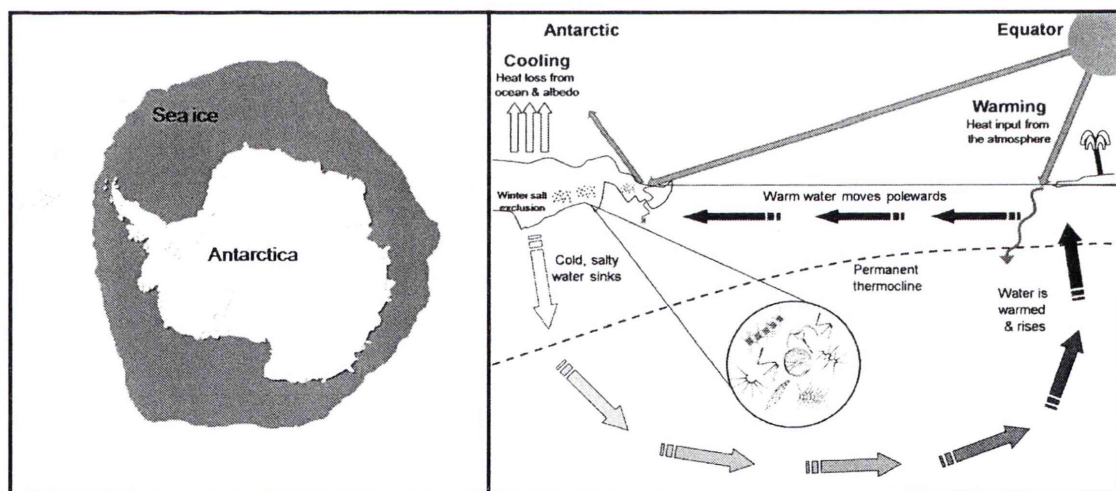


Figure 2.2 Schematic map of Antarctica (left panel), showing the Antarctic continent (white) and surrounding maximum winter sea ice extent (grey). Physiological processes that drive global thermohaline circulation and global temperature regulation (right panel) as a result of sea ice formation in the Antarctic. Interstitial microalgal communities within the ice matrix are also highlighted. Broken arrows indicate water circulation with colours representative of changes in temperature from cold (white) to warm (black).

The pelagic environment south of the polar front (060°S) is characterised by deeply mixed waters (Boyd 2002). This deep vertical mixing means phytoplankton are subjected to large fluctuations in irradiance. Furthermore, the Southern Ocean is the

largest high nutrient low chlorophyll (HNLC) region, characterised by high macronutrient concentrations and low phytoplankton biomass, now known to be due to low dissolved iron bioavailability (see Boyd et al 2007). Iron is essential for microalgal health and metabolic functioning, including various components of photosynthesis (Greene et al 1992). Iron-enriched proteins are critical for electron transport, and ferredoxin (iron-sulphur protein) is the electron donor used in nitrate reduction, N<sub>2</sub> fixation and the reduction of sulphate (Geider and La Roche 1994). In light of growing concerns over climate change, the productivity of the Southern Ocean has received increased attention in recent decades, due to its large contribution to atmospheric CO<sub>2</sub> drawdown, a result of its physical and chemical properties (Sabine et al 2004). Diatoms are the dominant primary producers in the Southern Ocean, but there is large heterogeneity in the distribution and composition of these diatom communities (Brierley and Thomas 2002). Understanding the physiological differences between species within this important phytoplankton group may provide some insight into the mechanisms that drive one species to succeed over another and determine the favourable and unfavourable conditions for their productivity.

## 2.2 ANTARCTIC PHYTOPLANKTON & PHYSIOLOGY

Given the remarkable diversity of microalgal communities in the Antarctic marine ecosystem—a result of the seasonal variability in environmental condition—it is important to understand the physiological responses to change within the environment.

Large variations in temperature and salinity are commonly experienced by Antarctic phytoplankton. Salinities vary seasonally from hyposaline meltwater conditions (< 34 psu) to the hypersaline conditions within the sea ice brine channels (> 140 psu) where temperatures can drop to as low as -15°C (Eicken 1992). Microalgal sensitivity to changes in salinity (Kottmeier and Sullivan 1988; Arrigo and Sullivan 1992; Krell et al 2007; Ralph et al 2007) and low temperature (Ralph et al 2005) have been reported in Antarctic species. However, many Antarctic microalgal species are adapted to variations in salinity and temperature (Vargo et al 1986; Ryan et al 2004; Mock and Hoch 2005), having evolved intracellular osmolytes for salinity regulation

(Mock and Thomas 2005), as well as cryoprotectants (Raymond and Knight 2003) and antifreeze proteins (Janech et al 2006) for dealing with the sub-zero temperatures.

In addition to metabolic adaptation, growth at low temperatures requires large reserves of carbon, nitrogen, phosphorus and in the case of diatoms, silicate (Arrigo et al 2010). These macronutrients are commonly in excess supply in the Southern Ocean. However, silicate can become limiting following a bloom (Gosselin et al 1990) and insufficient nitrogen to support sea ice algal growth has been reported previously (Lizotte and Sullivan 1992a; Robinson et al 1998). Furthermore, as with all photosynthetic organisms, Antarctic microalgae need to acclimate to changes in light climate. Sea ice algae are renowned for being shade-adapted organisms (Palmisano et al 1985; McMinn et al 2003, 2007; Lazzara et al 2007), having evolved the ability for low light ( $<1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) photosynthesis, with photoinhibition being measured at irradiances as low as  $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Palmisano et al. 1985; Robinson et al 1997). In summary, research to date has established that Antarctic microalgae are physiologically and metabolically active at low temperatures (Mock 2002; Price and Sowers 2004) and that they have evolved strategies to regulate photosynthesis under light limitation at sub-zero temperatures (Morgan-Kiss et al 2006). However, our understanding of photoacclimation, photoinhibition and photoprotective capacity under environmental stress remains largely unknown.

The key to understanding photosynthetic responses to variations in environmental parameters such as light, temperature and nutrient availability, requires an understanding of the balance between incoming excitation energy and outgoing demand for electrons used in carbon fixation (Kana et al 1997). Photosynthesis is the biological process of transforming light energy into oxygen and organic carbon compounds. The photosynthetic apparatus of a eukaryotic photoautotroph is comprised of two photosystems (PSII and PSI) that are linked by the electron transport chain via the Cytochrome *b<sub>6</sub>f* complex (Fig. 2.3). The functioning of PSII and PSI is closely coupled with carbon fixation, nitrate assimilation, respiratory processes and cell growth. For example, the assimilatory pathway of inorganic nitrogen is dependent on organic carbon substrates (GS and GOGAT), reductants (including NADPH) and ATP (Fig. 2.3), which are all supplied by the photosynthetic and respiratory pathways (Turpin 1991). In photosynthesis, ATP and NADPH are primarily responsible for the bioconversion of  $\text{CO}_2$  to carbohydrates utilising the enzyme ribulose-1,5-bisphosphate

carboxylase oxygenase, or Rubisco (Fig. 2.3). However, the relatively slow regeneration of rubisco in the photosynthetic carbon reduction cycle (PCR) is often a rate-limiting step in photosynthesis and can result in a diminished carbon sink capacity (Falkowski and Raven 2007). This has implications for photosynthetic plasticity, as it can upset the balance between absorbed energy and carbon sink turnover rates and therefore influence the capacity for the cell to respond to changes in environmental condition through photoacclimation.

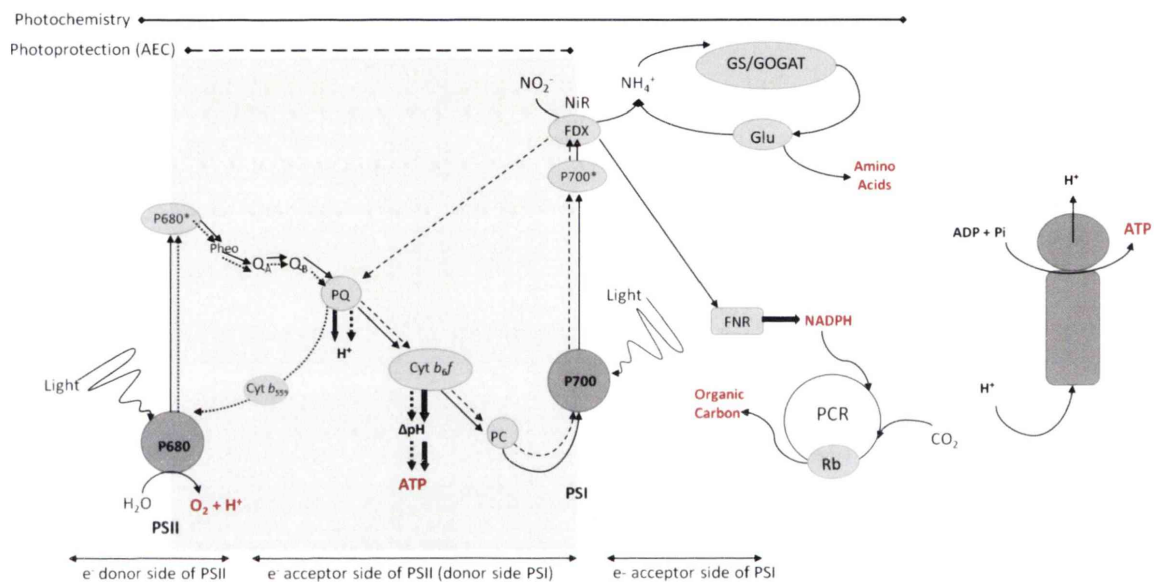


Figure 2.3 A schematic representation of the photosynthetic apparatus and processes in a eukaryotic photoautotroph, highlighting linear electron transport (LET) and alternative electron cycling (AEC) in the photosynthetic membrane. LET (solid lines) is the process of photo-oxidising a water molecule with the use of carbon dioxide ( $\text{CO}_2$ ) to produce oxygen and organic carbon via Rubisco. It involves electrons passing from PSII to PSI producing ATP (via a pH gradient ( $\Delta\text{pH}$ ) formed along the transport chain) and NADPH. NADPH is generated by the reduction of  $\text{NADP}^+$  by the enzyme ferredoxin NADP reductase (FNR), and is then used in the photosynthetic carbon reduction (PCR) cycle for the biosynthesis of sugars and in the reduction of nitrate to ammonia for the synthesis of amino acids. Photochemical pathway (solid line above) and photoprotective pathway (dashed line above) of electrons correspond to the two different modes of electron transfer. The two alternative electron cycling pathways shown are cyclic electron transport around PSII (dotted arrows) and PSI (dashed arrows). In CET around PSII (dotted arrows), electrons are circulated through the cytochrome  $b_6/f$  complex and returned to the electron donor side of PSII. In CET of PSI, electrons are passed around PSI (dashed lines), they are not passed on to the PCR, but recycled and only ATP is synthesised. The electron donor and acceptor sides are indicated (bottom arrows). Cyt  $b_6/f$ , cytochrome  $b_6/f$  complex; Cyt  $b_{559}$ , cytochrome  $b_{559}$  complex; FDX, ferredoxin; GOGAT, glutamine 2-oxoglutarate amino transferase; GS, glutamine synthetase; Glu, glutamate; NiR, nitrite reductase; Pheo, pheophytin; PC, plastocyanin; PQ, plastoquinone; PSII, photosystem two; PSI, photosystem one;  $\text{Q}_A$ , primary electron donor of PSII;  $\text{Q}_B$ , secondary electron donor of PSII; Rb, Rubisco.

Photoacclimation is a complex light response that results from changes in cellular activity and adjustment of physiological properties to balance photosynthetic electron transport with metabolic demands, such as nutrient uptake (Falkowski and LaRoche 1991). Photoacclimation is a phenotypic response to change in irradiance, not to be confused with photoadaptation, which involves an inherent genetic light response that has evolved with the species at evolutionary time scales (Moore et al 2006). Rapid photoacclimation (seconds to minutes) includes heat dissipation via xanthophyll cycle pigments (Fig. 2.4; Demmig Adams and Adams 1996) and is a photoprotective response induced at high light intensities or under stressed conditions (Allen 2003). In contrast, longer-term photoacclimation (minutes to hours) is implemented to establish a new photoacclimated state, which involves changes in gene expression, enzyme activity, antenna composition and photosystem stoichiometry (Fig. 2.4). These changes are regulated to allow the photosynthetic apparatus to maintain the balance between incoming excitation energy and electron utilisation (Falkowski and LaRoche 1991). In cases where light energy exceeds the capacity for photoacclimation, damage to the photosynthetic apparatus, specifically the PSII D1 protein, results (Müller et al 2001; Six et al 2007). Degradation of the D1 protein leads to photoinhibition, which can be dynamic—recovering rapidly when conditions return to normal or when D1 protein synthesis is able to match rates of degradation—or chronic; in which case electron flow cannot be re-established and damage to the photosystem follows.

Strategies of photoacclimation vary from one microalgal species to another (see Falkowski and LaRoche 1991; Moore et al 2006). Differences in photoacclimation strategy are due to the heterogeneity in photosynthetic structure and accessory pigment composition between species, influencing the rate and quantity of incoming photons (Wilhelm 1990). Some species acclimate by changing the size of the light harvesting antenna of the individual reaction centre, while others increase the total number of reaction centres, keeping antenna size constant (Falkowski and LaRoche 1991; Moore et al 2006). This variability in physiology results in a wide-range of light utilisation efficiency and photoprotective capacities from one phytoplankton species to another, making it important to investigate species-specific photosynthetic activity to understand what drives community composition and ultimately primary productivity. Furthermore, understanding the photosynthetic plasticity and photoprotective capacity of Antarctic phytoplankton to single and multiple stressors will provide insight into their ability to cope with rapid environmental change and lead to a better

understanding of the ecophysiology, distribution and abundance of phytoplankton within the Antarctic ecosystem. In summary, a detailed understanding of the photophysiology of single species and communities will link phytoplankton photosynthesis and ecological niche occupancy and possibly elucidate the drivers of acclimation, adaptation and long-term changing in community structure.

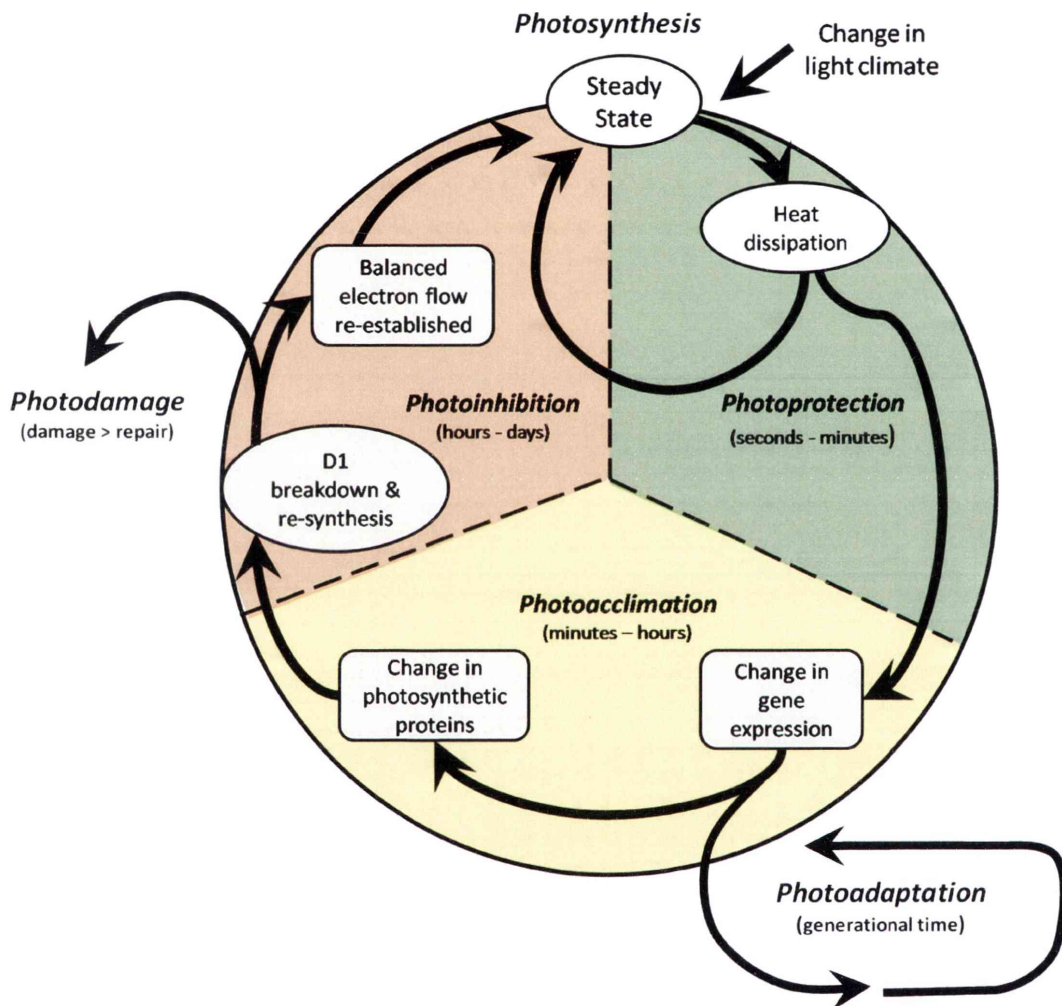


Figure 2.4 Schematic of the process of photoacclimation in microalgae. A change in light climate shifts cells from steady state photosynthesis into a series of physiological processes. If the photoprotective response of heat dissipation from the antenna is sufficient to deal with incoming light, then the cell is able to return to steady state photosynthesis in a matter of seconds to minutes. If however the change in light environment persists, changes in gene expression and proteins are necessary to acclimate to new conditions. If enzyme and protein acclimation is sufficient for dealing with new environmental conditions and D1 repair rates are fast enough to avoid permanent damage, cells will return to balanced electron flow and steady state photosynthesis. If however, the rate of D1 protein breakdown exceeds the rate of repair; irreparable damage to the photosynthetic apparatus will ensue.

## 2.3 THREATS FROM A CHANGING CLIMATE

*“It is not the strongest of species that survives, nor the most intelligent, but the one most adaptable to change” Charles Darwin*

### 2.3.1 PREDICTED ENVIRONMENTAL CHANGE

Change is an integral part of our planet’s history; past millennia have experienced major shifts in environmental condition and ecosystem structure. However, these rates of change were generally very slow, following geological time scales which permitted species to adapt, migrate, or in the case of those unable to do either, become extinct. In recent decades however, there is indisputable evidence that global atmospheric change is occurring at an alarming speed (Pachauri 2007), altering ocean chemistry, temperature and ocean circulation patterns (Doney et al 2009), driving species shifts and mass extinctions, increasing the efficacy of invasive species, and ultimately reducing ecosystem complexity. In the last 30 years alone, there has been a decline in the ocean’s annual primary production, with high latitude regions accounting for more than 70% of this decline (Gregg et al 2003). Continuing declines in marine primary productivity will have dire consequences for the marine environment, effecting ocean biogeochemistry, carbon sequestration and trophic dynamics (Falkowski et al 2000).

Rising atmospheric CO<sub>2</sub> concentrations and mean global temperatures pose serious threats to the World’s oceans (Hoegh-Guldberg and Bruno 2010). However, due to the complexity and sheer magnitude of the marine environment, knowledge about how climate change is affecting the functioning and diversity of this dominant ecosystem is still in its infancy (Thompson et al 2009; Hoegh-Guldberg and Bruno 2010). Ocean temperatures are rising (Levitus et al 2005; Domingues et al 2008), particularly at high latitudes and further warming over polar regions will invariably result in a decline in sea ice duration, extent and thickness (Mayewski et al 2009). Such structural changes to the Antarctic would weaken thermohaline circulation, which would alter global ocean currents and temperature, as well as having more regional effects on trophic dynamics (Moline et al 2004).

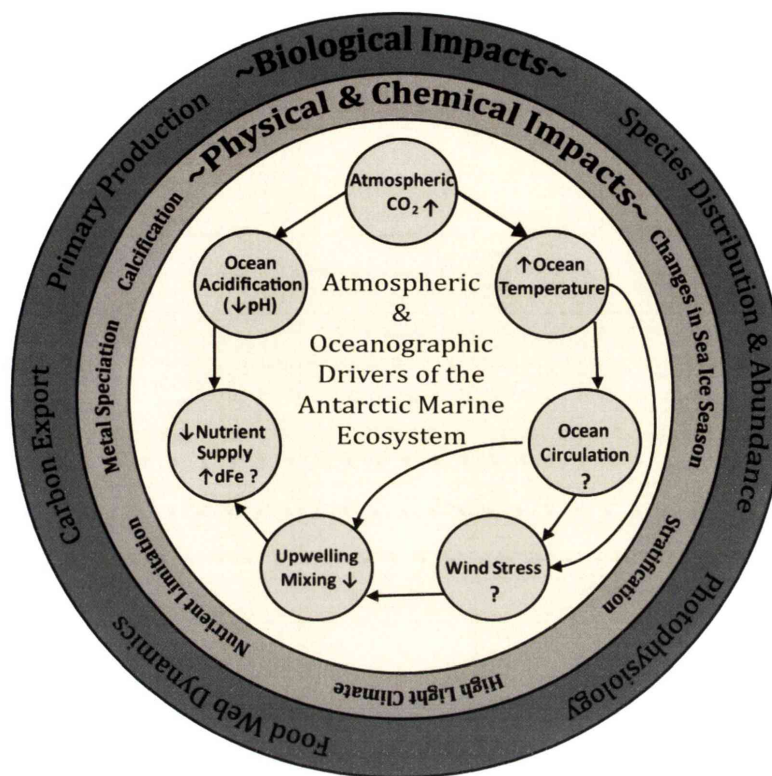


Figure 2.4 Atmospheric and oceanographic drivers of the Antarctic marine ecosystem. Arrows linking the inner bubbles identify the atmospheric and oceanic physical and chemical processes likely to change with increased atmospheric CO<sub>2</sub>. The innermost circle surrounding the identified drivers highlights the physical and chemical properties related to phytoplankton that are likely to be affected by these changes. The outermost circle highlights the biological impacts that the changes in the physical and chemical ocean properties are likely to cause. See text for further explanation. Figure adapted from schematic diagram by McKinnon et al (2007).

The cold high latitude waters of the Southern Ocean absorb around 30% of anthropogenic CO<sub>2</sub> annually (Sabine et al 2004). It is the world's largest CO<sub>2</sub> sink and therefore highly susceptible to acidification. A lowering of pH is likely to affect Southern Ocean biology in several ways (Fig. 2.4). Increased concentrations of hydrogen ions lead to aragonite and calcite undersaturation (McNeil and Matear 2008), having major implications for calcifying organisms, in particular, coccolithophorids and pteropods. Studies have shown changes in the morphology of coccoliths under different CO<sub>2</sub> concentrations (Riebesell et al 2000; Orr et al 2005) and dissolution of pteropod shells have been recorded below the aragonite saturation horizon (Honjo et al 2004). An indirect affect of increased hydrogen ion concentrations, is the influence lowered oceanic pH will have on nutrient availability and metal speciation. Negative effects of speciation include an increase in the toxicity of some metals, and possible influence on



nitrification by marine bacteria, impacting on nitrate supply to phytoplankton (Huesemann et al 2002). Conversely, acidification also has the potential to relieve widespread iron limitation (prevalent in the Southern Ocean) by increasing iron solubility (Breitbarth et al 2009b), enhancing the growth and productivity of some species. However, acidification also affects the ability for organic material to retain essential micronutrients (Fe, Zn, Cu, Co), and it is unclear whether this organically complexed iron will be available to sustain phytoplankton growth (Breitbarth et al 2009a).

Under a high CO<sub>2</sub> world, many flow-on effects to the physical and chemical properties of the ocean have been predicted. Sea surface temperature, wind stress and ocean currents exert strong influence over biological processes in the marine environment (Fig. 2.4). Surface temperatures control the distribution and abundance of phytoplankton and are crucial in triggering phytoplankton germination or resting stages, thereby influencing the timing of phytoplankton blooms (McQuoid and Hobson 1995). Generally, natural phytoplankton populations live at temperatures sub-optimal for photosynthesis, where communities are dominated by phytoplankton that show greatest growth at temperatures higher than the habitat mean (Moisan et al 2002). Thus, increasing sea surface temperatures are expected to result in increased photosynthesis and floristic shifts towards warmer-water species, while restricting cold-water species' ranges and reducing present biodiversity (Hays et al 2005). Changes in ocean currents and wind stress are expected to affect phytoplankton on a regional scale, with repercussions for primary productivity and CO<sub>2</sub> drawdown (Marinov et al 2010). The affect of wind stress on phytoplankton is predominantly indirect (Fig 2.4), where the interaction of wind and ocean currents can either enhance or suppress local upwelling (Boyd et al 2008). Furthermore, wind intensity can alter the depth and speed of vertical mixing, strongly influencing phytoplankton access to nutrients in the surface layers and determining light availability to phytoplankton for photosynthesis (Bopp et al 2001; Boyd and Doney 2002).

These CO<sub>2</sub>-driven modifications to the upper ocean (pH, temperature, wind-mixing, nutrients and light) will shape the function and ecology of phytoplankton, influencing their distribution, phenology and physiology (Edwards and Richardson 2004). Warmer temperatures alter wind stress, cloud cover and reduce vertical mixing, resulting in more stratified surface waters (Bopp et al 2001; Boyd and Doney 2002). For phytoplankton, this decline in mixed layer depth means that nutrient supply

(including iron) to the euphotic zone is diminished and photosynthetic efficiency potentially impaired (Fig. 2.3). Furthermore, reduced mixed layer depth with increase integrated daily irradiance delivered to phytoplankton in the surface waters (Marinov et al 2010), increasing the likelihood for prolonged photoinhibition. Indeed, the increase in temperatures, acidification and stratification of oceans has already resulted in changes in the distribution and abundance of phytoplankton communities, their phenology and productivity (Polovina et al 2008; Doney et al 2009).

### 2.3.2 RESPONSE OF ANTARCTIC PHYTOPLANKTON & GLOBAL IMPLICATIONS

Evidence of physiological impacts on Antarctic phytoplankton from a changing climate is largely anecdotal, due to the paucity of studies and observations. Knowledge of species' physiology and phenology is of critical importance to understanding ecosystem function and climate change responses. While many species within a community could be responding to changed conditions, it is the variability of the response and the sensitivity of each functional group that will lead to a loss in the synchrony of primary, secondary and tertiary producers (Edwards and Richardson 2004).

Species resilience to change will determine the ecosystems of the future. The vulnerability of one ecosystem compared with another is a function of exposure to change, sensitivity to that change and the capacity for acclimating and adapting to new conditions (Williams et al 2008). Of course this is ultimately determined by the response of the species contained within the ecosystem, which is in turn, constrained by individual phenotypic plasticity (Williams et al 2008). Most organisms are sufficiently plastic to accommodate normal variability experienced on short time scales within their life cycle and, when subsequent generations are exposed to different conditions they adjust through phenotypic plasticity (Bell and Collins 2008). However, when selection pressures become too great, populations begin to decline. In this case, migration poses an alternate option, but if neither relocation nor plasticity suffices, species must adapt or die (Bell and Collins 2008).

Using this model of plasticity with respect to Antarctic phytoplankton, the species' ability to acclimate or withstand change and the implications for ecosystem resilience can be assessed. Antarctic phytoplankton are evolutionarily adapted to

dynamic seasonal cycles from sea ice to oceanic environments, annually re-colonising the ice with the pelagic community. They therefore, possess substantial physiological plasticity. However, higher ocean temperatures will eventually lead to changes in ice extent, duration and thickness, disrupting this cycle (Smetacek and Nicol 2005) and potentially pushing some of these species beyond their thermal tolerance. Unlike temperate species, the possibility for migration to colder waters is not an option; therefore Antarctic phytoplankton must adapt or die. How well they will acclimate to altered physical and chemical properties that result from current climate forcings remains to be understood.

## 2.4 THESIS OUTLINE

This thesis investigates the photophysiological strategies and responses of Antarctic phytoplankton to environmental change. Photokinetics, net primary production, nutrient uptake, photosynthetic protein determination and pigment composition were studied in the laboratory on unicellular indicator microalgae from the sea ice, meltwater and pelagic environments, as well as on natural phytoplankton communities from the sea ice and pelagic Antarctic marine ecosystem.

Publication I investigates the effect of salinity and temperature on the photosynthetic plasticity and photoprotective capacity of three diatoms *Fragilariopsis cylindrus*, *Pseudo-nitzschia subcurvata* and *Chaetoceros* sp.. The photoprotective strategies and species-specific sensitivities are assessed in relation to ecological niche adaptation and species' distribution.

Publication II examines the link between species distribution and photosynthetic plasticity in *F. cylindrus*, *P. subcurvata* and *Chaetoceros* sp.. Ambient conditions experienced in the sea ice, meltwater and pelagic niche habitats and their influence on species-specific net primary production rates are considered.

Publication III addresses the question of obligate shade-adaptation in sea ice microalgae and investigates photoprotection and photoinhibition in bottom ice communities from the east Antarctic pack ice.

Publication IV explores the process of D1 protein breakdown and re-synthesis in sea ice diatoms. The effect of light on photoinactivation and photoinhibition in sea ice microalgal communities from the east Antarctic pack ice is investigated and the implications for thinning sea ice under future climate scenarios discussed.

Publication V examines the effect of nitrogen stress in the model polar diatom *F. cylindrus*. Investigations into the photophysiological strategies used by this species, addresses the question of why *F. cylindrus* is so successful in the Antarctic marine environment, particularly in its ability to cope with high light environments that are nutrient limited, such as the sea ice or stratified spring conditions.

Publication VI measures a community-based photophysiological response to high light stress under iron limiting conditions. The photosynthetic plasticity, pigment ratios and taxonomic changes are assessed and the implications of observed responses discussed in relation to primary productivity.

To conclude, the general discussion summarises the key findings and highlights new insights that this thesis has contributed to the understanding of photosynthetic plasticity in Antarctic microalgae. Possible implications for primary production, phytoplankton ecophysiology and ecosystem structure are evaluated in relation to changing climate and future research directions identified.

## 3 PUBLICATIONS

# 3 PUBLICATIONS

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## 3.1 LIST OF PUBLICATIONS

This doctoral thesis is based on the following six publications

- I. Katherina Petrou, Martina A. Doblin and Peter J. Ralph. (In press). Heterogeneity in the photoprotective capacity of three Antarctic diatoms during short-term changes in salinity and temperature. *Marine Biology*.
- II. Katherina Petrou and Peter J. Ralph. Variations in net primary productivity of three Antarctic diatoms: possible significance for their distribution in the Antarctic marine ecosystem. Ready for submission to *Limnology & Oceanography*.
- III. Katherina Petrou, Ross Hill, Martina A. Doblin, Andrew McMinn, Robert Johnson, Simon W. Wright and Peter J. Ralph (In Press). Photoprotection of sea ice microalgal communities from the East Antarctic pack ice. *Journal of Phycology* **47**.
- IV. Katherina Petrou, Ross Hill, Chirstopher M. Brown, Douglas A. Campbell, Martina A. Doblin, and Peter J. Ralph (2010). Rapid photoprotection in sea ice diatoms from the east Antarctic pack ice. *Limnology & Oceanography*. **55** (3) 1400-1407.
- V. Katherina Petrou, Sven A. Kranz, Martina A. Doblin and Peter J. Ralph. Photophysiological responses of *Fragilariopsis cylindrus* (Grunow) to nitrogen depletion at two temperatures. Submitted to *Journal of Phycology*.
- VI. Katherina Petrou, Christel S. Hassler, Martina A. Doblin, Kirsten Shelley, Veronique Schoemann, Rick van den Enden, Simon W. Wright and Peter J. Ralph (In Press) Iron limitation and high light stress on phytoplankton populations from the Australian Sub-Antarctic Zone (SAZ). *Deep Sea Research II, Antarctic biogeochemistry* (special issue).

### 3.2 DECLARATION OF THE CONTRIBUTION TO EACH PUBLICATION

#### Publication I

All laboratory work, data collection, data analyses and write up were undertaken by me. Olivia Sackett assisted with the setting up and maintaining cultures and flow cytometric analyses. HPLC analyses were done by Vinod Kumar and Marlene Zbinden.

#### Publication II

All laboratory work, data collection, data analyses and write up were undertaken by me. Olivia Sackett assisted with the setting up and maintaining cultures and chlorophyll *a* analyses.

#### Publication III

Sample collection and laboratory work were a joint effort undertaken by Ross Hill and myself. I was mostly responsible for the data analyses and write up of the manuscript.

#### Publication IV

Sample collection and laboratory work were a joint effort undertaken by Ross Hill and myself. Ross Hill undertook the immunoblot analyses with the assistance of Christopher M. Brown and Douglas A. Campbell in their Mount Alison laboratories. Douglas A. Campbell was instrumental in assisting me with the data analyses and I was primarily responsible for the write up of the manuscript.

#### Publication V

All laboratory work, data collection, data analyses and write up were undertaken by me. Dr Sven A. Kranz assisted with the setting up cultures and FIRe measurements.

#### Publication VI

All fluorescence, cell and community composition data were collected by me. Christel Hassler and Veronique Schoemann were responsible for the iron chemistry while Rick van den Eenden and Simon Wright performed the HPLC analyses. I was responsible for the data analyses and the majority of writing.

### 3.3 OTHER PUBLICATIONS

Publications not included in this doctoral thesis:

**Petrou K**, Smith R, Doblin M, Ralph P, Shelly K & Beardall J. (2008) State transitions and non-photochemical quenching of Nutrient-Induced Fluorescence Transients (NIFTs) in phosphorus-starved *Dunaliella tertiolecta*. *Journal of Phycology* **44**:1204-1211.

Cassar N, DiFiore PJ, Barnett BA, Bender ML, Bowie AR, Tilbrook B, **Petrou K**, Westwood K, Wright S & Lefevre D (2010) The influence of iron and light on net community production in the Subantarctic and Polar Frontal Zones. *Biogeosciences Discussions* **7**:5649-5674.

Ralph P, Wilhelm C, Lavaud J, Jakob T, **Petrou K** & Kranz S. Fluorescence as an assay to understand aspects of the physiology of light regulation. *In Advances in applied phycology* (Book Series). Chapter 12 (Eds. D. Suggett & O. Prasil); *in press*.

Doblin MA, Ralph P, **Petrou K**, Shelly K, Westwood K, Van den Ended R, Wright S & Griffiths B. (2010) Diel variation of chl *a* fluorescence, phytoplankton pigments and productivity in the Sub-Antarctic Zone (SAZ). *Deep Sea Research II*; *in press*.



# PUBLICATION I

HETEROGENEITY IN THE PHOTOPROTECTIVE CAPACITY OF THREE ANTARCTIC DIATOMS DURING  
SHORT-TERM CHANGES IN SALINITY AND TEMPERATURE

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Running head: Photoprotective capacity of three Antarctic diatoms

**ABSTRACT**

The Antarctic marine ecosystem changes seasonally, forming a temporal continuum of specialised niche habitats including open ocean, sea ice and meltwater environments. The ability for phytoplankton to acclimate rapidly to the changed conditions of these environments depends on the species' physiology and photosynthetic plasticity and may ultimately determine their long term ecological niche adaptation. This study investigated the photophysiological plasticity and rapid acclimation response of three Antarctic diatoms—*Fragilariopsis cylindrus*, *Pseudo-nitzschia subcurvata* and *Chaetoceros* sp.—to a selected range of temperatures and salinities representative of the sea ice, meltwater and pelagic habitats in the Antarctic. *Fragilariopsis cylindrus* displayed physiological traits typical of adaptation to the sea ice environment. Equally, this species showed photosynthetic plasticity, acclimating to the range of environmental conditions, explaining the prevalence of this species in all Antarctic habitats. *Pseudo-nitzschia subcurvata* displayed a preference for the meltwater environment, but unlike *F. cylindrus*, photoprotective capacity was low and regulated via changes in PSII antenna size. *Chaetoceros* sp. had high plasticity in non-photochemical quenching, suggesting adaptation to variable light conditions experienced in the wind-mixed pelagic environment. While only capturing short-term responses, this study highlights the diversity in photoprotective capacity that exists amongst three dominant Antarctic diatom species and provides insight into links between ecological niche adaptation and species' distribution.

Keywords: Photoprotection; diatoms; xanthophyll cycling ; light harvesting antenna

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Petrou, K., Doblin, M. & Ralph, P. (2011). Heterogeneity in the photoprotective capacity of three Antarctic diatoms during short-term changes in salinity and temperature. *Marine Biology*. **158** (5) 1029-1041. DOI: 10.1007/s00227-011-1628-4

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# PUBLICATION II

Net primary production of three Antarctic diatoms: possible significance for  
their distribution in the Antarctic marine ecosystem

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Running head: Primary productivity in Antarctic diatoms

## Acknowledgements

Thanks to Olivia Sackett for experimental assistance and Dr Isabel Jimenez-Denness for her support, helpful discussions and guidance. Financial support was provided by the Australian Research Council grant (DP0773558) awarded to PJR, Aquatic Processes Group and Department of Environmental Sciences, University of Technology, Sydney. KP was supported by an Australian Postgraduate Award and the Commonwealth Scientific and Industrial Research Organisation (CSIRO) top-up scholarship.

## Abstract

This study investigated photosynthesis and net primary productivity of three Antarctic diatoms, *Fragilariopsis cylindrus*, *Pseudo-nitzschia subcurvata* and *Chaetoceros* sp., to rapid temperature and salinity changes representing a range of conditions found during a seasonal cycle. *Fragilariopsis cylindrus* displayed the highest rates of relative electron transport and net primary productivity under all salinity and temperature combinations. It showed adaptive traits to the sea ice environment, but also plasticity to perform well under all conditions. *Pseudo-nitzschia subcurvata* displayed a preference for low saline conditions where production rates were greatest. However, there was evidence of photosynthetic sensitivity to the lowest temperatures and highest salinities, suggesting a lack of adaptation for dealing with the sea ice environment. *Chaetoceros* sp. showed high plasticity, acclimating well to all conditions, but showing a general preference for the pelagic environment. When this data was modelled over different seasons, integrated daily net primary production was greatest under summer conditions in the pelagic environment. There was also evidence to suggest sensitivity to low saline conditions. This study shows Antarctic net primary productivity is a function of light availability and can be influenced by ambient environmental conditions. Therefore, it is likely to vary on a seasonal basis and community primary production rates are highly dependent on community composition. Furthermore, this study demonstrated niche adaptation in Antarctic diatoms, adding to the understanding of phytoplankton dominance and distribution in the Antarctic ecosystem.



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Petrou, K. & Ralph, P.J. (2011). Photosynthesis and net primary productivity in three Antarctic diatoms: possible significance for their distribution in the Antarctic marine ecosystem. *Marine Ecology Progress Series* **437**. DOI: 10.3354/meps09291

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# PUBLICATION III

PHOTOPROTECTION OF SEA ICE MICROALGAL COMMUNITIES FROM THE  
EAST ANTARCTIC PACK ICE<sup>1</sup>

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Running title: LIGHT STRESS IN SEA ICE MICROALGAE

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## ABSTRACT

All photosynthetic organisms endeavour to balance energy supply with demand. For sea ice diatoms, as with all marine photoautotrophs, light is the most important factor for determining growth and carbon fixation rates. Light varies from extremely low to often relatively high irradiances within the sea ice environment, meaning that sea ice algae require moderate physiological plasticity that is necessary for rapid light acclimation and photoprotection. This study investigated photoprotective mechanisms employed by bottom Antarctic sea ice algae in response to relatively high irradiances to understand how they acclimate to the environmental conditions presented during early spring, as the light climate begins to intensify and snow and sea ice thinning commences. The sea ice microalgae displayed high photosynthetic plasticity to increased irradiance, with a rapid decline in photochemical efficiency that was completely reversible when placed under low light. Similarly, the photoprotective xanthophyll pigment diatoxanthin (Dt) was immediately activated, but reversed during recovery under low-light. The xanthophyll inhibitor, dithiothreitol (DTT), and state transition inhibitor, sodium fluoride (NaF) were used in under-ice *in situ* incubations and revealed that non-photochemical quenching via xanthophyll cycle activation was the preferred method for light acclimation and photoprotection by bottom sea ice algae. This study showed that bottom sea ice algae from the east Antarctic possess a high level of plasticity in their light acclimation capabilities and identified the xanthophyll cycle as a critical mechanism in photoprotection and the preferred means by which sea ice diatoms regulate energy flow to PSII.

KEYWORDS

Chlorophyll *a* fluorescence, OJIP transients, photoprotection, sea ice microalgae, xanthophyll cycle.

ABBREVIATIONS

Dd, diadinoxanthin; Dt, diatoxanthin; DTT, dithiothreitol;  $F_v/F_M$ , maximum quantum yield of PSII;  $F_0$ , minimum fluorescence;  $F_M$ , maximum fluorescence; PSI, Photosystem I; PSII, Photosystem II;  $Q_A$ , primary plastoquinone acceptor of PSII;  $Q_B$ , secondary plastoquinone acceptor of PSII; VAZ, violaxanthin, antheraxanthin and zeaxanthin.

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Petrou, K., Hill, R., Doblin, M., McMinn, A., Johnson, R., Wright, S.W. & Ralph, P.J. (2011). Photoprotection of sea ice microalgal communities from the East Antarctic pack ice. *Journal of Phycology*. **47**(1) 77-86. DOI: 10.1111/j.1529-8817.2010.00944.x

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# PUBLICATION IV

## Rapid photoprotection in sea-ice diatoms from the East Antarctic pack ice

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### *Abstract*

Photoinhibition and D1 protein re-synthesis were investigated in bottom-dwelling sea-ice microalgal communities from the East Antarctic pack ice during early spring. Bottom-dwelling sea-ice microalgal communities were dominated by diatoms that exhibited rapid photoprotection when exposed to a range of different light levels (10  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , 50  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , and 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). Photosynthetic capacity of photosystem II (PSII) dropped significantly over 3 h under 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , but largely recovered when placed in a low-light environment (10  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) for an additional 3 h. PSII repair rates increased with increasing irradiance, and the D1-protein pool remained steady even under high light (200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). Sea-ice diatoms showed a low intrinsic susceptibility to photoinactivation of PSII across all the light treatments, and a strong and irradiance-dependent induction of nonphotochemical quenching, which did not depend upon chloroplast protein synthesis, was also seen. These highly plastic organisms, once thought to be adapted to shade, are in fact well equipped to withstand rapid and relatively large changes in light at low temperatures with minimal long-term effect on their photosynthetic machinery.



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Petrou, K., Hill, R., Brown, C.M., Campbell, D.A., Doblin, M.A. & Ralph, P.J. (2010). Rapid photoprotection in sea-ice diatoms from the East Antarctic pack ice. *Limnology and Oceanography*. **55**(3) 1400-1407. DOI: 10.4319/lo.2010.55.3.1400

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# PUBLICATION V

PHOTOPHYSIOLOGICAL RESPONSES OF *FRAGILARIOPSIS CYLINDRUS*  
(GRUNOW) TO NITROGEN DEPLETION AT TWO TEMPERATURES<sup>1</sup>

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Running title: NITROGEN STRESS IN *F. CYLINDRUS*

<sup>1</sup>Received \_\_\_\_\_ Accepted \_\_\_\_\_

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## ABSTRACT

The photosynthetic efficiency and photoprotective capacity of the sea ice diatom *Fragilariopsis cylindrus* (Grunow) grown in a matrix of nitrogen repletion and depletion at two different temperatures (-1°C and +6°C) was investigated. Temperature showed no significant effect on photosynthetic efficiency or photoprotection in *F. cylindrus*. Cultures under nitrogen depletion showed enhanced photoprotective capacity with an increase in non-photochemical quenching (NPQ) when compared with nitrogen replete cultures. This was achieved at no apparent cost to the photosynthetic efficiency ( $F_V/F_M$ ) of PSII. Nitrogen depletion yielded a partially reduced electron transport chain, even in darkness, and maximum fluorescence ( $F_M$ ) could only be obtained by adding DCMU.  $Q_A^-$  reoxidation curves showed the presence of  $Q_B$  non-reducing PSII centres under nitrogen depletion. Fast induction curves (FICs) and electron transport rates revealed a slowing of the electrons transferred from the primary ( $Q_A$ ) to the secondary ( $Q_B$ ) quinone electron acceptors of PSII. The data presented show that nitrogen depletion in *F. cylindrus* leads to the formation of  $Q_B$  non-reducing PSII centres within the photosystem. On a physiological level, the formation of  $Q_B$  non-reducing PSII centres in *F. cylindrus* provides the cell with protection against photoinhibition by facilitating NPQ through xanthophyll pigment production. This strategy provides an important ecological advantage, especially during the Antarctic spring, maintaining photosynthetic efficiency under high light and nutrient limiting conditions.

## KEYWORDS

Diatom, *F. cylindrus*, Photoprotection, NPQ,  $Q_B$  non-reducing PSII centres

## ABBREVIATIONS

$F_0$ , minimum fluorescence in the dark;  $F_M$ , maximum fluorescence in the dark;  $F_V/F_M$ , maximum quantum yield of PSII (dark adapted); NPQ, non-photochemical quenching;  $Q_A$ , primary plastoquinone acceptor of PSII;  $Q_B$ , secondary plastoquinone acceptor of PSII; PQ, plastoquinone

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Petrou, K., Kranz, S.A., Doblin, M.A. & Ralph, P.J. (2012). Photophysiological responses of *fragilariopsis cylindrus* (bacillariophyceae) to nitrogen depletion at two temperatures. *Journal of Phycology*. **48**(1) 127-136. DOI: 10.1111/j.1529-8817.2011.01107.x

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# PUBLICATION VI

## **Iron-limitation and high light stress on phytoplankton populations from the Australian Sub-Antarctic Zone (SAZ)**

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**Abstract**

The high nutrient low chlorophyll (HNLC) surface waters of the Southern Ocean are characterised by high concentrations of nitrate and phosphate, low concentrations of dissolved iron and deep vertical mixing. Future climate scenarios predict increased surface temperatures and ocean stratification in the region. These changes to vertical mixing will result in a slowdown of nutrient supply to surface waters and an increase in the integrated irradiance in the upper mixed layer. To investigate the influence of iron-limitation and high irradiance on phytoplankton growth and physiology, a six-day shipboard incubation experiment was conducted during the SubAntarctic Zone Sensitivity to Environmental Change (SAZ-Sense) voyage using phytoplankton populations from the upper mixed layer in the north-eastern SAZ region. Iron-limitation was induced with an organic siderophore and was compared with a 1 nM iron-enriched incubation and an unamended treatment (under silicate replete conditions). As expected, iron enrichment led to dominance by large diatoms and enhanced photosynthetic performance, while the iron-limited community showed a decline in total chl *a* and photochemical efficiency. Under the added stress of high light, the iron-limited community was able to cope with the shift from in situ ( $< 150 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) to incubation (mean =  $765 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) irradiance by increasing the proportion of photoprotective pigments and diverting excess light energy via energy-dependent quenching ( $q_E$ ). The responses to iron-limitation under high light showed that the phytoplankton community was able to acclimate to these conditions, but exhibited an overall decline in photosynthetic activity. Data presented here suggest the community shifts, in particular the decrease in diatoms, and the decline in photosynthetic performance of phytoplankton under low iron-high irradiance conditions has the potential to impact future ocean productivity and biogeochemical cycling.



**Keywords**

Light stress, iron, phytoplankton, xanthophyll cycling, Southern Ocean

**Abbreviations**

DD, diadinoxanthin; DFB, desferroxamine B; DT, diatoxanthin; EPPS, 4-(2-Hydroxyethyl)-1-piperazinepropanesulfonic acid;  $F_0$ , dark-adapted minimum fluorescence;  $F_M$ , dark-adapted maximum fluorescence;  $F_M'$ , light-adapted maximum fluorescence; FUCO, fucoxanthin;  $F_V/F_M$ , maximum quantum yield of PSII; HNLC, high-nutrient low-chlorophyll; HEX, 19'-hexanoyloxyfucoxanthin; NPQ, non-photochemical quenching; NPP, non-photosynthetic pigments; PFG, phytoplankton functional group; PSII, photosystem II;  $q_E$ , energy-dependent quenching;  $q_I$ , photoinhibitory quenching; SAZ, Sub-Antarctic Zone; TAC, 2-(2-thiazolylazo)-p-cresol;  $\Phi_{PSII}$ , effective quantum yield of PSII.

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Petrou, K., Hassler, C.S., Doblin, M.A., Shelly, K., Schoemann, V., van den Enden, R., Wright, S. & Ralph, P.J. (2011). Iron-limitation and high light stress on phytoplankton populations from the Australian Sub-Antarctic Zone (SAZ). *Deep-Sea Research Part II: Topical Studies in Oceanography*. **58** (21-22) 2200-2211. DOI: 10.1016/j.dsr2.2011.05.020  
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# 4 GENERAL DISCUSSION

## 4 GENERAL DISCUSSION

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The publications presented in this thesis investigated the photosynthetic plasticity of Antarctic phytoplankton exposed to environmental change. Results obtained from these studies have provided new insights into the photosynthetic efficiency, photoprotective capacity and adaptive photosynthetic traits of Antarctic phytoplankton. Furthermore, the combination of field and laboratory studies delivered new information on phytoplankton responses to environmental stress at the sub-cellular, species and community levels. The key findings and implications from these new insights are discussed in the following sections. Given this new information, possible ecosystem-based responses to climate change are proposed and future research directions to emerge from this thesis are presented.

### 4.1 HISTORY OF RESEARCH ON ANTARCTIC PHYTOPLANKTON

Polar research has a history spanning more than 170 years (Mock and Thomas, 2008). The earliest records of polar microalgae come from the Norwegian explorer Fridtjot Nansen (1897) on his voyage across the Arctic as he observed '*...unicellular pieces of slime that live by the millions, in pools on very nearly every ice-floe all over this endless sea of ice, which we like to call a place of death!*'. In the south, due to the isolation of Antarctica and the difficulty of working under such extreme conditions, it was not until the establishment of stations on the Antarctic continent in the 1950s that significant advances in scientific research began. The majority of research into Antarctic microalgae from the last 50 years has focused primarily on taxonomic diversity (Mock and Thomas 2005), meaning that even after half a century of research, there are still many gaps in scientific knowledge on the basic physiology and biochemistry of these organisms, without which a complete understanding of the functioning and resilience of this unique ecosystem remains elusive.

In light of this paucity in basic physiological understanding, the last decade has brought about a growing interest in the physiology of polar microalgae, particularly in regard to their role in global climate. *In situ* and laboratory studies have shown that sea ice diatoms are physiologically active at low temperatures (Mock 2002; Price and

Sowers 2004) and there is a growing body of evidence to show that these species are evolutionarily adapted to life at low temperatures (Morgan-Kiss et al 2006). The studies contained within this thesis have contributed to improving the mechanistic understanding and physiological strategies that these unique organisms adopt for survival and success. In particular, this thesis has addressed some of the gaps in understanding physiological responses with respect to a changing climate, including increased temperature, increased light and nutrient limitation. New insights into the mechanistic understanding of the physical and biological drivers within the ecosystem—and their role in regional and global atmospheric regulation—will make predictions of ecosystem responses to climate change more attainable.

## 4.2 PHOTOSYNTHETIC PLASTICITY AND ECOPHYSIOLOGY OF ANTARCTIC PHYTOPLANKTON: A NEW UNDERSTANDING

### 4.2.1 SUB-CELLULAR RESPONSES TO ENVIRONMENTAL STRESS

Until now, the photoprotective capacity of Antarctic diatoms has been largely unexplored; however, studies on temperate diatoms have revealed this important functional group of microalgae to possess rapid and very high xanthophyll activity in response to increases in irradiance (Lavaud et al 2004; Ruban et al 2004). This same photoprotective trait has now been observed in several key bloom-forming Antarctic diatom species and communities (Publication I and III). Previous studies have also revealed variability in photoprotective strategies among temperate diatoms from different oceanographic regions (Dimier et al 2007, 2009; Lavaud et al 2007), a trait also observed among Antarctic species (Publication I). Many investigations on sea ice microalgal photosynthesis have found them to be among the most shade-adapted species on the planet (Palmisano et al 1985; Lizotte and Sullivan 1991a; McMinn et al 2003, 2007; Lazarra et al 2007), but with high capacity for photoacclimation (Lizotte and Sullivan 1991b, 1992b; Publications III and IV). Furthermore, several mechanisms and photophysiological strategies responsible for this flexibility have been uncovered (Publications III and IV) including a large PSII antenna size, that provides the cells with a high capacity for photoacclimation (Publication III), rapid xanthophyll cycling for immediate photoprotection (Kropuenske et al 2009; Publication III), and efficient *de novo* synthesis of carotenoid pigments for long-term sustainability of non-photochemical quenching (Publication III). Evidence of alternative electron cycling

(AEC) as a mechanism for photoprotection (Lavaud et al 2002) was also detected (Publication II), but not fully explored in this thesis.

Alternative electron cycling is a natural stress response in photosynthetic organisms. It plays a vital role in photoacclimation strategies, by providing a trigger for the dissipation of unusable light that has been absorbed by the PSII chl *a* molecules (Allen 2003). The PQ pool also plays a key role in regulating photosynthetic electron transport by modulating the amount of absorbed energy in the PSII reaction centres that is directed to linear electron flow. As photochemical energy exceeds utilisation, there is an increase in the pH gradient of the thylakoid membrane leading to the reduction of the PQ pool (Müller et al 2001). This reduction causes the cytochrome *b<sub>6</sub>f* complex to activate the cycling of electrons through PSII or PSI reaction centres (Prasil et al 1996). As the PQ pool re-oxidises in the dark, cyclic electron transport ceases (Prasil et al 1996). Cyclic electron flow around PSI is closely linked with ADP phosphorylation in the chloroplast and is primarily activated when additional ATP is required, such as in active nutrient uptake. Similarly, cyclic electron transport around PSII may occur in response to high light, a slowing of assimilatory enzymes — such as might occur under low temperature or nutrient stress — or when there is a mismatch between light and dark photosynthetic reactions (Prasil et al 1996). It is essential for PSII down-regulation and the dissipation of excitation energy occurs without the oxidation of water and is independent of thermal deactivation in the antenna (Prasil et al 1996). While no direct measurement of cyclic electron transport of PSII were made, it seems highly likely that the differences detected between the fluorescence and oxygen measurements (Publication II) in this thesis were attributed to cyclic electron transport around PSII.

A review by Mock and Thomas (2005) identified a lack of information on photoinactivation and photodamage in sea ice microalgae when exposed to high irradiances at low temperatures. This thesis has shown, for the first time, that photoinhibition in pack ice microalgal communities is largely avoided, with D1 repair rates able to keep pace with rates of photoinactivation, subsequently avoiding photosystem damage (Publication IV). This capacity for photoprotection in sea ice microalgae and subsequent lack of photoinhibitory damage has also been demonstrated through the rapid recovery of  $F_V/F_M$  after exposure to high irradiance. In a natural sea ice population dominated by *Nitzschia frigida*, photoinhibited  $F_V/F_M$  returned to 99.5% of its original  $F_V/F_M$  value after 10 min in the dark (McMinn and

Hattori 2006). This same reversible photoinhibition was measured in several Antarctic species used in this thesis, with high recovery rates of  $F_V/F_M$  under a number of stress conditions (Publications I, III, V and VI).

Investigations into the influence of nutrient requirements on phytoplankton growth and photosynthesis have received considerable attention in recent decades, particularly with respect to iron-limitation (Boyd et al 2007). It has been demonstrated that iron-limited cells display signs of high-light acclimation, with increased investment into photoprotection at the expense of photosynthetic plasticity (van Leeuwe and Stefels 1998; Publication VI). This diminished photosynthetic capacity would likely result in a decline in overall productivity, as predicted by models (Bopp *et al.*, 2001; Boyd and Doney, 2002), due to more energy being dissipated from the light harvesting antenna (photoprotection) than is being used in photosynthesis. The community-based response measured in this thesis following six days of light/iron stress, resulted in measurable changes in pigment ratios, photosynthetic capacity and taxonomic contributions to the total population (Publication VI). Furthermore, the observed community shifts, in particular an absence of diatom dominance, could have large implications for biogeochemical cycling, including iron remineralisation and carbon and silicate drawdown.

In contrast to the countless studies into iron as a limiting nutrient for Antarctic phytoplankton, nitrogen has largely been ignored, yet has been reported to limit growth in the sea ice (Lizotte and Sullivan 1992a; Robinson et al 1998). Nitrogen limitation leads to changes in lipid concentration and composition in Antarctic microalgae (Mock and Kroon 2002). By changing lipid composition, cells are able to maintain membrane integrity while protein and pigment concentrations are low (Mock and Kroon 2002). Nitrogen limitation in three sea ice diatoms lead to a decline in photosynthetic efficiency and electron transport rates, due to an increase in  $Q_B$  electron acceptors (Mock and Kroon 2002). A similar photosynthetic response was observed in *F. cylindrus* when subjected to nitrogen depletion (Publication V). There was a slowing of the electron transport chain which lead to the formation of  $Q_B$  non-reducing centres, but no change in  $F_V/F_M$  was detected (Publication V).

## 4.2.2 SPECIES RESPONSES TO ENVIRONMENTAL STRESS

Observations of Antarctic species successions and distribution have been investigated previously (Lizotte 2001; Kopczynska et al 2007; Roberts et al 2007; Almandos et al 2008; Beans et al 2008), with some studies correlating observed distribution with physical and chemical oceanic parameters (Almandos et al 2008; Beans et al 2008). Few if any, have linked the physiology and photosynthetic plasticity to the observed distribution and abundance of the species. Publications I and II bring empirical evidence of species-specific sensitivities to changes in salinity and temperature and new information on physiological differences based on photoacclimation strategies. In agreement with other studies (Lavaud et al 2007; Dimier et al 2009), the photoprotective capacity of the three Antarctic diatoms can be linked with their ecological niche occupancy (Publication I). Species comparisons identified variability in photophysiological responses and strategies for coping with environmental stressors including photoprotection and photosynthetic down-regulation (Publications I and II). As found in studies with temperate diatoms, Antarctic diatoms show niche-specific adaptive traits as a function of light (Sakshaug et al 1987; Lavaud et al 2007; Publication II), but also as a function of their photoprotective capacity (Dimier et al 2009; Publication I).

The dominance of one species in an ecosystem is usually a result of that species being the best-adapted to that ecosystem, less likely to be preyed upon and the most competitive given the resources available. The physiological strategy of such a species could be termed a 'generalist', able to adapt easily to changes in environmental conditions, particularly light, with large investment in photoprotection to allow for uninterrupted photosynthesis (Fig. 4.1). Field studies have observed the dominance of *F. cylindrus* in the Antarctic sea ice (Lizotte 2001; Kopczynska et al 2007; Roberts et al 2007), and have also described its success in the meltwater zones (Beans et al 2008), yet there have been surprisingly few studies into its photophysiology (Mock and Kroon 2002; Kropuenske et al 2009). New evidence has shown that *F. cylindrus* is able to regulate photosynthesis with large fluctuations in light (Kropuenske et al 2009; Publication I and V), strong changes in salinity and temperature (Publication I) and nitrogen limitation under high light stress (Publication V). This new information might help to explain why *F. cylindrus* is so successful in the polar marine environment. In particular, it provides insight into how this species might cope with seasonal shifts from the pelagic to the sea ice environment, where essential nutrients can be limiting



and light initially excessive. Similarly, it may help uncover why *F. cylindrus* is also able to flourish under extremely light limited conditions of the sea ice in the late winter and explain its ability to rapidly acclimate from this light-limited environment and come to thrive in the sunlit, stratified conditions of spring meltwater. The physiology and wide distribution of *F. cylindrus* would indicate that it is a generalist species, able to consistently dominate different Antarctic environments. The alternative physiological strategy is that of the 'opportunist'. This species, unlike the generalist, simply survives until conditions become favourable and growth can be maximised, forming large blooms (Fig. 4.1). Opportunistic species are usually adapted to stable conditions, such as those provided by the meltwater environment and show little photosynthetic plasticity. *Pseudo-nitzschia subcurvata* showed many of the physiological traits of an opportunist, where plasticity was sacrificed at the expense of large investment in protein and pigment storage for maximal growth when conditions were optimal (Publications I and II).

#### 4.2.3 COMMUNITY RESPONSES TO ENVIRONMENTAL STRESS

Information on the physiology of dominant phytoplankton species can provide considerable insight into ecosystem responses, but they are constrained by not capturing any of the biotic interactions. Manipulative experiments on natural populations are useful in determining the response of a community to a specific environmental perturbation or stressor, particularly with respect to understanding floristic shifts. Shifts in phytoplankton assemblages towards a diatom-dominated community have been observed under iron enrichment, both in large-scale iron fertilisation experiments (Timmermans et al 2001; de Baar et al 2005) as well as bottle experiments (Takeda et al 1998; Boyd et al 2001; Hutchins et al 2001; Publication VI). Similarly, overall photoprotective capacity expressed by a community, provides insight into how primary productivity and carbon cycling changes. Community photosynthetic responses presented here have brought to light new information on photoacclimation and photoprotective strategies of sea ice and pelagic microalgal communities (Publication III, IV and VI, respectively). However, it is obviously limited to the specific communities captured by the particular sampling program.

## GENERAL DISCUSSION

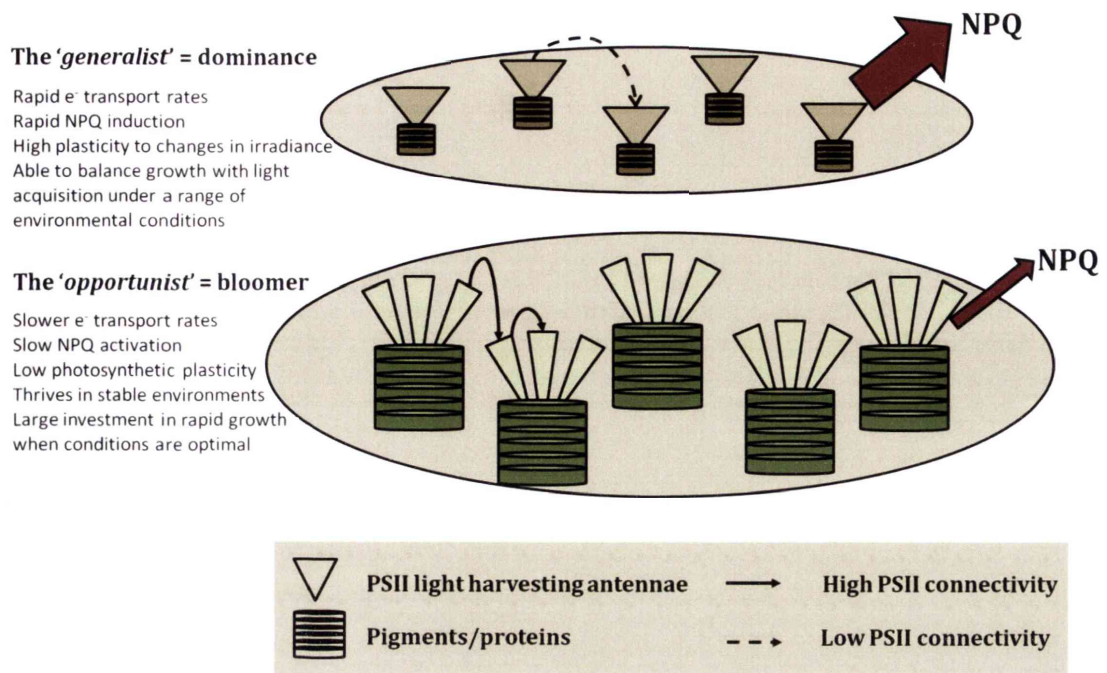


Fig. 4.1 Two models of photosynthetic physiology based on contrasting photoacclimation strategies in Antarctic diatoms. The models are derived from the structure of photosynthetic machinery, total pigment concentration and investment, xanthophyll activity and plasticity to changes in irradiance. The red arrows indicate the capacity for non-photochemical quenching (NPQ).

### 4.2.4 ECOSYSTEM RESPONSES TO ENVIRONMENTAL STRESS

Linking sub-cellular strategies, species-specific traits and community responses provides a better overview of the ecosystem responses, as well as an improved insight into the processes driving this complex ecosystem.

Physiological data are particularly important for improving estimates of net primary production from the marine ecosystem (Behrenfeld et al 2005). Net primary production is a function of phytoplankton biomass and its physiological status; yet, determining this from space remains a complex and difficult task (Behrenfeld et al 2005) particularly for the sea ice environment. Satellite data use conversion factors to calculate photosynthesis (Behrenfeld et al 2005), which results in significant uncertainty, and further highlights the need for a greater understanding of physiological responses at a species, community or ecosystem level to changes in physical environment (light, nutrients and temperature) as well as the need for empirical data on carbon fixation. One of the more prominent limitations to models is that they assume balanced growth, yet in nature, physical perturbations often result in

unbalanced growth (Falkowski and Raven 2007) making the relationship between chlorophyll *a* and carbon more complex. For example, in the Antarctic haptophyte *Phaeocystis antarctica*, the chlorophyll *a* to carbon ratio can change by a factor of 3 under iron limitation and low light (van Leeuwe and Stefels 1998; Schoemann et al 2005). Therefore, physiological data, including that collected in this work, are essential for determining these relationships under a variety of environmental conditions for incorporation into large ecosystem and global production models.

### 4.3 SIGNIFICANCE FOR THE ANTARCTIC MARINE ECOSYSTEM & IMPLICATIONS FOR PRODUCTIVITY UNDER A CHANGING ENVIRONMENT

*“One planet, one experiment” Edward O Wilson*

The complex interactions and multiple feedback mechanisms involved in biogeochemical and biological processes, makes characterising an ecosystem and predicting its response to environmental change very difficult. The Antarctic marine ecosystem, like the rest of the planet, is changing in response to increases in atmospheric carbon dioxide concentrations. In southern latitudes, projected changes in nutrient supply and light climate as a result of stratification will likely result in regional changes in net primary production (Bopp et al 2001; Boyd and Doney 2002), where previously light-limited areas would see an increase in net primary production (NPP), whereas in nutrient-limited areas, NPP would decline (Arrigo and Thomas 2004). A 10% increase in primary productivity has been predicted with loss of sea ice (Arrigo and Thomas 2004), but much of this change is dependent on the resultant shift in species. If communities were to shift from diatom dominated to non-diatom dominated, the result could be an increase in primary production rates, as nutrient utilisation efficiency and carbon fixation is generally lower in diatoms (Arrigo et al 1999). Alternatively, productivity could decline with a loss of seed populations from the sea ice (Arrigo and Thomas 2004). An example of potential change to productivity can be drawn from the work in this thesis. This study shows evidence that if a highly plastic species like *F. cylindrus* were to dominate the ecosystem even more than it currently does; it could lead to greater productivity. Net primary production in *F. cylindrus* is controlled by light (Publication II), and would therefore, be predicted to increase under

greater light as a result of thinner ice or reduced mixed layer depth. Furthermore, productivity is dependent on nutrient availability which is predicted to decline under future conditions, this makes *F. cylindrus* an able competitor, as it has been shown to cope with nitrogen limitation at little cost to its photosynthetic efficiency (Publication V). However, if silicate were also limited, there could be a floristic shift away from diatoms and hence *F. cylindrus*, greatly influencing the global silicate cycle and regional carbon fluxes.

Based on the information currently available, some general hypotheses can be generated as to how marine communities may respond in the future. Firstly, there is likely to be a shift towards the more plastic species (those with the greatest phenotypic plasticity and genetic potential to adapt). Strong evidence is emerging of systematic changes in plankton community structure with increased ocean temperatures around the globe (Hays et al 2005). There has been a measureable decline in krill abundance over the past few decades with a concomitant increase in the abundance of salps in the Southern Ocean (Atkinson et al 2004). Similarly, increases in jellyfish abundance in the Bering Sea (Brodeur et al 1999) and the North Sea (Lynam et al 2004) have been recorded. Given that salps and jellyfish are a much poorer nutritional source than krill and copepods, great implications of such compositional changes can be expected for the higher trophic levels (Hays et al 2005).

Secondly, there is the potential for increased competition from invasive species, that is, species that are able to increase their distribution southward as waters warm, restricting cold-adapted species distributions. Range expansions into higher latitudes have been observed, where warm-water species of copepods have successfully expanded their distribution northward (Beaugrand et al 2002). Similarly, evidence of a retraction in range for the cold-water species dinoflagellate *Ceratium* sp. has been documented (Bernard et al 2004). Knowledge of phenological relationships are also essential to understanding ecosystem functioning, and any decoupling of predator-prey relationships across functional groups and trophic levels could result in the complete collapse of a given region's ecology (Edwards and Richardson 2004).

Thirdly, with the predicted changes in ocean chemistry, there is likely to be a shift towards those species least affected by ocean acidification, as many species exhibit reduced calcification rates and physiological impacts under high-CO<sub>2</sub> conditions (Riebesell et al 2000). For the Antarctic marine ecosystem, prominent calcifiers like the

pteropod *Limacina helicina* (Hunt et al 2008), are under imminent threat from the predicted undersaturation of aragonite in the Southern Ocean (McNeil and Matear 2008). Pteropods can comprise up to 25% of total zooplankton biomass in the Southern Ocean (Boysenennen et al 1991; Hunt et al 2007) and are major contributors to Antarctic carbonate and organic carbon export (Honjo et al 2004). They form aragonite shells which are vulnerable to dissolution under low carbonate ion concentrations (Honjo et al 2000, 2004) and any widespread loss of pteropod populations will inevitably have large flow-on effects for the Antarctic marine food web, as well as regional biogeochemistry (McNeil and Matear 2008). Combined or in isolation, these selection pressures of temperature, nutrients and pH not only have consequences for the distribution and abundance of phytoplankton species in the Antarctic, but also broader implications for higher trophic organisms, biogeochemical cycling, carbon export and ultimately carbon sequestration. Therefore, future research needs to consider these pressures in combination when investigating ecosystem responses to climate change.

Finally, several major climate change scenarios were investigated throughout this thesis, including increased irradiance due to ice thinning and stratification of surface waters, reduced nutrient supply and temperature increases. These experiments indicated sub-cellular, species and community level responses over relatively short time scales. In light of these new data and given the general hypotheses mentioned above, two conceptual models on plankton community shifts and their influence on carbon drawdown and primary production are proposed (Fig 4.2). Both depict the changes in physical and chemical properties predicted for the Antarctic marine ecosystem, including lowered pH, shallower mixed layer depth and a decline in nutrient input from deep water. In the first model there is a dramatic shift in the plankton community structure. Typical oceanic species such as diatoms and copepods are replaced with picophytoplankton, cyanobacteria, jellyfish and tunicates in response to the increases in temperature and light (Fig. 4.2). Both temperature and light are important selection pressures in polar ecosystems and are projected to result in an increase in the biomass and abundance of small phytoplankton species (Marinov et al 2010). Also in this conceptual model, calcifying organisms are primarily lost, due to the undersaturation of aragonite from increased hydrogen ions. Such species shifts result in a significant loss of biodiversity and cause a reduction in carbon sequestration and regional primary productivity.

The inclusion of iron in the second model leads to a completely different outcome (Fig 4.2). Iron is a common limiting micronutrient in the Southern Ocean. Due to the isolation, dust deposition from terrestrial sources and continental margin inputs into the Southern Ocean are limiting and often seasonal. Therefore, biological recycling of iron seems to be of paramount importance for phytoplankton in the Southern Ocean (McKay et al 2005; Bowie et al 2009). Dissolved iron is strongly complexed by the organic material in the ocean, thus the availability of iron for phytoplankton uptake is greatly influenced by its chemical form, biological cycling and the uptake strategies of the phytoplankton (Breitbarth et al 2009a). However, more hydrogen ions, as a result of increased CO<sub>2</sub> concentrations, have recently been shown to slow iron complexation and oxidation rates and increase dissolved iron concentrations (Breitbarth et al 2009b). This speciation of iron into a more bioavailable form under acidified conditions may result in relieving iron limitation many oceanic regions. Thus, only a minor shift in plankton assemblage, such as a move towards larger diatoms (Publication VI, de Baar et al 1995; Boyd et al 2000; 2007; Coale et al 2004), longer chains, and the removal of calcifiers, is proposed (Fig. 4.2). This new iron-rich community has the potential to increase carbon acquisition and export (Riebesell et al 2007; Breitbarth et al 2009b), maintaining much of its biodiversity and favouring diatom growth. The increase in diatom size and chains will also influence grazing control, as larger cells are able to escape predation more easily (Sarhou et al 2005).

In contrast to the first conceptual model, which proposes a loss in carbon drawdown and primary production, the broader implications of the second model is that the increased productivity may provide a negative feedback mechanism on atmospheric CO<sub>2</sub> concentrations. The second model however, does not take into account the potentially limiting effect of lower macronutrient availability such as silicate, which would put a cap on diatom growth becoming the limiting nutrient (Sarhou et al 2005), as co-limitation of Fe and Si has been measured in oceanic HNLC

GENERAL DISCUSSION

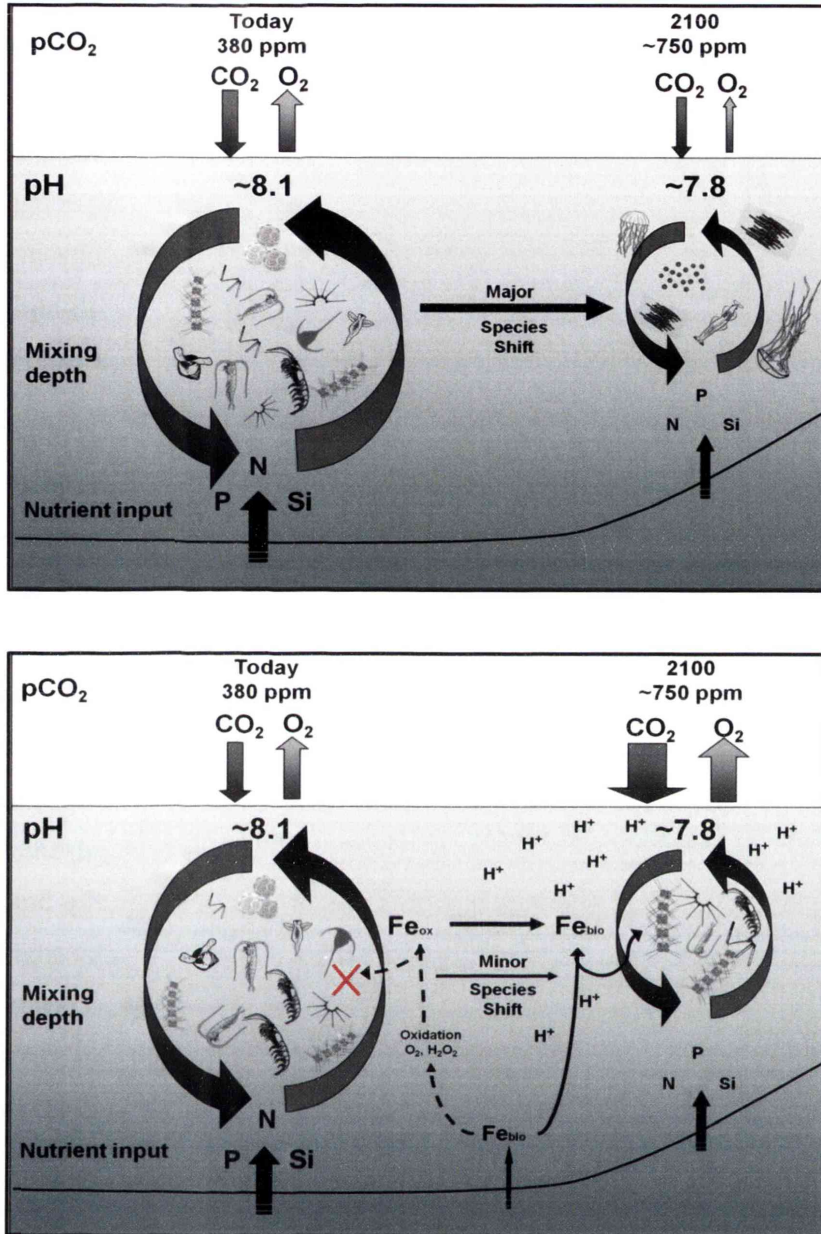


Fig. 4.2 Changes in Antarctic plankton community structure and its effect on carbon export and sequestration under projected hydrographic conditions. Model I (upper panel) shows a decline in species diversity and a major shift in community structure from large diatoms, dinoflagellates, coccolithophores, copepods, krill, and pteropods to a community of very low nutritional value dominated by picoplankton, cyanobacteria, jellyfish and tunicates. It represents a positive feedback mechanism for atmospheric  $\text{CO}_2$  concentrations. Model II (lower panel) depicts the influence of iron on community productivity. Under present day conditions (left-hand side) Fe is rapidly oxidized ( $\text{Fe}_{\text{ox}}$ ), becoming biologically unavailable to phytoplankton (denoted by the red X). However, the changes in iron speciation to more bioavailable iron ( $\text{Fe}_{\text{bio}}$ ) under an acidified ocean (right-hand side), leads to increased productivity and helps maintain a diverse plankton community, with the exception of some calcifiers. Under these future conditions, carbon export and productivity are increased with potential to fuel a negative feedback mechanism for atmospheric  $\text{CO}_2$  concentrations.

regions previously (LeBlanc et al 2005). However, macronutrients are typically in excess in the Southern Ocean and therefore a reduction in their concentration may still be enough (in the presence of bioavailable iron) to increase productivity in the region. These conceptual models are clearly an oversimplification and have many limitations, including ignoring the possibility of restricted diatom growth from the seasonal variability in silicate concentrations. If this were to happen, there could be a shift toward a non-diatom dominated community, perhaps toward the prymnesiophyte *Phaeocystis antarctica*.

The physiological plasticity of Antarctic marine phytoplankton demonstrated in this thesis provides new insight into the adaptability of these microalgae to changes in ambient environment. Furthermore, species-specific and community-based responses provide new information essential for the assessment of ecosystem vulnerability. Future research should continue to focus on understanding the mechanisms behind this plasticity and determine whether these physiological traits have developed across all Antarctic species alike. The physiological study on nitrogen depletion in *F. cylindrus* for instance (Publication V) could be applied to other dominant Antarctic species, such as the prymnesiophyte *Phaeocystis antarctica*. Any similarities in the photosynthetic plasticity and photoprotective capacity between these two species could provide greater insight into the allocation of cellular energy that result in their dominance of the community. Conversely, any differences in their photophysiology, however small, could translate into major differences in their resilience to change, having significant implications for carbon cycling and food web dynamics at an ecosystem level.

#### 4.4 PERSPECTIVES FOR FUTURE RESEARCH

The publications within this thesis provide new information on the strategies of photoacclimation, photoprotection and photoinhibition in this important group of organisms. A number of questions have arisen from these findings and should be addressed in future research. Publications I and II showed that species-specific differences in photosynthetic traits and photoprotective capacities exist between Antarctic diatom species. To increase knowledge of the generality of these responses, future research should focus on conducting photophysiological studies with an increased number of species. By comparing the physiological responses of dominant species to an environmental stress, a more complete picture of ecosystem function in



relation to species dominance and successions can be obtained. Furthermore, through the use of multi-species competition studies a better understanding of potential community shifts and the implication for trophic dynamics and carbon cycling at a large scale can be obtained.

High photoprotective capacities and low photoinhibition that was measured in the pack ice microalgae (Publications III and IV) may be a result of the timing of sampling and thickness of the ice sampled. Therefore, further experiments on natural community responses need to examine numerous communities from different depths, locations and seasons to determine whether high photoprotective capacity is a general trait in sea ice diatoms. Furthermore, testing photoinhibitory responses to irradiances greater than  $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  would provide information on the irradiance threshold at which irreversible damage occurs. Similarly, the high photoprotective capacities observed (Publications I, III, V, VI) require further study to isolate xanthophyll activity from possible alternative electron cycling mechanisms. This question should also address photoprotective mechanisms in species from across the entire ecosystem and not only the sea ice environment. Furthermore, the use of molecular tools, such as gene expression and regulation of genes and proteins, will provide valuable information on the possible physiological adaptation within Antarctic microalgal species, filling some of the knowledge gaps on the poorly understood genetic traits that allow these species to adapt so successfully. Genetics could also help determine adaptive capacity. One example would be to use *Cylindrotheca closterium*—a common temperate diatom and highly successful sea ice coloniser—for looking at genetic and physiological changes in response to environmental condition. By comparing genetic expression and physiological traits at both temperate and polar conditions, this species could potentially reveal the genes or changes in physiology responsible for low temperature adaptation.

Community shifts in response to environmental perturbation and the extent of sensitivity to changes in ambient environment varies from one species to another, and no doubt differs across trophic levels. For Antarctic phytoplankton, floristic shifts were observed (Publication VI) and similarly, species-specific sensitivities identified (Publication I and II). Future research needs to be cross-disciplinary to determine the physiological plasticity and response to environmental factors across a broad range of trophic levels within a marine community. Understanding responses of numerous species within an ecosystem are essential to determine any mismatch between

functional groups and across all trophic levels. Therefore, climate change effects on phytoplankton floristics, or ecosystem biodiversity, requires that new research be conducted using mesocosms which better mimic what happens in nature. They also need to be long-term experiments to better reflect the timelines relevant to environmental change. These mesocosms would need to address seawater chemistry (Fe, Si, NO<sub>x</sub>, pCO<sub>2</sub>,) and temperature, but also biological complexity (microbiology, multiple species competition, grazing). Only with such detailed and complex experiments could we discriminate which conceptual model proposed (Fig. 4.2) might apply, or whether an entirely different scenario will eventuate.

In order to appreciate the gravity of the current and future global condition, identified stressors must be considered together. It is not enough to only investigate responses to individual stressors in isolation of potential synergistic or antagonistic effects. For example, the increase in salinity in isolation of temperature shifts were detrimental to the photosynthetic efficiency of *F. cylindrus* at +5°C, whereas when temperature dropped to -1.5°C, *F. cylindrus* was able to maintain photosynthetic efficiency at high salinities (Publication II). By measuring responses to combined changes in environmental factors such as salinity and temperature (Publications I and II), nitrogen and temperature (Publication V) or iron and light (Publication VI), an improved and possibly more accurate determination of future outcomes can be obtained. Future research needs to focus on investigating the simultaneous changes in physical and chemical variables that will result from climate change. As one of the largest CO<sub>2</sub> sinks, understanding effects of CO<sub>2</sub>, particularly in combination with increased temperature is important for understanding the synergistic effects on metabolism and species range shift (Smetacek and Nicol 2005). The effect of increased CO<sub>2</sub> on phytoplankton is a rapidly growing field, with a few studies already conducted on carbon acquisition and uptake kinetics in Antarctic phytoplankton (Mitchell and Beardall 1996; Cassar et al 2004; Tortell et al 2008, 2010). The physiological and ecological responses to combined changes will provide a better understanding of possible biodiversity loss that can be expected as well as providing invaluable insight into the failing or prevailing health of the marine ecosystem as a whole.

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