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L Delizo

WO Smith
Virginia Institute of Marine Science

J Hall

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Taxonomic composition and growth rates of phytoplankton assemblages at the Subtropical Convergence east of New Zealand

LIZA DELIZO[1†], WALKER O. SMITH[1]* AND JULIE HALL[2]

[1]VIRGINIA INSTITUTE OF MARINE SCIENCES, COLLEGE OF WILLIAM AND MARY, GLOUCESTER POINT, VA 23062, USA AND [2]NIWA, PO BOX 11-115, HAMILTON, NEW ZEALAND

[†]PRESENT ADDRESS: FLORIDA ATLANTIC UNIVERSITY, BOCA RATON, FL 33431, USA

*CORRESPONDING AUTHOR: wos@vims.edu

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Off the eastern coast of New Zealand, warm, saline, nutrient-poor Subtropical Waters (STW) are separated from cool, fresher, relatively nutrient-rich Sub-Antarctic Waters (SAW) by the Subtropical Convergence (STC). The Chatham Rise, a submarine rise, restricts the latitudinal movement of the STC as well as mixing of STW and SAW. Due to this restriction, this sector of the STC is characterized by sharp gradients in temperature, macro- (nitrate, silicate and phosphate) and micro- (iron) nutrient concentrations. Shipboard incubations were conducted during austral spring 2000 and 2001 to test the hypothesis that these gradients affect the taxonomic composition and/or growth rates of phytoplankton on either side of and at the STC. Maximum chlorophyll a *concentrations during 2000 were 0.39* $\mu g\ L^{-1}$*, but were an order of magnitude higher in 2001. During both years, STC phytoplankton were dominated by diatoms (77% of the total chlorophyll* a *during austral spring 2000 and 70% during spring 2001), whereas cryptophytes and prasinophytes dominated STW assemblages (27 and 36% during 2000, and 63 and 17% during 2001). Chlorophyll in the SAW was dominated by procaryotes and photosynthetic nanoflagellates during 2000 (17% procaryotes, 68% nanoflagellates), and by diatoms during the austral spring 2001 cruise (53%). Growth rates of the phytoplankton assemblage were determined by* ^{14}C*-labeling of chlorophyll* a *and photosynthetic pigments. During 2000, temperature-normalized growth rates were near maximal at the STC, and decreased on average to less than half of the maximum north and south of that front, whereas in 2001 both absolute and relative growth rates were low at all stations. Growth rates did not closely parallel biomass of the various taxa, suggesting that nutrient limitation and/or grazing were significantly impacting standing stocks. It appeared that growth was strongly influenced by nutrients and light, but that biomass was more strongly influenced by grazing. The STC is a globally important region of enhanced biomass and productivity; however, the phytoplankton assemblage reflects control by both top–down and bottom–up processes that makes a predictive understanding of the area's biogeochemical cycles extremely difficult.*

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INTRODUCTION

Oceanic food webs largely depend on the fixation of carbon dioxide into organic matter by the phytoplankton, which consists of a variety of taxa that vary both temporally and spatially in response to both biological and oceanographic controls. The variations in time and space are a function of the net growth rates of individual species, defined as the difference between growth (μ) and losses of the individual species (or functional groups). In order to characterize the flow of organic matter through a pelagic ecosystem, accurate determination of both the phytoplankton biomass and growth rate are necessary.

Knowledge of phytoplankton assemblage composition is essential to completely characterize the biological pump. In locations where the removal of CO_2 via phytoplankton growth is substantial, a flux into the ocean of atmospheric CO_2 occurs. Flux of organic matter to depth is another component of the biological pump, and this export is mediated by either passive sinking of phytoplankton or the production of fecal pellets and aggregates, both of which are related to size and taxonomy. The major phytoplankton functional groups have varied impacts on energy and material cycles (Boyd and Newton, 1995). For example, diatoms can have very rapid growth rates under nutrient replete conditions and often are responsible for much of the flux of organic matter from the surface layer (e.g. Armstrong *et al.*, 2000), whereas coccolithophorids exert a strong influence on the alkalinity and carbon budgets of the water column (Archer *et al.*, 2000), and other prymnesiophytes (e.g. *Phaeocystis* spp.) significantly influence the sulfur cycle (Liss *et al.*, 1994). Models have explicitly incorporated the different biogeochemical functions of critical taxa (Armstrong, 1999; cf. Anderson, 2005).

High (or low) phytoplankton biomass does not necessarily indicate high (or low) absolute growth rates. Low biomass potentially can be due to either low absolute growth (regulated by bottom–up factors such as nutrients or light), or elevated growth balanced by high rates of grazing or other losses (Banse, 1991; Goericke, 1998). Furthermore, different taxa have different sizes and growth rates and are exposed to different grazing pressures. For example, microzooplankton remove certain species and sizes of phytoplankton (generally the smaller sizes) and affect only their target species within the assemblage (Verity, 1991; Jakobsen and Hansen, 1997). Because microzooplankton are similar in size to their phytoplankton prey, their growth rates are similar (Banse, 1994; Strom, 2000). Larger zooplankton (e.g. copepods) tend to ingest larger phytoplankton (Harris, 1996); however, their life cycles do not always allow them to rapidly respond to increased standing stocks of fast growing phytoplankton, such as diatoms. This can lead to a decoupling of phytoplankton growth and zooplankton grazing, often resulting in a phytoplankton "bloom" and accumulation of biomass that is not a direct consequence of more rapid growth. However, because of the complexity of the interactions among functional groups and the environment (including herbivores), it is extremely difficult within a single experiment or field study to assess the importance of the individual linkages between growth rates of individual taxa and their biomass.

Photosynthetic pigments have long been used as indicators of phytoplankton biomass. The use of high performance liquid chromatography (HPLC) has facilitated the separation of photosynthetic pigments and been used to quantify the biomass of phytoplankton groups (Bidigare and Ondrusek, 1996). The use of pigments to estimate biomass assumes that there is a consistent relationship between accessory pigment concentrations and the biomass of the algal group (Goericke, 1990). Thus, while photoprotective pigments such as diadinoxanthin are unreliable as an estimate of biomass, light-harvesting pigments such as fucoxanthin can be used (Strom and Welschmeyer, 1991). Furthermore, numerical techniques allow us to account for the presence of a diagnostic pigment in more than one taxon. CHEMTAX (Mackey *et al.*, 1996) is a method for calculating phytoplankton class abundances using pigment concentrations and estimated class pigment composition (e.g. Mackey *et al.*, 1996; DiTullio *et al.*, 2003).

Previously, it has been difficult to measure carbon-specific growth rates and algal carbon due to our inability to isolate phytoplankton from other particulate matter, such as bacteria and detritus (Redalje and Laws, 1981). Hence, calculated growth rates that combine productivity measurements (bulk ^{14}C-uptake measurements) with particulate carbon determinations (Eppley, 1980; Smith *et al.*, 1999) overestimate actual growth rates. Other techniques to assess growth rates also introduce errors and use assumptions that are difficult to verify. For example, the dilution technique estimates absolute growth rates in the absence of grazing, but assumes phytoplankton growth is the same in both diluted and undiluted seawater (Landry and Hassett, 1982; Landry *et al.*, 1995). The HPLC pigment-labeling technique (Redalje, 1993) allows us to accurately quantify phytoplankton growth rates, as there is no significant interference from other sources of particulate carbon such as bacteria or detritus. One of the assumptions of this technique is that a pigment's specific activity is equal to the total carbon-specific activity of living cells, which was verified by Welschmeyer and Lorenzen (1984),

who showed that net growth rates for POC and chlorophyll *a* were not statistically different, and that total carbon and chlorophyll were labeled at the same rate. This is also true for carotenoids, at least during balanced growth (Eppley, 1980). However, concentrations of some carotenoids, and indeed all chlorophylls, can change rapidly during incubation due to photoacclimation (e.g. Brunet *et al.*, 1993), a problem that is exacerbated by on-deck incubations. The assumption of balanced growth is at least partially met through the use of long (24 h or more) incubations (Eppley, 1981; Goericke and Welschmeyer, 1993a, b). Zooplankton grazing does not introduce errors in the pigment-labeling technique because the ratio of specific activity of pigments to the total pigment concentrations is unaltered by grazing.

The Subtropical Convergence (STC) off the eastern coast of New Zealand separates two very different water masses [Subtropical Waters (STW) and Sub-Antarctic Waters (SAW)], and their mixing is constrained temporally and spatially by the Chatham Rise. STW north of the STC have been previously characterized by warm, saline waters, seasonally elevated algal biomass, surface primary production ranging from 5.4 to 120 mg C m^{-3} day^{-1} (Gall *et al.*, 1999), decreased macronutrient concentrations, dissolved iron concentrations greater than 1 ng kg^{-1}, phytoplankton assemblages dominated by diatoms in spring and dinoflagellates in winter and decreased levels of microzooplankton grazing. In contrast, SAW south of the STC are characterized by colder waters, decreased salinity, low algal biomass, rates of surface primary production that range from 2.6 to 10.7 mg C m^{-3} day^{-1} (Gall *et al.*, 1999), elevated nitrate, silicate and phosphate concentrations, sub-nanomolar dissolved iron concentrations, phytoplankton assemblages apparently dominated by cyanobacteria and significant grazing by microzooplankton (Nodder, 1997; Bradford-Grieve *et al.*, 1998; James and Hall, 1998; Boyd *et al.*, 1999). Satellite images of the Chatham Rise area show increased phytoplankton pigment concentrations, particularly when compared to the two water masses on either side of the Rise, that are persistent regardless of season (Nodder and Alexander, 1998). Increased phytoplankton production at the STC (Nodder, 1997) apparently sustains a higher biological production throughout the food web, especially when compared to STW and SAW, as the Chatham Rise supports a major fishery for hoki, a demersal fish species and orange roughy (*Hoplostethus atlanticus*).

We hypothesized that the variations in phytoplankton taxa biomass were largely the result of variations of growth rates of different functional groups in the different water masses. Because the biomass of small autotrophs is often limited by rates of grazing and that of diatoms by nutrients (e.g. Landry *et al.*, 1996), we also hypothesized that diatom growth would covary with nutrient concentrations, whereas other groups (such as cyanobacteria and microflagellates) would covary with other factors such as temperature and grazing. This paper reports the results of measurements made during two cruises in consecutive years along a north–south transect across the STC during austral spring. We conclude that the distribution of phytoplankton taxa was controlled by a combination of chemical, physical and biological constraints that varied strongly in space and time.

METHOD

Field site and water sampling

Two cruises were conducted during austral spring in 2000 (5–19 October) and 2001 (29 September–14 October) on the *R.V. Tangaroa*. Samples were taken along a north–south transect (178°30.0 E) east of New Zealand (Fig. 1). Water was collected from four stations north and south of the Chatham Rise and from one on the Rise itself. Water was collected at each station during predawn casts using a rosette fitted with 12 10 L Niskin bottles, a CTD and fluorometer. A depth of 10–20 m was sampled as irradiance levels were saturating for photosynthesis at those depths, but not inhibiting, and it was well within the mixed layer. Temperature and salinity values were binned at 1 m intervals and mixed layers derived from their distributions. Nutrients were analyzed at sea using automated techniques.

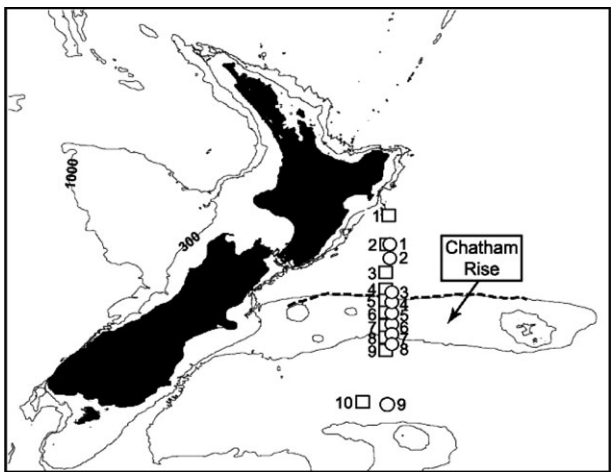

Fig. 1. Map of study site showing the location of the stations sampled in austral spring, 2000 (•) and spring, 2001 (□; station numbers in italics). Approximate location of the STC (dashed line) and Chatham Rise are also shown.

Analytical techniques

Water samples at each station were collected for HPLC determinations, growth rate measurements and fluorescence microscopy. Both pigments and growth rates were determined on the same sample. To determine taxon-specific growth rates (μ), replicate bottles of whole seawater were inoculated with ^{14}C-labeled bicarbonate and incubated in a deck-mounted, flow-through seawater incubator at 50% of surface irradiance (Redalje and Laws, 1981). Samples were incubated for at least 24 h, but less than 36 h, to obtain sufficient ^{14}C-labeling of pigments. Long incubations are necessary to insure that pigments and phytoplankton carbon achieve equal isotopic labeling (Redalje and Laws, 1981; Goericke and Welshmeyer, 1993a), in contrast to rate process measurements like primary productivity measurements, where artifacts are introduced through long incubations. Incubated water was filtered under low light and low vacuum (<10 mmHg) through a 25 mm Whatman GF/F filter. These filters were flash-frozen in liquid N_2 and stored at -80°C until analyzed. Subsamples were collected to assess total primary productivity, and total activity was measured by counting 0.1 μL of unfiltered sample directly.

Filters for pigment analyses were placed in 90% acetone in a 1.5 mL microcentrifuge tube, sonicated for 15 min in an ice-water slurry and extracted in the dark at -20°C for at least 24 h. The pigment extract was transferred to a second tube and centrifuged for 3 min at $1.10 \times 10^4 \times g$. Aliquots of the centrifuged extract were diluted with Milli-Q water for analysis. Photosynthetic pigments and pigment-specific activity were quantified using a Waters Spherisorb ODSU C-18 HPLC column and Waters HPLC system (Waters 600 controller and pump with 1000 μL sample loop, Waters 474 scanning fluorometer detector, and Waters 996 photodiode array detector) and a Hewlett-Packard 500TR Series in-line flow radiodetector (Pinckney *et al.*, 1996). The separation scheme utilized the following HPLC-grade solvents: solvent A consisted of 85% methanol: 15% ammonium acetate (pH 7.5) buffer (v/v; 0.5 M ammonium acetate), solvent B was made up of 87.5% acetonitrile: 12.5% Milli-Q water (v/v), and solvent C was 100% ethyl acetate. The following pump gradient was used: 0 min, 95%A, 5%B; 1 min, 100%B; 11 min, 78%B, 22%C; 27.5 min, 10%B, 90%C; 29 min, 100%B; and 30–35 min, 95%A, 5%B. Solvent flow rate was kept at 1 mL min^{-1} (Jeffrey *et al.*, 1997). Pigment peaks were identified using Waters Millenium Chromatography Manager 3.05.01 or Waters Empower Pro software by comparing absorption spectra and elution time to pigments of known absorption spectra and elution times (Jeffrey *et al.*, 1997). Certain pigments were incompletely resolved due to overlaps in elution peaks (e.g. chlorophyllide *a* peak overlapped chlorophyll *c*3 peak), leading to a possible underestimation of these pigments. Chlorophyll *c*1 and chlorophyll *c*2 were incompletely separated (only one peak was distinguishable), so were considered as one (chlorophyll *c*1 + *c*2). Zeaxanthin concentrations may be due to prochlorophytes, but we were unable to consistently resolve and identify their marker (divinyl chlorophyll *a*) to confirm prochlorophyte presence and concentration. Pigments quantified and used to distinguish taxonomic differences are listed in Table I.

Two different Waters Spherisorb ODSU HPLC columns were used for calibration and data collection. The two columns were intercalibrated by running known volumes of the same sample on both columns and using area under pigment peaks to determine

Table I: List of pigments used in this study to differentiate functional group distributions and growth rates, and the major phytoplankton divisions/classes that contain that pigment

Pigment	Abbreviation	Phytoplankton taxa
19-butanoyloxyfucoxanthin	19-BUT	Chrysophytes and prymnesiophytes
19-hexanoyloxyfucoxanthin	19-HEX	Prymnesiophytes
Alloxanthin	ALLO	Cryptophytes
Chlorophyll *a*	CHL *a*	All autotrophic forms
Chlorophyll *b*	CHL *b*	Chlorophytes and prasinophytes
Chlorophyll *c*1 + *c*2	CHI *c*1 + *c*2	Diatoms, prymnesiophytes, chrysophytes and dinoflagellates
Chlorophyll *c*3	CHL *c*3	Prymnesiophytes and chrysophytes
Dinoxanthin	DINO	Dinoflagellates
Fucoxanthin	FUCO	Diatoms, prymnesiophytes and chrysophytes
Lutein	LUT	Chlorophytes and prasinophytes
Peridinin	PERI	Dinoflagellates
Phaeophytin *a*	PHAEO *a*	Chlorophyll *a* degradation product
Prasinoxanthin	PRASINO	Prasinophytes
Violaxanthin	VIOLA	Chlorophytes and prasinophytes
Zeaxanthin	ZEA	Cyanobacteria, prochlorophytes and chlorophytes

conversion factors between HPLC columns. The first column was calibrated for photosynthetic pigments using the three-point calibration method; the second column was calibrated using gradually increasing concentrations of pigment within the expected range. Purified pigments were obtained from pure cultures or mixed phytoplankton assemblages. Pigment concentrations were determined using a Perkin-Elmer Lambda 25 UV/VIS Spectrophotometer and known extinction coefficients.

Aliquots of the 2001 cruise extracts were checked for radiochemical purity of chlorophyll *a*. The samples were acidified with 0.1 N HCl, and then neutralized with 0.5 M ammonium acetate solution (Goericke, 1992). Pigments were separated using HPLC and in-line radioanalysis, and phaeophytin *a*, the product of chlorophyll *a* acidification, was quantified. Contamination of the chlorophyll *a* peak with co-eluting, colorless, radiolabeled molecules was checked by converting the chlorophyll *a* to phaeophytin *a* and processing the sample again, but no significant amounts of colorless coelutants were detected. Growth rates of phytoplankton were determined using the method and equations described by Redalje (Redalje, 1993). The ability to determine growth rates using this technique is partly determined by the *difference* between the signal of pigment-incorporated ^{14}C and background. Because some pigments were poorly labeled, only 19-BUT, FUCO, 19-HEX, ALLO, CHL *b* and CHL *a* were used to estimate growth rates in the spring, 2000 cruise. In 2001, higher concentrations of ^{14}C-bicarbonate were used, allowing growth rates for CHL *a*, CHL *b*, CHL *c*3, ALLO, 19-BUT, FUCO, 19-HEX and PRASINO to be derived. We had no data to quantify the effects of photoacclimation during incubations, so for carotenoids we simply assumed balanced growth throughout. Peridinin was adequately labeled, but cannot be used to estimate growth, as it is synthesized only in the light, violating the assumption of balanced growth (Goericke and Welschmeyer, 1993b). Because of the sharp gradient in temperature at the STC, growth rates were compared using specific growth rates, where growth rates quantified by pigment labeling were expressed as a percentage of the temperature-limited maximum growth rate (Eppley, 1972).

To supplement HPLC data on phytoplankton taxonomic distribution and abundance, whole seawater samples were collected for epifluorescence microscopy at each station. Whole water samples were preserved with gluteraldehyde (5 mL total volume, 2% gluteraldehyde final concentration), placed in darkness for 15 min, flash-frozen in liquid nitrogen and stored at −80°C. Seawater samples were treated according to Booth (Booth, 1993) and examined using epifluorescence microscopy. A green excitation (530–550 nm) and a 590 emission filter from a 200 W mercury lamp were used (Jeffrey *et al.*, 1997).

Statistical analyses

Pigment and growth rate estimates were analyzed using paired *t*-tests, one-factor Analysis Of Variance (ANOVA) with Tukey multiple comparisons test (Zar, 1999), and chemical taxonomy (CHEMTAX) analysis (Mackey *et al.*, 1996). A paired *t*-test (used due to the low number of replicates) was used to test for differences in pigment concentration and phytoplankton growth rates with distance from the STC. This test examines differences in means of the populations; these values were compared two by two. Thus, each datum in one sample was correlated with one, and only one, datum in a second (Zar, 1999; e.g. the end-member of STW is correlated with the end-member of SAW). The next closest station to the STW end-member was then correlated with the next-closest station to the SAW end-member, etc. A Tukey multiple comparison test was performed in order to determine differences in pigment concentrations at stations representative of the different types of water at this sector of the STC. A Tukey's test was performed using the end-member of the STW (St. 1), STC (St. 6 for 2000 cruise, St. 5 for 2001 cruise) and SAW (St. 10 and 9 for 2000 and 2001, respectively). This test determines whether the mean pigment concentrations at each station are equal in a pairwise fashion (i.e. STW versus STC, SAW versus STC and STW versus SAW).

CHEMTAX was used to estimate taxa abundances from chlorophyll and carotenoid pigments (Mackey *et al.*, 1996; Wright and van den Enden, 2000). The procedure estimates the contributions of different phytoplankton taxa to the pigment and/or chlorophyll *a* concentrations via factor analysis and a steepest descent algorithm to find the best fit to the data based on an initial estimate of the pigment ratios. Two main assumptions are made: (i) pigment ratios within any group are constant over the domain encompassed by the data set, and (ii) variations in the abundance of different algal groups are not correlated (Goericke and Montoya, 1998). One of the fundamental assumptions of this study is that environmental stresses, specifically nutrient limitation, may be responsible for changes in taxonomic composition and growth rates of phytoplankton assemblages over distances within this sector of the STC. Studies have shown a dependence of cellular chlorophyll *a* concentrations on environmental and physiological parameters, such as irradiance, growth rate and nutritional state. Goericke and Montoya (Goericke and

Montoya, 1998) recommend using regression analysis only for those accessory pigments whose concentrations covary tightly with chlorophyll *a* (e.g. FUCO, VIOLA, PERI). Because of the sharp changes in environmental parameters and nutrient concentrations associated with the region (and their effects on pigment ratios), two separate CHEMTAX analyses were performed on subsets of the data (SAW end-member to STC, and STC to STW end-member) using the pigment ratios determined by DiTullio *et al.* (DiTullio *et al.*, 2003) to account for differences in environmental conditions. A complete description of all statistics is given in Delizo (Delizo, 2003).

RESULTS

Oceanographic and nutrient data

Oceanographic data were within previously reported ranges for STW and SAW during both cruises (Bradford-Grieve *et al.*, 1998; Nodder and Alexander, 1998). In 2000, water temperatures ranged from 8.9 to 14.2°C and salinities ranged from 34.3 to 35.3 (Table II). Temperature and salinity values at the STC were intermediate between the two end-members. Average ammonium, nitrate, silicic acid and phosphate levels were higher in SAW than in STW (0.44 versus 0.34, 2.27 versus 0.64, 1.19 versus 0.46 and 0.25 versus 0.09 μmol L^{-1}, respectively), and chlorophyll *a* values were higher in STW than SAW (means 0.60 and 0.29 μg L^{-1}; Table II). Spatial distributions were generally similar in 2001, but STW water temperatures were warmer than expected for this time of the year (>15°C during austral summer). Salinity values ranged from 34.1 to 35.4. Nitrate and phosphate values were higher in SAW (>1.79 and 0.35 μmol L^{-1}, respectively, at the extreme) and lower in STW (always less than 0.95 and 0.21 μmol L^{-1}). Silicate values were higher in STW and SAW than at the STC, but in all cases they were <2.5 μmol L^{-1} (Table II). Chlorophyll values in 2001 were substantially greater than those in 2000 throughout the entire transect.

Primary productivity

In both years, mean primary productivity was greatest at the STC, although it was twice as great in 2001 (Table III). Light-saturated productivity averaged 2.32 and 5.71 mg C m^{-3} h^{-1} at the STC in the 2 years, which is approximately equal to 0.39 and 1.11 g C m^{-2} day^{-1} when integral productivity is estimated by the equation of Falkowski *et al.* (Falkowski *et al.*, 1998). Productivity was generally lowest in SAW (0.31 and 0.84 g C m^{-2} day^{-1} in 2000 and 2001, respectively) and intermediate in the STW (0.47 and 0.81 g C m^{-2} day^{-1} in the 2 years). Chlorophyll-specific productivity was greatest in both years in the STC [5.40 and 2.19 mg C (mg Chl)$^{-1}$ h^{-1} in 2000 and 2001, respectively] and was slightly decreased both north and south of the front (Table III). Assimilation numbers were greatest in 2000 and markedly decreased in 2001 [from 4.11–5.40 to 1.44–2.19 mg C (mg Chl *a*)$^{-1}$ h^{-1}, respectively].

Phytoplankton pigments

Photosynthetic pigments were spatially variable in both years. Chlorophyll *a* concentrations in 2000 were significantly higher at the STC than at the STW or SAW end-members (0.39 versus 0.13 and 0.08 μg L^{-1}, respectively; Tukey's test, $\alpha = 0.05$), indicating enhanced autotrophic biomass at the STC (Fig. 2a). Fucoxanthin concentrations were also highest at the STC and lowest at the SAW (Fig. 2a), and prasinoxanthin concentrations were substantial in the STW

Table II: Means and ranges of oceanographic variables assessed during the two cruises based on the three water masses (STW, STC and SAW)

	Spring 2000			Spring 2001		
Variable	STW[a]	STC[b]	SAW[a]	STW[a]	STC[b]	SAW[a]
Temperature (°C)	13.0 (9.0–14.7)	11.2	9.5 (9.0–10.7)	14.1 (13.1–15.0)	11.9	10.3 (9.2–11.7)
Salinity	35.24 (35.03–35.5)	34.81	34.43 (34.32–34.70)	35.29 (35.19–35.43)	34.90	34.46 (34.15–34.85)
Nitrate (μmol L^{-1})	0.64 (0.44–0.77)	1.23	2.27 (1.52–2.93)	0.70 (0.31–0.95)	0.33	1.64 (0.26–1.79)
Phosphate (μmol L^{-1})	0.09 (0.03–0.12)	0.68	0.25 (0.17–0.31)	0.17 (0.14–0.21)	0.19	0.24 (0.12–0.35)
Silicic acid (μmol L^{-1})	0.46 (0.35–0.65)	0.30	1.19 (0.47–2.52)	0.76 (0.48–1.07)	0.54	0.64 (0.30–1.08)
Ammonium (μmol L^{-1})	0.34 (0.11–0.64)	0.58	0.44 (0.29–0.67)	nd	nd	nd
Chlorophyll *a* (μg L^{-1})	0.27 (0.13–0.33)	0.39	0.10 (0.19–0.52)	1.76 (0.79–3.52)	2.84	1.96 (0.38–4.39)

Data are from the upper 20 m. Chlorophyll concentrations derived from HPLC analyses.
[a]$n = 4$.
[b]$n = 1$.

Table III: Mean primary productivity and chlorophyll specific productivity (± 1 standard deviation) from stations within the three water masses during 2000 and 2001

Water mass	2000 primary productivity (mg C m^{-3} h^{-1})	2001 primary productivity (mg C m^{-3} h^{-1})	2000 Chl-specific Productivity [mg C (mg chl)$^{-1}$ h^{-1}]	2001 Chl-specific Productivity [mg C (mg chl)$^{-1}$ h^{-1}]
STW	1.48 ± 0.60 (0.47)	2.52 ± 1.76 (0.81)	4.68 ± 1.25	1.44 ± 0.39
STC	2.32 ± 0.17 (0.39)	5.71 ± 0.13 (1.11)	5.40 ± 1.40	2.19 ± 0.27
SAW	0.37 ± 0.15 (0.31)	1.52 ± 1.01 (0.84)	4.11 ± 1.23	1.64 ± 0.82

Values in parentheses represent the integrated daily production (g C m^{-2} day^{-1}) using the equation of Falkowski *et al.* (1998).

(Fig. 2b). Statistical analysis of 2001 pigments showed no difference in concentrations with distance from STC (Fig. 2c and d; two-tailed *t*-test, $n = 3$, $\alpha = 0.05$) with the exception of alloxanthin ($t = 7.40$, $P = 0.002$), a marker pigment for cryptophytes (Fig. 2d).

All pigment concentrations in 2000 at St. 1, 6 and 10 were statistically different between the STW end-member and STC, the STC and SAW end-member and the STW and SAW end-members ($\alpha = 0.05$) except for peridinin (Fig. 2a). Several spatial patterns were observed. Some pigments were low in STW, high at STC and low in SAW (CHL *a* and FUCO), and some were high in STW and low at STC and SAW (ALLO, LUT, PRASINO and VIOLA), but a few were low at STW and STC and high at SAW (19-HEX and ZEA). PRASINO, a marker for prasinophytes, was significantly higher at the STW end-member when compared with the STC (Tukey's test, $\alpha = 0.05$; paired *t*-test, $n = 3$, $P = 0.02$, $\alpha = 0.05$), but chlorophyll *b* was not.

Analysis of photosynthetic pigment concentrations from 2001 (two-tailed *t*-test, $n = 4$, $\alpha = 0.05$) showed statistically significant differences in pigments with distance from the STC for PRASINO, VIOLA and ALLO (Fig. 2b); all these pigments had concentrations that were higher on the STW side of the Rise. Assessment of pigment concentrations at St. 1 (STW), St. 5 (STC) and

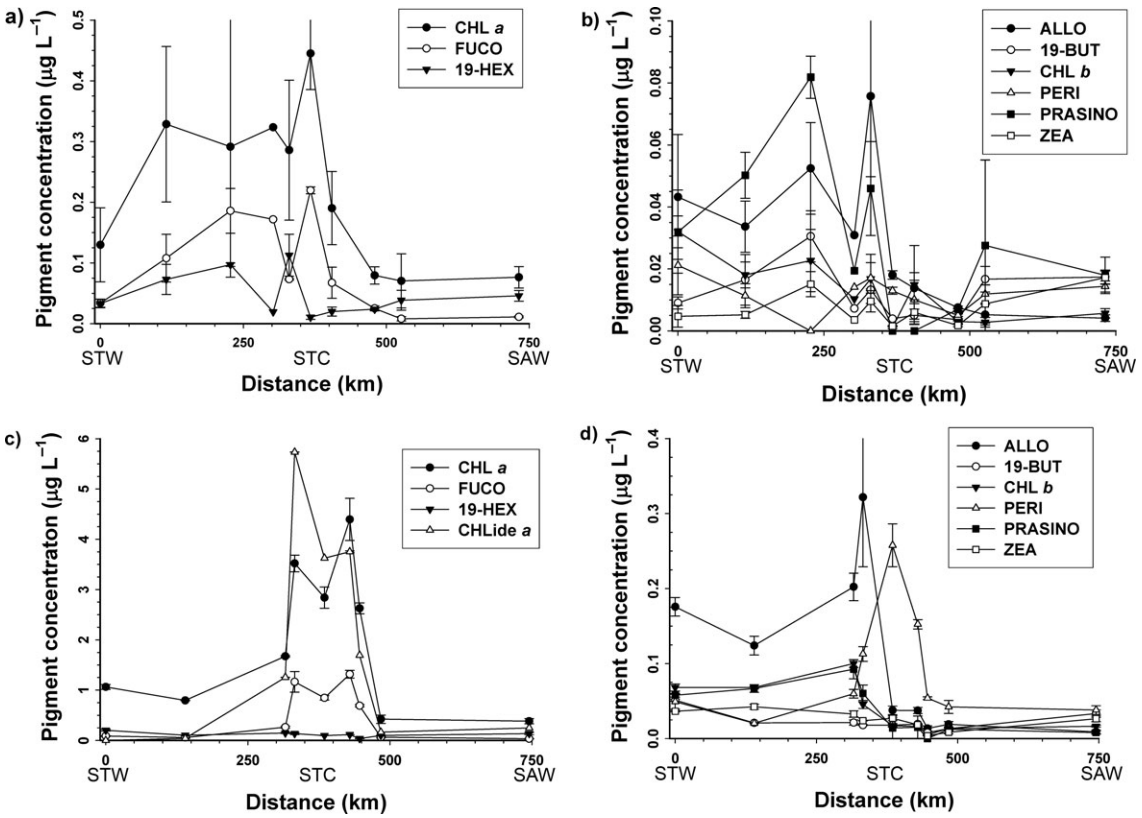

Fig. 2. Distribution of (**a**) chlorophyll *a*, fucoxanthin and 19-hexanoylfucoxanthin during austral spring, 2000, (**b**) other accessory pigments during 2000, (**c**) chlorophyll *a*, fucoxanthin, 19-hexanoylfucoxanthin and chlorophyllide *a* during austral spring, 2001 and (**d**) other accessory pigments during 2001. Location of the end-members of STW and SAW indicated, as is the STC. Error bars represent standard deviations.

St. 9 (SAW) showed that all pigment concentrations were statistically different between STW and STC, STC and SAW and STW and SAW (Tukey's test, $\alpha = 0.05$) except for zeaxanthin. Two distribution patterns were observed. The first exhibited low concentrations of pigments (CHL *a*, FUCO, LUT and PERI) in STW and SAW but high in the STC, whereas the second showed high concentrations (ALLO, 19-BUT, 19-HEX, PRASINO and VIOLA) in STW but low at the STC and SAW. Fucoxanthin and peridinin concentrations at both SAW and STW end-members were significantly lower than STC concentrations, a pattern also seen in chlorophyll *a* concentrations.

One unusual difference between the 2 years was the rather large concentration of chlorophyllide *a* in 2001 (Fig. 2c). Concentrations at some sites exceeded those of chlorophyll *a* and other accessory pigments. Maxima were noted at the STC, but also were elevated to the north and south of the front, but decreased to zero at the two ends of the transect.

CHEMTAX analysis

CHEMTAX analysis of STW and STC locations (St. 1–6) sampled in 2000 showed the contribution of diatoms to total chlorophyll *a* tended to be fairly large (albeit variable) except for St. 1, where the diatom contribution was zero (Fig. 3a). Diatom contributions at the other stations ranged from 7 to 77%, with the highest contribution occurring at the STC. Cryptophyte contribution to total chlorophyll *a* was fairly consistent (7–28%), and dinoflagellate chlorophyll increased with the distance from the STC (Fig. 3a). Although prymnesiophyte and prasinophyte contributions were variable, there was a general pattern of increased contribution to the north. Diatom chlorophyll decreased rapidly to the south from the STC (71% at STC, 14% at St. 8), with no contribution from diatoms at St. 9 and 10 (Fig. 3a). The contribution of cryptophytes followed the same trend: cryptophyte contribution was 16–27% at St. 6–8, but absent at St. 10. In contrast, dinoflagellate and procaryote chlorophyll increased south of the STC. Chrysophytes and prasinophytes contributed little to chlorophyll *a* anywhere. Prymnesiophyte and pelagophyte chlorophyll also increased south of the STC (Fig. 3a). There was good agreement between the results of the two CHEMTAX analyses that used different initial pigment ratios (e.g. diatom chlorophyll was ca. 70% for both analyses).

In 2001 cryptophytes were by far the largest component of phytoplankton standing stocks in the STW, where they contributed between 47 and 63% of total chlorophyll *a* (Fig. 3b). Diatoms were important in the

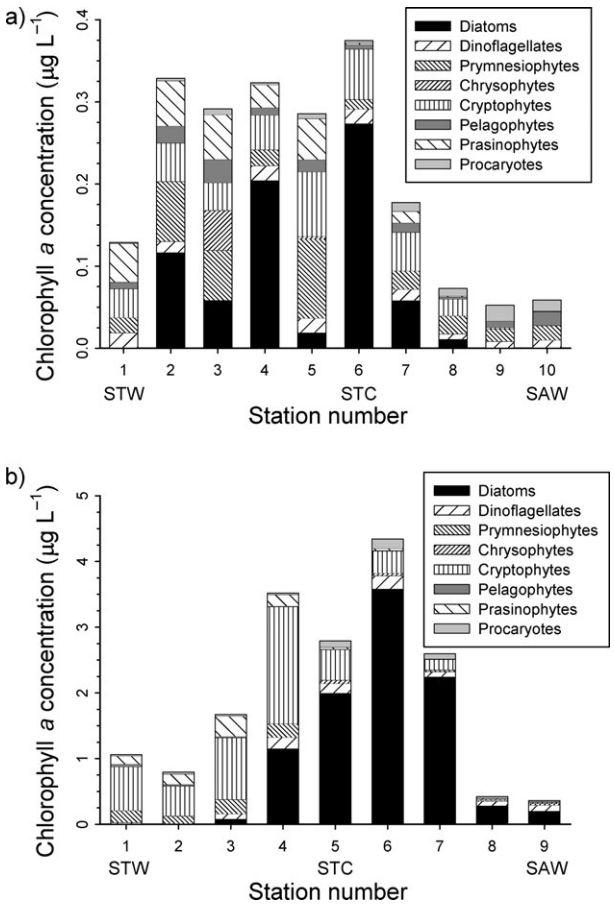

Fig. 3. Distribution of the amount of chlorophyll attributed to various taxa (**a**) during austral spring, 2000 in STW (St. 1–5), the STC (St. 6) and SAW (St. 7–10) and (**b**) during austral spring, 2001 in Subtropical Waters (St. 1–4), the STC (St. 5) and SAW (St. 6–9).

vicinity of the STC (~33% at St. 4 and 70% at St. 5). Prasinophyte and prymnesiophyte contributions were relatively constant among St. 1–3, but decreased towards the STC. Dinoflagellate chlorophyll increased from St. 1–5, but the percentage of total chlorophyll *a* was always low (1–5% at St. 1–4, 15% at St. 5). Contributions by chrysophytes, procaryotes, chlorophytes and pelagophytes were small (<3%; Fig. 3b). Diatom chlorophyll at the STC and SAW (St. 5–9) was high (53% of chlorophyll *a* at St. 9, 70% at St. 5) (Fig. 3b). Prymnesiophyte standing stocks increased to the south of the STC, from 5 to 24%, as did prasinophyte chlorophyll, but the percentage of contribution was always low (≈1% at St. 9). Dinoflagellate chlorophyll decreased south of the STC. Contributions due to chrysophytes, cryptophytes, chlorophytes, procaryotes and pelagophytes were negligible (0–6%; Fig. 3b). The CHEMTAX results of St. 5 at the STC using northern

section initial pigment ratios differed from those when the southern section pigment ratios were used. Contribution of diatoms was 28% using northern ratios, but using southern pigment ratios it was 53% of the total chlorophyll. Cryptophyte and prymnesiophyte chlorophyll was 47 and 5% with northern ratios, but 4 and 24% with southern pigment ratios.

Cellular abundance

In 2000, large numbers of diatoms were observed from the STW north of the Chatham Rise and at the STC (Fig. 4a). Direct counts of preserved samples also indicated that there were high numbers of photosynthetic nanoflagellates and prokaryotes (prochlorophytes and cyanobacteria). Higher numbers of photosynthetic prokaryotes were seen in STW and SAW, and lower numbers were observed at the Chatham Rise (Fig. 4a). Photosynthetic nanoflagellates were higher in STW. When compared with the number of nanoflagellates and prokaryotes, the abundance of diatoms was low, but because they were mostly large centric forms, the carbon biomass of this group was high. No pattern was observed with dinoflagellate abundance (Fig. 4a). In 2001, there were more diatoms at the stations immediately adjacent to the STC (St. 4, 6 and 7) than at the end-members; however, actual numbers were low (Fig. 4b). Again, no pattern was discerned for dinoflagellates. The numbers of autotrophic nanoflagellates were high, and there appeared to be more nanoflagellates at the SAW end-member (Fig. 4b). Photosynthetic prokaryotes were higher towards the STW and SAW end-member stations.

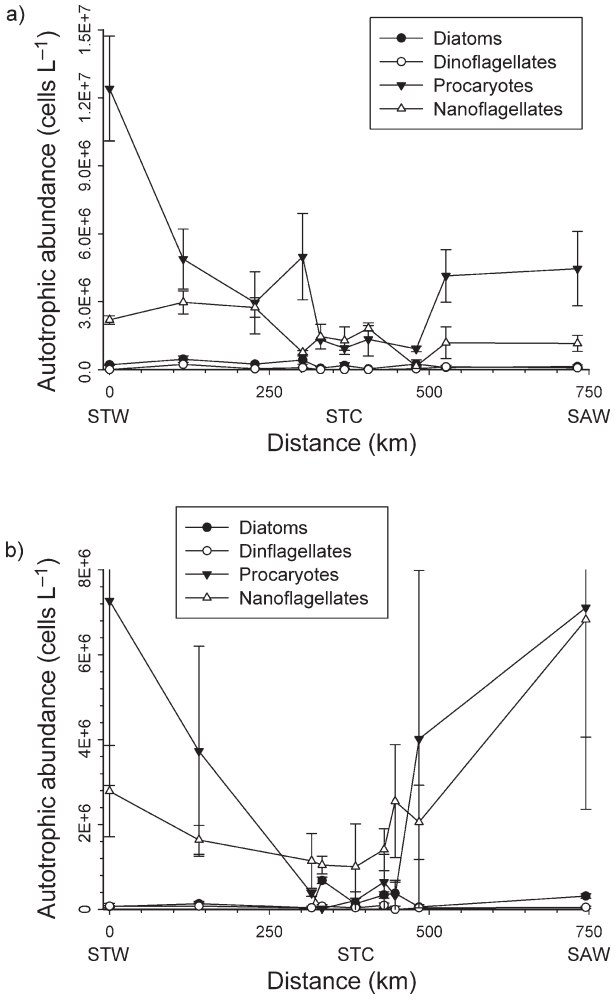

Fig. 4. Distribution of taxa abundance determined by microscopy (**a**) during austral spring, 2000 in STW (St. 1–5), the STC (St. 6) and SAW (St. 7–10) and (**b**) during austral spring, 2001 in STW (St. 1–4), the STC (St. 5) and SAW (St. 6–9). Error bars represent standard deviations.

Absolute phytoplankton growth rates

Absolute growth rates of phytoplankton in 2000 (based on CHL *a*) ranged from 0.10 day^{-1} at St. 3 to 1.18 day^{-1} at St. 6 (STC; Table IV). Growth rates were highest at the STC ($\mu = 1.18$ day^{-1}), and decreased in SAW (mean $\mu = 0.49$ day^{-1}) and STW (mean $\mu =$ 0.55 day^{-1}). Absolute growth rates based on CHL *b* ranged from 0.38 day^{-1} at St. 3 to 1.72 day^{-1} at the STC (Table IV). Mean CHL *b* growth rates were less in STW than in SAW (0.55 and 1.01 day^{-1}, respectively); the same trend was seen for those based on ALLO (0.38 and 0.64 day^{-1}), FUCO (0.73 and 0.82 day^{-1}), 19-BUT (0.59 day^{-1} and 0.96 day^{-1}) and 19-HEX (0.53 and 0.85 day^{-1}) (Table IV).

In 2001, absolute growth rates for the total assemblage (based on chlorophyll *a*) were relatively low along the entire transect, ranging from 0.30 to 0.57 day^{-1} (Table IV). The differences between the STW, STC and SAW were much less than that observed in 2000. Growth rates for diatoms were low at the region of the STC (0.47 day^{-1}) and much higher at the STW and SAW end-members (1.31 and 0.90 day^{-1}, respectively; Table IV). Indeed, all pigment-based growth rates showed a minimum at the STC, with the exception of ALLO and ZEA. Cryptophyte growth rates were low north of the Chatham Rise (0.29 to 0.38 day^{-1}), and higher at the STC and to the south (1.17d^{-1} at the Rise, and 0.57 to 1.09 day^{-1} in SAW; Table IV); procaryotes showed a similar spatial pattern.

Table IV: Phytoplankton growth rates (mean, standard deviation, minimum and maximum) derived from various pigments within the transect

	2000 Growth Rate (day^{-1})			2001 Growth Rate (day^{-1})		
Pigment	STW	STC	SAW	STW	STC	SAW
Chlorophyll *a*	0.55 ± 0.37 (0.10–0.86)	1.18	0.49 ± 0.14 (0.39–0.70)	0.47 ± 0.12 (0.30–0.57)	0.35	0.38 ± 0. 07 (0.31–0.48)
19-butanoyloxyfucoxanthin	0.59 ± 0.15 (0.41–0.77)	1.42	0.84 ± 0.20 (0.61–1.10)	1.07 ± 0.16 (0.90–1.21)	0.99	1.16 ± 0.47 (0.71–1.63)
19-hexanoyloxyfucoxanthin	0.53 ± 0.39 (0.06–1.00)	0.93	0.84 ± 0.30 (0.45–1.17)	1.22 ± 0.41 (0.67–1.52)	0.62	0.82 ± 0.24 (0.50–1.08)
Alloxanthin	0.38 ± 0.19 (0.10–0.56)	0.69	0.62 ± 0.16 (0.46– 0.79)	0.34 ± 0.04 (0.29–0.38)	1.17	0.89 ± 0.24 (0.57–1.09)
Chlorophyll *b*	0.55 ± 0.12 (0.38–0.67)	1.72	0.83 ± 0.36 (0.49–1.26)	1.12 ± 0.34 (0.64–1.34)	0.84	0.93 ± 0.30 (0.70–1.36)
Fucoxanthin	0.73 ± 0.38 (0.17–1.03)	0.52	0.89 ± 0.23 (0.65–1.21)	1.31 ± 0.41 (0.92–1.70)	0.47	0.90 ± 0.46 (0.42–1.31)
Prasinoxanthin	nd			0.70 ± 0.37 (0.33–1.10)	0.11	0.39 ± 0.51 (0.00–1.07)
Zeaxanthin	1.08 ± 0.46 (0.70–1.70)	nd	0.76 ± 0.35 (0.43–1.07)	1.12 ± 0.44 (0.63–1.70)	1.64	1.18 ± 0.28 (0.94–1.46)

nd, no data.

Relative growth rates

The maximum relative growth rates after being normalized to temperature (Eppley, 1972) in 2000 were greatest at the STC and generally greater in colder waters (i.e. SAW) than farther north. Chlorophyll growth rates were 40 and 56% of the predicted maximum in STW and SAW, respectively, and 99% at the STC (Fig. 5). Growth rates derived from accessory pigments averaged 41% of maximum growth in STW and 68% in SAW (Fig. 6a and b). Specific growth rates on either side of the Rise were not, however, statistically different from each other.

In contrast to the results in 2000, austral spring 2001 temperature-normalized assemblage growth rates showed no significant difference as distance increased from the STC (two-tailed, $\alpha = 0.05$, $n = 4$), with the exception of those of cryptophytes ($t = -5.23$, $P = 0.014$; Fig. 5c), which were higher in SAW. Chlorophyll-based growth rates were lower and relative invariant, ranging from 15 to 29% of the maximum (Fig. 5). The contribution of individual taxa to the assemblage growth rate varied considerably, however (Fig. 6c and d). Some groups (e.g. procaryotes) had growth rates that were consistently greater than those of the total assemblage, but because their biomass was small, the net impact on bulk assemblage growth rates was modest.

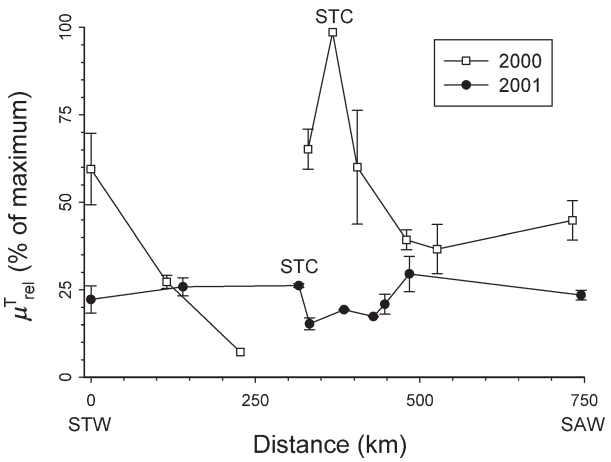

Fig. 5. Distribution of phytoplankton growth rates determined from chlorophyll *a* labeling during austral spring, 2000 and 2001. Error bars represent standard deviations.

DISCUSSION

The STC is a good region to examine the relationship between assemblage composition, biomass and growth rates because there is substantial oceanographic variability over relatively short distances that may influence all three. In general, the STC is considered to be a zone of enhanced biomass. CZCS images of the STC east of New Zealand between 1978 and 1986 showed elevated chlorophyll *a* concentrations ($\sim 3\ \mu g\ L^{-1}$) during austral spring (http://seawifs.gsfc.nasa.gov/SEAWIFS/CZCS_DATA/australia.html). Recent SeaWiFS images also consistently show that the shallow region east of New Zealand is elevated in pigments (http://seawifs.gsfc.nasa.gov/). Banse (Banse, 1996) compiled data from a variety of sources and showed that the frontal regimes (both the STC and those farther south) were sites of enhanced chlorophyll concentrations, but later argued (Banse and English, 1997) that pigment concentrations had been overestimated due to the effects of clouds, and that only two (of 197) pixels were greater than $1\ \mu g\ L^{-1}$. Although few field studies have been conducted in this area of the STC, those that have showed substantial seasonal variations, with spring chlorophyll *a* levels 6-fold greater than those found in winter (Chang and Gall, 1998). During this study, diatoms dominated at the STC, but during winter, in the STW, dinoflagellates dominated and diatoms were again dominant in spring. Nanoflagellates were dominant in SAW during both

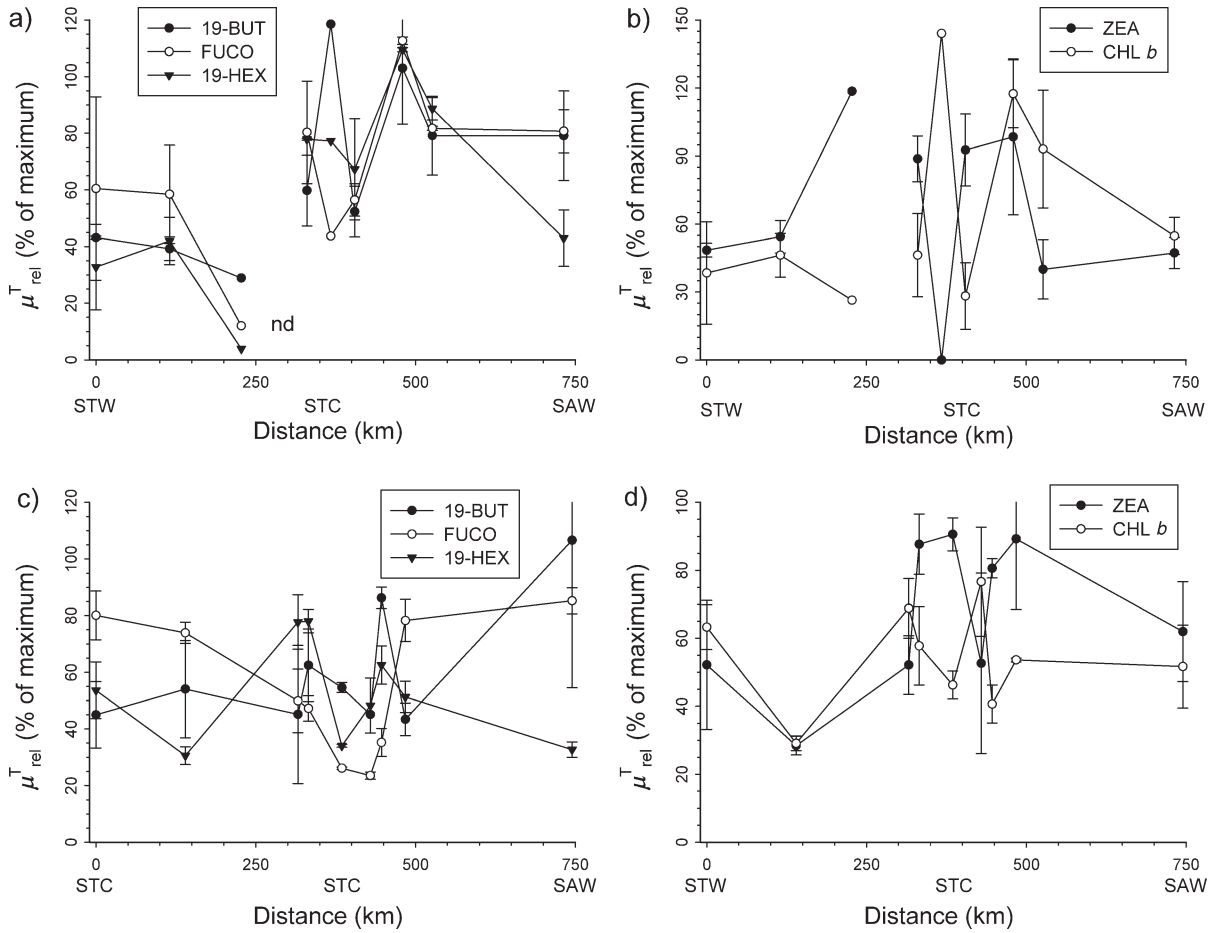

Fig. 6. Distribution of growth rates determined from accessory pigment labeling during austral spring, 2000 (**a** and **b**) and spring, 2001 (**c** and **d**). Error bars represent standard deviations.

seasons. Primary productivity was highest in spring and lowest in winter (Gall *et al.*, 1999). James and Hall (James and Hall, 1998) observed that microzooplankton abundance was similar in all water masses in winter, but significantly higher in spring, suggesting that grazing rates were likely greater in spring. Our chlorophyll values exceeded those detected by Banse and English (Banse and English, 1997) and were similar to those found in more satellite and recent field studies (Chang and Gall, 1998). Concentrations were greatest in 2001 and reached 5.6 $\mu g\ L^{-1}$ and clearly show that the region in austral spring is one of elevated biomass, especially for one that is relatively deep and largely removed from neritic influences.

Primary productivity

Phytoplankton productivity was only assessed at one depth, so it cannot be easily related to integrated water column estimates normally made. Falkowski *et al.* (Falkowski *et al.*, 1998) derived a relationship between surface chlorophyll concentrations and integrated productivity, and by using this equation, we estimate that productivity ranged from 0.68 to 1.04 $g\ C\ m^{-2}\ day^{-1}$ in 2000 and from 1.82 to 2.52 $g\ C\ m^{-2}\ day^{-1}$ in 2001 and was greatest in the STC (Table III). Assimilation numbers (chlorophyll-specific productivity) were also greatest in the STC, although the increase was not as great as that for absolute productivity. Assimilation numbers were much lower in 2001 (see *Controls of Growth and Biomass*), which suggests that the Falkowski *et al.*'s relationship may overestimate productivity in 2001.

Pigment concentrations and assemblage composition

Pigment concentrations showed substantial spatial variability in SAW and STW as well as at the STC east of

New Zealand during austral springs 2000 and 2001. Chlorophyll *a* concentrations were significantly greater at the STC, indicating higher autotrophic biomass at the STC than in either STW or SAW. However, chlorophyll *a* values throughout the entire region during 2000 were low (from 0.19 to 1.21 $\mu g\,L^{-1}$) relative to 2001 (from 0.22 to 5.26 $\mu g\,L^{-1}$; Fig. 2a and b). The chlorophyll *a* spatial distribution paralleled that of fucoxanthin in 2000, suggesting that diatoms (and perhaps cryptophytes) were responsible for most of the increased biomass at the STC (84% of the chlorophyll *a* at St. 6 was due to diatoms and cryptophytes; Fig. 3). Diatom standing stocks were also elevated in STW, but the correlation between cell abundance and pigment concentrations was less marked at the STC (Figs 3 and 4). Cryptophyte biomass was significantly higher north of the STC, a pattern also found by Chang and Gall (Chang and Gall, 1998). Prasinophyte biomass was higher at the STW end-member that at the STC (Fig. 3), but prymnesiophyte biomass was decreased at the STC and elevated in the waters north and south of the front. Differences between all other pigments (except alloxanthin) with distance from the STC were not statistically significant in 2000. However, the spatial pattern was variable (high at the STC, low at both or one of the end-members or low at the STC and high at both or one of the end-members), confirming the substantial spatial variability of pigment concentrations within the study site.

There was similarly a high degree of spatial variability of photosynthetic pigments during austral spring 2001. Much of the autotrophic biomass at and near the STC was again due to diatoms. Pigment concentrations in 2001 showed that the contribution of diatoms to total chlorophyll *a* was lower at the stations closer to STW and SAW end-members and much higher at the STC as well as at the stations closest to the STC (~85% at St. 7; Fig. 3b). Cell abundances also showed that diatom abundances were high at stations closest to the STC (St. 4, 6 and 7; Fig. 4b). CHEMTAX analysis also indicated that there was spatial change in taxonomic dominance of the phytoplankton assemblage along the transect: prasinophytes and cryptophytes co-dominated on the STW side and diatoms dominated at the STC and in SAW. Although they did not contribute a large percentage to chlorophyll *a*, prymnesiophytes increased in importance towards the SAW and the STW end-members. Procaryote biomass was low in the STW, but contributions by procaryotes to chlorophyll *a* during 2001 increased with distance from the STC (from 1% of the chlorophyll *a* at STC to 23% at SAW end-member). Procaryotes (cyanobacteria and prochlorophytes) are ubiquitous in much of the ocean and are most commonly found in tropical and STW (Jeffrey *et al.*, 1997).

The discrepancy in CHEMTAX results for the STC station using different pigment ratios (northern versus southern sections) may be due to the use of inexact initial pigment ratios in the CHEMTAX analysis. Diatom biomass was high at the STC, but nutrient data suggest that phytoplankton may have been subjected to nitrate stress there, as ambient concentrations were less than reported half-saturation constants (<0.1–$3\ \mu mol\,L^{-1}$) (Chang and Gall, 1998). Thus, nutrient effects on pigment ratios may have been significant. The STC assemblage composition was more similar to those of SAW (COMPAH analysis was based on presence or absence of pigments at each station); therefore, at the time of the 2001 cruise CHEMTAX analysis, using southern pigment ratios for analysis of STC pigment concentrations may have been more appropriate. In contrast, the 2000 data showed good agreement between the two different results for the STC station, and COMPAH analysis showed STW and SAW stations were more similar to each other than to the STC station.

Phytoplankton growth rates

Growth rates of the entire assemblage in 2000 were greatest at the STC and averaged 1.18 day^{-1} (Table IV). Relative growth rates were near maximal at the STC, and while variable away from the STC, they were generally close to half of the maximum, temperature-limited rate (Fig. 5). Growth rates of diatoms were relatively high across the entire transect, but were slightly decreased at the STC, a pattern that was inverse of the diatom pigment distribution. Prasinophyte (chlorophyll *b*-based) growth rates were higher south of the STC (Table IV). Chlorophyll *b* and prasinoxanthin concentrations showed prasinophyte biomass was higher in STW, but chlorophyll *b* growth rates were higher in SAW (Fig. 3a). This suggests that the prasinophyte biomass in SAW was growing faster, but their accumulation was precluded due to grazing and/or export. Absolute growth rates of prymnesiophytes were relatively high at all stations along the transect (Fig. 6a).

In 2001, growth rates based on chlorophyll *a* were low and showed little variability along the cruise transect (Table IV, Fig. 5). In contrast, diatom growth rates were high in both STW and SAW end-members but low at the STC. A paired *t*-test of temperature-normalized cryptophyte growth rates was statistically significant (Table IV), with cryptophyte growth significantly higher in SAW. However, cryptophyte biomass was higher in

STW. Although growth rates based on chlorophyll *b* (prasinophytes) did not vary along the transect, concentrations were higher in STW. This same pattern was seen in chrysophyte and prymnesiophyte growth rates. Thus, grazing and/or export of cryptophytes, prasinophytes, and prymnesiophytes are likely important in SAW in limiting biomass accumulations of those taxa.

Comparison of 2000 and 2001 cruises

Environmental factors varied only modestly between the two cruises, far less than the dramatic (order of magnitude) differences in chlorophyll concentrations we observed. For example, whereas nitrate values were highest in SAW during both years, and approximately equal in the STW, differences between years were $<1\ \mu mol\ L^{-1}$. Nitrate concentrations during spring 1993 (Chang and Gall, 1998) were higher than those during these cruises (16.7 versus 2.3 $\mu mol\ L^{-1}$ in 1993 and 2000, respectively), and whereas silicate concentrations were less in our study, they were decreased to a greater extent than nitrate in 1993 (3.2 versus 1.2 $\mu mol\ L^{-1}$ in 1993 and 2000, respectively; Table II). Removal of large amounts of nitrate relative to silicic acid can be explained by an overwhelming contribution to nitrate uptake by non-siliceous forms, exacerbated by an altered Si:N uptake ratio via the effects of iron (Hutchins and Bruland, 1998). No data exist to verify that more iron may have been injected into the region during our study than 1993.

As discussed previously, pigment concentrations during both cruises showed spatial variations within the transects. Chlorophyll *a* concentrations were an order of magnitude higher during 2001 than in 2000 (4.5 and 0.4 $\mu g\ L^{-1}$ at the STC). However, chlorophyll *a* concentrations were higher on the STW side during 2000, but higher on the SAW side during 2001. It is possible that this difference reflected an interannual difference in the onset of the spring bloom, but the magnitude of the difference suggests that other processes were more important in generating the variation. Fucoxanthin concentrations showed the same pattern (fucoxanthin contribution to chlorophyll *a* was higher during 2001) (Fig. 3). Although no significant trend in peridinin concentrations was seen during 2000, concentrations during 2001 were higher at the STC when compared withs STW or SAW (Fig. 2). It is possible that a nutrient-mediated shift from diatoms to dinoflagellates was occurring at the STC during 2001, as both nitrate and silicic acid were below 1 $\mu mol\ L^{-1}$. Cryptophyte chlorophyll during 2000 was about 20% of the total at all stations, but during 2001 it was more variable both in percentage contribution and in absolute amount (from 47 to 63% of chlorophyll *a* was contributed by cryptophytes in STW, but only 6% in SAW). Perhaps the most marked difference between cruises was the large amount of chlorophyllide *a* found in 2001. Enhanced levels of this chlorophyll precursor have been observed previously in the Pacific sector of the Southern Ocean (Lance *et al.*, 2007) and may be a result of either senescence or iron-limitation.

Control of biomass and growth

Growth of phytoplankton represents a relatively short-term process, whereas the accumulation of biomass by different taxa represents the cumulative effects of various growth and loss processes over a variety of time scales. By comparing growth with biomass distributions, it is possible to infer the importance of biological loss processes as well as potential environmental controls.

Nutrients were quite low throughout much of the study area, with both silicic acid and nitrate being low and near or much below measured half-saturation constants. Chang and Gall (Chang and Gall, 1998) found that average K_s for silicate uptake by diatoms was 2.3 μM, which suggests that diatoms may have been stressed by silicate availability. Chlorophyllide *a*, which is found in senescent tissue (Jeffrey *et al.*, 1997), was found in significant amounts near the STC during 2001 as well (Fig. 3b) and was coincident with the large diatom abundance (Fig. 2c). We suggest that diatoms, especially near the STC, were under severe silicic acid stress and had entered senescence and that other taxa may have been similarly stressed by nitrogen availability. The decreased relative growth rates (Figs 5 and 6) also suggest the potential for senescence. No such condition was noted in 2000. Hence at the time of the 2001 cruise, we believe that growth of some taxa was being severely restricted by nutrients, particularly in the area of the STC, but that other taxa, despite the low ambient nutrient concentrations, still were growing at near their maximum potential rates. These forms may have been using regenerated nitrogen (NH_4^+) and contributed to the development of the classical microbial food web.

The general area of the STC was the one with the highest chlorophyll concentrations of the region. A number of physical mechanisms have been suggested as means to bring nutrients into the surface layer, as well as to retain cells there (i.e. decrease losses). The region is shallower than the rest of the transect, so vertical mixing rates may be enhanced and provide input of nutrients from below. Mesoscale frontal circulation (generation of a convergence) also might allow cells to accumulate to a greater extent than throughout the rest of the transect. Enhanced vertical motion might reduce

the net sinking rates of larger taxa such as diatoms and allow them to flourish. Our results cannot distinguish among the various possible causes of the enhanced standing stocks, but the taxonomic distributions could be used in conjunction with detailed physical measurements to test the importance of biophysical interactions.

Certain taxa exhibited rather low standing stocks but relatively high rates of growth. For example, zeaxanthin concentrations were low in both years, but the growth rates were quite high throughout (approaching 100% of the maximum temperature-mediated growth rate at some stations; Fig. 6b, Table IV). This strongly suggests that procaryotes were being grazed nearly as fast as they grew. James and Hall (James and Hall, 1998) concluded that microzooplankton grazing on picoplankton in STW (as determined by dilution experiments) was greater than growth, which would be consistent with our results. Similarly, absolute growth rates of cryptophytes and diatoms were near maximal at the extremes of the SAW, but the biomass was very low. This again implies that removal processes may have been important for controlling the abundance of these taxa. Indeed, many taxa had relatively rapid or at least intermediate growth rates, but particularly in 2000, quite restricted standing stocks. While oceanographic factors may have been important in impacting growth rates, we believe that the biomass of the phytoplankton taxa was strongly regulated and controlled by grazing as suggested for other oceanic regions (e.g. Miller, 1993; Banse, 1994).

In conclusion, this region of the STC is highly dynamic, with pigment concentrations, phytoplankton assemblage structure, dominant taxa and growth rates fluctuating substantially during spring. The dynamic nature of this sector of the STC may be due to the two very different water masses forming a front and interacting over a very short distance (150 km) because of the bathymetry of the Chatham Rise. The area "is a region of stirring with warm and cold plumes of frontally modified water intertwining", with mixing strongest at the surface (Sutton, 2001). STW have lower levels of macronutrients (nitrate, silicate, phosphate) and higher levels of micronutrients (such as iron; Boyd *et al.*, 1999), but SAW have relatively high levels of macronutrients and decreased iron concentrations. These spatial changes result in a mosaic of biological distributions during austral spring, and ultimately result in both regulation of growth by nutrients and limitation of taxa standing stocks by grazing. Phytoplankton growth rates may be dependent upon the availability of nutrients; assemblage composition, however, may be more strongly regulated by biological removal processes. The interplay between oceanographic influences and biological processes no doubt leads to the substantial spatial variability observed in this region.

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