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Structure and dynamics of the pelagic microbial food web of the Subtropical Convergence region east of New Zealand

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ABSTRACT: The Subtropical Convergence (STC) region to the east of New Zealand was sampled in both winter and spring to establish the food web structure and dynamics in 3 water masses. Subtropical (ST) waters to the north were warm with high salinity, and in spring macronutrient concentrations were potentially limiting to phytoplankton growth. Subantarctic (SA) waters to the south in both seasons were cold, with lower salinity and high macronutrient concentrations with chlorophyll *a* concentrations of 0.12 to 0.19 µg l^{-1}. The frontal zone between these water masses (STC) had maximum chlorophyll *a* concentrations ranging from 0.39 to 3.42 µg l^{-1}. In SA waters in both seasons and ST waters in spring the pelagic food web in the mixed layer was dominated by the microbial components with up to 98% of the phytoplankton biomass in the <20 µm size fraction and the bacterial C/phytoplankton C ratio ranging from 0.9 to 1.9. In comparison, in STC waters in both seasons and subtropical waters in winter the >20 µm phytoplankton dominated the phytoplankton biomass with ratios of 0.2 to 0.3 bacterial C/phytoplankton C. Despite significant differences in the food web structure, primary grazers of the phytoplankton in all water masses in both seasons were microzooplankton with 78 to 118% of the primary production being grazed on a daily basis. This suggests that the food web was dominated by recycling processes, and phytoplankton export fluxes from the upper mixed layer were low in all water masses at the time of sampling.

KEY WORDS: Microbial food web · Subtropical Convergence · Grazing · Microzooplankton

INTRODUCTION

The south-west Pacific Ocean has been identified as one of the largest sinks for atmospheric CO_2 (Takahasi & Azevedo 1982, Murphy et al. 1991). One of the highly productive areas in this region is the Subtropical Convergence (STC) which lies between 40 and 50° S. It has been proposed that the CO_2 flux in this zone is driven not only by physical processes but also by biological processes (Currie & Hunter 1998). One important factor in determining carbon export fluxes from the upper ocean is the structure and size composition of organisms in the planktonic food web (Eppley & Peterson 1979, Michaels & Silver 1988). Fortier et al. (1994) hypothesise that turnover time of biogenic carbon is a direct function of the ratio between the size of organisms and that of their food particles. In systems where the microbial food web is dominant, most of the biogenic material is rapidly recycled within the euphotic layer (Fortier et al. 1994). Burkill et al. (1995) estimated that up to 271% of the daily primary production in the Bellingshausen Sea was consumed by microzooplankton. In these systems the microzooplankton play a pivotal role in transferring carbon from the microbial food web to the larger grazers. In ecosystems where larger phytoplankton dominate the algal biomass the mesozooplankton and macrozooplankton are the primary grazers, and export fluxes from the upper water column are via direct sinking of large phytoplankton and sink-

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ing of zooplankton faecal pellets (Small et al. 1979, Gonzalez et al. 1994).

The microbial food web has been widely shown to dominate food web structure in low-nutrient, low-chlorophyll *a* (chl *a*) systems (e.g. Azam et al. 1983, Joint 1986, Cushing 1989, Søndergaard et al. 1991, Legendre & Rassoulzadegan 1995). However, it has also been suggested that the microbial food web may be dominant in high-nutrient, low-chl *a* systems where micronutrients such as Fe may be limiting phytoplankton growth (Miller et al. 1991, Boyd et al. 1995a).

The STC region is well defined to the east of New Zealand and offers an ideal study site for evaluating the importance of the microbial food web in different systems. To the north, warm, low-macronutrient, subtropical (ST) waters are potentially macronutrient-limited (Longhurst 1995) and to the south, cold subantarctic (SA) waters, which are a typically high-nutrient, low-chl *a* systems, are potentially micronutrient-limited (Banse 1996, Sedwick et al. 1997) The frontal zone between these water masses of the STC is a region of maximum chl *a*.

The information for this paper was collected on 2 cruises in 1993 to the STC region east of South Island, New Zealand, as part of the New Zealand contribution to the JGOFS (Joint Global Ocean Flux Study) programme.

The aim of this paper is to evaluate the structure and dynamics of the microbial food web in the mixed layer and the importance of the microbial food web in water masses of the STC region east of New Zealand.

METHODS

Samples were collected from 2 replicate stations in the SA, ST and STC waters in winter (June) and spring (October) 1993 (Fig. 1). Each station was sampled 3 times in a 24 h period with a full suite of process experiments conducted once at each station. Samples were collected at 10 m using Niskin water bottles and a rosette sampler. A Sea Bird 9/11 plus CTD profiler was deployed at each station to record conductivity, temperature and depth. Conductivity was calibrated using a Guildline Autosal Salinometer MODEL 8400A.

Chl *a* was measured by filtering 500 ml of sample through a Whatman GF/F filter. The filters were stored frozen until analysed spectrofluorometerically on a Perkin-Elmer LS 50B (Strickland & Parsons 1972). Primary production was assessed from daily incubations with ^{14}C bicarbonate as described in Bradford-Grieve et al. (1997).

Ammonia-nitrogen (NH_4-N), and nitrate-nitrogen (NO_3-N) analyses were carried out on the samples that had been passed through acid-washed Whatman GF/F filters; the filters were retained and stored frozen until analysed for particulate nitrogen and particulate phosphorus using Kjeldahl digestion (Vincent et al. 1991). NH_4-N determination used the colorimetric method of Crooke & Simpson (1971), modified for use on the Technicon autoanalyser (M. T. Downes unpubl. data). NO_3-N concentrations were determined using a modification of the method described in Nydahl (1976). Dissolved reactive silica (DRSi) was analysed by the method of Smith & Milne (1981).

Samples for heterotrophic bacterial enumeration were passed through a 2 µm polycarbonate Nuclepore filter, fixed with formalin to a final concentration of 4% and stored in the dark at 4°C for a maximum of 24 h. The prefiltration was shown not to lead to an underestimation of bacterial numbers. A 5 ml subsample of this was stained for 5 min with Acridine Orange (0.01% final concentration) and filtered onto 0.2 µm Nuclepore filters (Hobbie et al. 1977) using a Whatman GF/C as a backing filter. Filters were mounted in immersion oil

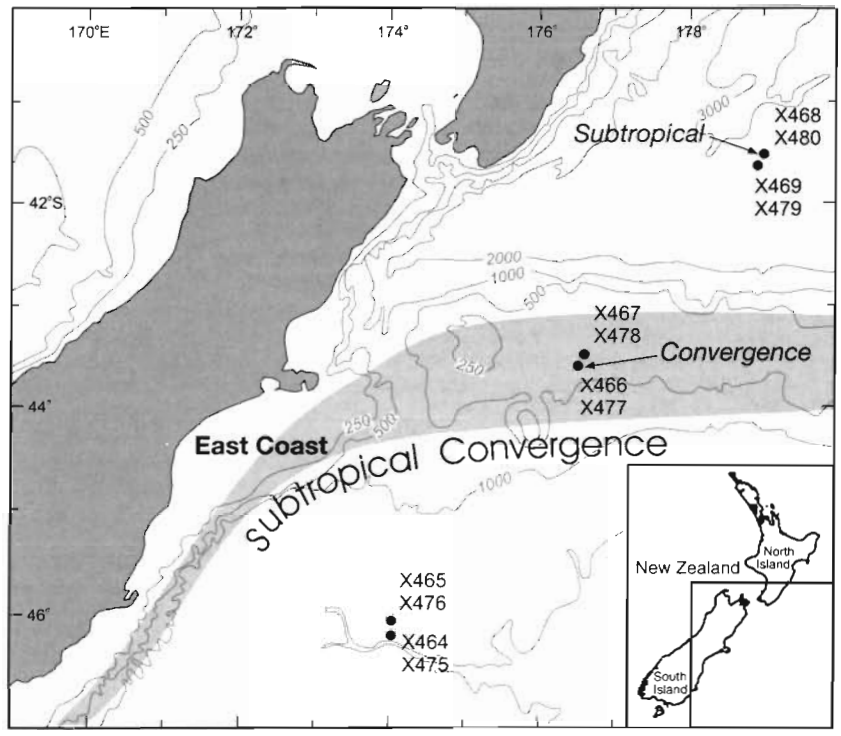

Fig. 1. Location of sampling stations in the Subtropical Convergence to the east of New Zealand

and stored frozen. Bacterial cells were enumerated with blue light excitation (Leica filter block 13) at 1000× magnification with a minimum of 20 fields or 200 cells being counted.

Heterotrophic bacterial productivity was measured using (methyl-^{3}H) thymidine as detailed in Smith & Hall (1997). The extraction procedure followed Wicks & Robarts (1987) modified TCA precipitate method, which involved rinsing the TCA precipitate with phenol-chloroform followed by ethanol. Following filtration the non-filtering area of the filter was removed (Robarts et al. 1986) with a wadding punch and the filters stored frozen in glass scintillation vials until counted. Tritium incorporation was determined with a liquid scintillation counter (LKB, 1217 Rackbeta) using OptiPhase HiSafe 3 (Wallac) as the scintillation fluor. Counts were corrected for quench by external standards. In order to convert mol thymidine to g C we used Fuhrman & Azam's (1982) conversion factor of 2.4×10^{18} cells per mol thymidine incorporated, and Lee & Fuhrman's (1987) estimate of 20×10^{-15} g C cell^{-1}. Doubling time was determined as the natural log of 2 divided by the specific growth rate.

Samples for picophytoplankton enumeration were passed through a 2 µm Nuclepore filter before being fixed with 1 ml of paraformaldehyde (0.2% final concentration) for at least 1 h. Duplicate 50 ml subsamples were then filtered onto pre-dyed 0.2 µm filters and the duplicate filters mounted in a gelatin/glycerol mix, sealed onto glass slides and frozen (Hall 1991). Enumeration of eukaryotic picophytoplankton was conducted under blue light excitation (Bandpassfilter [BP] 450–490 excitation, LP 515 barrier filter, RPK 510 dichromatic beam splitter), resulting in a red fluorescence for eukaryotic cells. Enumeration of prokaryotic picophytoplankton was conducted under green light excitation (BP 530–560 excitation, LP 580 barrier filter, RPK 580 dichromatic beam splitter), resulting in an orange fluorescence. Prochlorophyte numbers were not evaluated as appropriate methods were not available.

Samples collected for nanoflagellate enumeration were size-fractionated through a 20 µm nylon mesh. The filtrate was then fixed with an identical volume of ice-cold glutaraldehyde (2% final concentration) for 1 h (Sanders et al. 1989). Fixed samples were filtered onto prestained 0.8 µm black polycarbonate Nuclepore filters, stained for 5 min with 2 ml primulin, rinsed twice with 2 ml of tris HCl, mounted on slides and stored frozen (Caron 1983, Bloem et al. 1986). Nanoflagellates were counted under UV excitation using a Leica compound microscope (BP 450–490 nm excitation, LP 520 barrier filter, FT 510 dichromatic beam splitter). Autotrophic nanoflagellates were differentiated from heterotrophic nanoflagellates by chl *a* fluorescing red under blue light excitation (BP 450–490 excitation, LP 515 barrier filter, RPK 510 dichromatic beam splitter). Forty randomly selected fields were counted per filter. Nanoflagellate biovolumes were calculated from measurements on a minimum of 200 cells, from each of the 3 samples collected at 10 m for each station. Biovolumes were then averaged for each station. Biovolumes were calculated from direct measurements taken during analysis. Cells were regarded as spheres or the closest geometrical shapes and the volumes calculated accordingly (Chang 1988).

Water samples for enumeration of microzooplankton were preserved in 1% Lugol's iodine. Samples were left to settle for 48 h and the supernatant removed. The remaining sample was transferred to a 25 ml Utermöhl chamber. The microzooplankton were identified to genus where possible and enumerated using a Wild inverted microscope (James et al. 1996). There was no differentiation of plastidic ciliates.

Carbon estimates were based on those used by Lee & Fuhrman (1987) for bacteria 20 fg C cell^{-1}, and for picophytoplankton 250 fg C cell^{-1} (Li et al. 1992). The phytoplankton carbon biomass was estimated from cell counts and calculated cell volumes as described in Chang & Gall (1998). Ciliate biomass was estimated from dimensions of 10 to 20 randomly chosen individuals of each taxa measured from 1 station in each water mass. The volumes were estimated from approximate geometric shapes and were converted to carbon biomass using a factor of 0.19 pg C µm^{-3} (Putt & Stoecker 1989).

Grazing was measured using the dilution technique of Landry & Hassett (1982). This method is based on changes in prey concentrations and using different proportions of filtered sea water to manipulate microzooplankton abundance. Four dilutions were used in each experiment and samples were taken from each bottle for chl *a* analysis at the beginning of the experiment. Samples for enumeration of heterotrophic bacteria, picophytoplankton, nanoflagellates, ciliates and macronutrient concentrations were taken from the bulk water collected for the experiments. The experimental bottles were incubated at ambient temperature and 50% surface irradiance using a flow-through incubation chamber. At the end of the incubation duplicate subsamples were taken from each bottle for chl *a* analysis and picophytoplankton enumeration. In spring heterotrophic bacterial numbers were also enumerated at the end of the incubations. Macronutrient and ciliate samples were collected from the 100% natural water incubations (James & Hall 1998).

RESULTS

The STC to the east of South Island, New Zealand, is a region of significant gradients. ST waters to the north

were warmer, more saline and had lower macronutrient concentrations than either the STC or the SA waters. Temperature and salinity decreased rapidly with distance from north to south across the front, and ranged from 14.1 to 8.7°C and 35.2 to 34.2 in winter and from 13.6 to 8.0°C and 35.3 to 34.3 in spring (Table 1). The depth of the mixed layer also varied between water types; in winter it was greatest in ST waters and decreased in depth towards the south in STC and SA waters, ranging from 140 m in ST waters to 90 m in the SA waters. In spring the pattern was not so clear, with both the deepest and shallowest mixed layer depth being recorded at ST stations. STC and SA waters had similar mixed layer depths.

There were also gradients in macronutrients and chl *a* concentrations across the region. In both winter and spring, ST waters had the lowest NO_3-N concentrations. In the STC, NO_3-N concentrations were halved between winter and spring from a mean of 10.1 µmol in winter to 5.2 µmol in spring. In SA waters, NO_3-N concentrations did not vary between seasons (Table 1). DRSi concentrations were similar in all water types in winter. In spring the lowest concentrations of DRSi were observed in the STC with the highest occurring in SA waters (Table 1). Chl *a* concentrations were highest in STC waters in both seasons, with a 6-fold increase in concentrations between winter and spring. Chl *a* concentrations were substantially lower in both SA and ST waters than in STC waters in both seasons (Table 1).

In winter, phytoplankton biomass ranged from 5.7 mg C m^{-3} in SA waters to 26.6 mg C m^{-3} in STC waters. In spring, SA waters also had the lowest biomass with a mean of 16.3 mg C m^{-3} compared to 99 mg C m^{-3} in the STC. In ST waters in both seasons, carbon biomass varied between the paired stations. The size structure of the phytoplankton biomass differed between water masses. In winter, the picophytoplankton (<2 µm) contributed a much higher proportion of the phytoplankton carbon biomass in SA waters than observed in STC or ST waters (Fig. 2). In spring, the contribution of the picophytoplankton to carbon biomass decreased in both SA and STC waters, whereas in ST waters their proportion increased (Fig. 2). The composition of the picophytoplankton also changed between seasons, with eukaryotic forms being undetectable in winter, whereas in spring they contributed 95, 33 and 73% of the total picophytoplankton biomass in SA, STC and ST waters, respectively. There was also a difference between the contribution of the <20 µm size fraction between water types and seasons. In the SA waters the greatest contribution to phytoplankton carbon biomass was by the <20 µm fraction (Fig. 2). In STC and ST waters the contribution of the <20 µm size fraction increased between winter and spring (Fig. 2).

The contribution of the picophytoplankton (<2 µm) to primary production was greatest in SA waters in winter and least in STC waters. In spring there was high variability in the contribution of the picophytoplankton between stations within water types. The contribution of the <20 µm phytoplankton to primary production was substantial in all water masses in winter ranging from 60 to 100%. In spring, however, their contribution in the STC was much lower and variable (Fig. 2). In ST and SA waters in spring 88 to 100% of the primary production was contributed by the <20 µm phytoplankton (Fig. 2).

Heterotrophic bacterial numbers increased between winter and spring with a 5-fold increase observed in ST waters. In winter, bacterial numbers were lowest in the ST waters and highest in SA waters ranging from 2.4 to 4.8 × 10^5 cells ml^{-1}. In spring the gradient between water masses was reversed, with highest numbers in ST waters and lowest in SA waters, with

Table 1. Physical, chemical and biological characteristics of samples from 10 m for each station sampled in each water mass. ST: subtropical, STC: Subtropical Convergence, SA: subantarctic

Season	Water type	Stn	Date sampled (d/mo)	Temperature (°C)	Salinity (‰)	Mixed layer depth (m)	NO_3 (µM)	Si (µM)	Chl *a* (µg l^{-1})
Winter	ST	X468A	01/7	14.11	35.24	130	4.1	2.6	0.13
		X469A	02/7	12.81	34.95	140	2.2	2.1	0.25
	STC	X466I	26/6	10.93	34.62	120	9.4	1.7	0.39
		X467F	27/6	10.79	34.61	120	10.8	2.0	0.58
	SA	X464C	24/6	8.71	34.24	90	16.1	2.0	0.13
		X465E	23/6	8.66	34.24	100	16.0	1.7	0.12
Spring	ST	X479H	19/10	13.61	35.26	80	2.8	2.5	0.87
		X480H	17/10	13.22	35.18	30	3.2	1.6	0.86
	STC	X477F	16/10	10.81	34.69	55	5.2	0.6	3.42
		X478F	15/10	10.94	34.69	55	5.2	1.0	2.49
	SA	X475J	12/10	8.00	34.33	55	16.6	3.2	0.19
		X476J	11/10	8.30	34.32	50	16.8	3.2	0.19

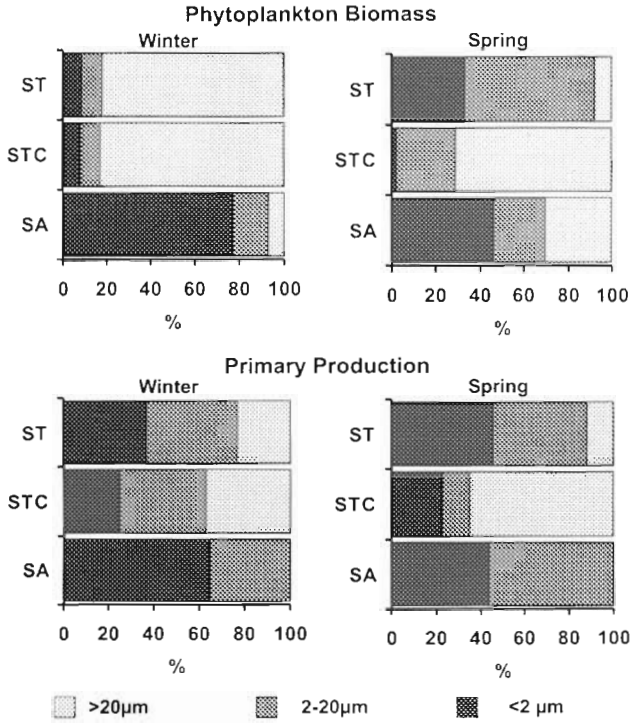

Fig. 2. Contribution to total phytoplankton biomass and primary production of the <2 µm, 2 to 20 µm and >20 µm size fractions at 10 m. Data are averaged for each of the paired stations

numbers ranging from 7.5 to 12.0 × 10^5 cells ml^{-1}. Heterotrophic bacterial production was also greatest in spring. In winter, bacterial production ranged from 0.02 to 0.10 µg C l^{-1} h^{-1} with greatest production occurring in SA waters and least production in STC waters. In spring, however, the lowest production was recorded in SA waters at 0.05 µg C l^{-1} h^{-1} compared to a maximum of 0.7 µg C l^{-1} h^{-1} in STC waters.

The ratio of bacterial carbon to phytoplankton carbon was variable between water masses and seasons. In SA waters in winter bacteria dominated; however, in spring bacteria and phytoplankton had a similar biomass (Table 2). In the STC phytoplankton dominated in both seasons, whereas in ST waters phytoplankton dominated biomass in winter but not in spring (Table 2).

The relationship between bacterial production and primary production was highly variable both between water masses and between seasons. In winter in the SA waters bacterial production was greater than primary production, but in STC waters bacterial production represented only a small proportion of primary production (Table 2). In spring in STC waters the proportion increased, in contrast to the ST waters where the proportion decreased.

The biomass (as carbon) of microzooplankton (heterotrophic flagellates and ciliates) increased between the winter and spring (Table 3). Little difference was observed between water types. The composition of microzooplankton also changed between seasons with the proportion of the total carbon contributed by heterotrophic flagellates increasing in each water type in spring. The proportion of heterotrophic flagellates increased in spring (Table 3). Overall the larger 720 µm heterophic dinoflagellates contributed very little biomass to the total microzooplankton biomass (Chang & Gall 1998).

The grazing pressure exerted by the microzooplankton on different size fractions of phytoplankton also varied between seasons and water masses. In both seasons in STC waters the contribution of picophytoplankton to the microzooplankton algal diet was 13% or less (Table 3). In contrast, in SA and ST waters, the proportion of picophytoplankton in the microzooplankton algal diet ranged from 26 to 70%. A reduction in the

Table 2. Bacterial parameters for paired stations in each water mass at 10 m. Order of the station numbers is the same as in Table 1. –: no data

Season	Water type	Bacterial biomass (mg C m^{-3})	Bacteria C/phytoplankton C	Bacterial production as % primary production
Winter	ST	6.7	0.3	47
		4.9	0.5	–
	STC	7.4	0.3	5
		6.8	0.3	6
	SA	8.9	1.6	178
		9.7	1.6	101
Spring	ST	24.7	0.8	15
		24.5	1.9	14
	STC	19.3	0.3	36
		23.1	0.2	47
	SA	14.7	0.9	14
		14.7	0.9	43

Table 3. Microzooplankton parameters for each station in each water mass at 10 m. Order of the station numbers is the same as in Table 1. –: no data

Season	Water type	Microzooplankton biomass (mg C m^{-3})	Heterotrophic flagellate carbon as % of microzooplankton carbon	<2 µm size fraction phytoplankton as % of phytoplankton grazed	% daily primary production grazed	Bacteria as % of total carbon grazed
Winter	ST	1.6	50	56	–	–
		1.9	77	38	117	–
	STC	1.1	52	6	119	–
		1.0	44	13	–	–
	SA	1.0	14	70	71	–
		1.1	46	45	121	–
Spring	ST	2.1	–	49	74	62
		9.1	88	47	82	71
	STC	5.4	63	10	100	21
		6.4	–	10	126	26
	SA	1.7	66	36	41	47
		7.9	89	26	126	–

proportion of picophytoplankton consumed in the SA waters was observed between winter and spring (Table 3).

The proportion of the primary production grazed by the microzooplankton population was high in all water masses and both seasons. In winter, results for all but one SA station showed grazing to be greater than primary production (Table 3). A similar result was observed in spring in STC and SA waters; however, in ST waters, growth of phytoplankton was greater than grazing (Table 3). The grazing impact on picophytoplankton ranged from 13 to 75% of standing stock and 27 to 297% of picophytoplankton production.

DISCUSSION

In the STC region to the east of New Zealand the microbial food web plays an important role in food web structure and energy transfer. In SA waters in both seasons and in ST waters in spring the microbial food web was the dominant pathway for carbon and energy flow. In comparison, in STC waters in both seasons and in ST waters in winter the phytoplankton population was dominated by the large >20 µm phytoplankton, suggesting that the microbial food web was less important. The composition of the phytoplankton population is important in determining food web structure and energy flows.

Phytoplankton

In conjunction with differences in total phytoplankton biomass there were distinct differences in the composition of the phytoplankton populations between water types and seasons (Fig 2). The domination of larger phytoplankton in STC waters is probably the result of the potential for an intermittent supply of macronutrients from SA waters and micronutrients from ST waters and/or the New Zealand land mass (Bradford-Grieve et al. 1997). The observations of Froneman & Perissinotto (1996a) south of South Africa in winter (June) showed that picophytoplankton contributed 38 to 54% of phytoplankton biomass in STC waters, in contrast with the 1 to 8% in early winter and spring east of New Zealand. In ST waters there was a substantial change in the composition of the phytoplankton population at 10 m between winter and spring, with larger cells dominating during winter. In spring, however, the picophytoplankton and <20 µm fraction increased in importance, with the <20 µm fraction dominating both biomass and primary production. In contrast, in macronutrient-rich SA waters, the picophytoplankton population consistently dominated both biomass and production. The dominance of picophytoplankton in SA waters may be a result of their capacity for growth under micronutrient limitation compared to larger phytoplankton as suggested by Banse (1996) for SA waters and Miller et al. (1991) for the subarctic Pacific. This hypothesis is also consistent with the observation of Hawes et al. (1997), who noted the low quantum efficiency of photosynthesis in late summer in SA waters in this region and suggested it was linked to micronutrient stress. Frost (1991) suggested that the factors resulting in phytoplankton populations being dominated by small cells in high nutrient, low chl *a* systems may be more complex, with an interaction occurring between grazer control of the phytoplankton population and the role of Fe in controlling a phytoplankton assemblage in which small-celled phytoplankton are favoured.

The composition of the phytoplankton population within the different size fractions may also be nutritionally important. The picophytoplankton contributed a different proportion of the total biomass in each water type, and the composition of the picophytoplankton population changed substantially and in a similar way in all water types. Prokaryotic forms contributed 100% of the picophytoplankton biomass in winter; however, in spring they contributed between 5 and 66% of the picophytoplankton biomass, with the eukaryotic population usually contributing the majority of the picophytoplankton biomass in ST and SA waters. This change in the composition does not appear to be attributable to changes in macronutrient concentrations, particularly NO_3, as suggested by Hall & Vincent (1990), as NO_3-N concentrations were above potentially limiting concentrations in all water masses in both winter and spring (Table 1). Changes in the composition of the picophytoplankton population may be important to the energy transfer from the microbial food web if, as Azam et al. (1991) suggested, the prokaryotic picophytoplankton are not digestable by metazoan herbivores.

Heterotrophic bacteria

Bacterial numbers and biomass observed in the region were similar to those in other low chl *a* waters (Cho & Azam 1990, Boehme et al. 1993, Robarts et al. 1996). In winter, bacterial biomass dominated phytoplankton biomass in SA waters with a mean ratio of bacterial C/phytoplankton C of 1.6. Bacteria also dominated at 1 station in the ST waters in spring with a ratio of 1.9. These ratios are consistent with ratios recorded in other low chl *a* waters (Fuhrman et al. 1989, Cho & Azam 1990). In the STC in both seasons and in ST waters in winter the biomass was dominated by phytoplankton at ratios of 0.2 to 0.5, similar to those recorded by Lochte et al. (1996) in the Atlantic sector of the Southern Ocean.

The importance of the bacterial populations can also be evaluated by considering bacterial production relative to primary production. In this study these proportions were highly variable. In winter in SA waters bacterial production was greater than primary production (Table 2), highlighting the importance of the bacterial population in the SA waters. The low proportion of bacterial production to primary production in the STC in winter was consistent with observations by Lochte et al. (1996), who found much lower ratios of bacterial production to primary production in frontal zones than in other waters. In spring, however, the ST waters had the lowest bacterial production/primary production ratios (Table 2).

The factors controlling bacterial numbers and production are often difficult to identify. Correlation analysis (of bacterial numbers and production against chl *a* and primary production) showed that the only significant ($p < 0.05$) correlation was between bacterial numbers and chl *a* concentrations in ST waters in spring. This suggests substrate limitation of bacterial growth did not occur widely during this study. Another approach used to evaluate factors controlling bacterial numbers and production has been suggested by Billen et al. (1990) and uses the slope of a log/log plot of bacterial biomass against bacterial production. In the present study analyses of data from each water mass in each season showed all slopes to be <0.27, well below the 0.4 to 0.55 suggested by Dufour & Torreton (1996) to indicate moderate 'bottom-up' control. This suggests that the bacterial populations in this study were potentially 'top-down' controlled by grazing pressure (Ducklow 1992). These results are consistent with those of Smith & Hall (1997) and Safi & Hall (1997), who suggested that in both seasons during this study the heterotrophic nanoflagellates were potentially food-limited, indicating that top-down grazing pressures may be limiting bacterial populations in the region. In this study the bacterial biomass was almost as great or greater than phytoplankton biomass in SA waters in both seasons and in the ST waters in spring, suggesting that the microbial food web was playing a significant role in the overall food web structure in these water masses and seasons.

Microzooplankton

Microzooplankton are considered to play a pivotal role in the transfer of microbial biomass to higher trophic levels as they are the primary grazers of bacteria and picophytoplankton (Sherr & Sherr 1983, Sanders et al. 1992, James et al. 1996) and have been estimated to consume up to 71% of daily primary production (Burkill et al. 1995). In the STC region, in contrast to the bacterial and phytoplankton biomass, the microzooplankton biomass was relatively constant across the water masses in each season. However, biomass increased from 1.0 mg C m^{-3} in winter to 6.4 mg C m^{-3} in spring. These observations contrast with those made by Boyd et al. (1995a) from the North Pacific, where microzooplankton biomass changed little between seasons and ranged from 7 to 13 mg C m^{-3}. Microzooplankton biomass in winter in the STC region was considerably lower than in the subarctic North Pacific. This may be a result of higher winter primary production due to the shallower mixed layer of 100 to 120 m maintained in winter, and in the North Pacific due to permanent halocline (Boyd et al. 1995b).

The composition of the microzooplankton population also changed between seasons. The proportion of the biomass contributed by heterotrophic nanoflagellates increased between winter and spring in all water types. The lower proportion of heterotrophic nanoflagellates in winter may be due to increased grazing pressure by ciliates, which may have also resulted in the decrease in size of the heterotrophic nanoflagellates observed (Safi & Hall 1997). These results are consistent with Boyd et al. (1995a), who also showed that the ciliate population was a larger proportion of the microzooplankton population in winter in the subarctic North Pacific. In spring the heterotrophic nanoflagellate population contributed a larger proportion of the microzooplankton population, had a larger cell size, and had higher ratios of potential prey, suggesting potential bottom-up control of this population (Safi & Hall 1997). The lower ciliate to heterotrophic nanoflagellate ratios may be a result of increased predation pressure on ciliates by the larger mesozooplankton populations in all water masses in spring (Bradford-Grieve et al. 1997).

Although microzooplankton biomass was similar between water masses, the composition of the phytoplankton in the diet varied between water masses. In ST and SA waters picophytoplankton contributed 38 to 49% and 26 to 70% of the diet, respectively, over both seasons. In STC waters, however, the picophytoplankton contributed only 1 to 13% of the total phytoplankton consumed. In the STC in both seasons over 100% of the primary production was grazed even though 37 and 65% for winter and spring, respectively, of the primary production was in the >20 µm size fraction. This suggests that contrary to the findings that microzooplankton prefer particles <20 µm (Verity et al. 1993, Froneman & Perissinotto 1996a), the microzooplankton in the convergence zone grazed a reasonable proportion of the >20 µm phytoplankton. The phytoplankton population in STC waters were dominated numerically by the diatoms *Lauderia annulata* and *Hemiaulus* sp. (Chang & Gall 1998), which have small cells that form chains. It is possible that these small-celled forms are prey items for microzooplankton (Strom & Strom 1996).

The proportion of the primary production grazed by the microzooplankton ranged from 41 to 126% of the primary production, which is bigger than the 56 to 69% for STC waters and the 76 to 81% for subantarctic waters reported by Froneman & Perissinotto (1996b) but similar to the 80 to 100% reported by Verity et al. (1993) in subarctic waters. It was only in STC waters that grazing was consistently below 100% (74 and 82%). Grazing on bacterial populations was also very high, ranging from 79 to 250% of the bacterial production with bacteria contributing between 21 and 62% of the total biomass grazed, with the proportion being consistently lower in STC waters.

When these grazing rates are considered, it must be remembered that the dilution method for assessing grazing rates of the microzooplankton is likely to overestimate grazing rates due to the exclusion of zooplankton >200 µm which are predators on microzooplankton populations. This overestimate could be considerable as copepod predation has been shown to account for over 50% of daily ciliate production (Atkinson 1996). In this study grazing pressure on the microzooplankton is likely to be high as there was an unusually small fraction of zooplankton in the 200 to 500 µm fraction and the phytoplankton met only a small fraction of the basic metabolic requirements of the >200 µm zooplankton (Bradford-Grieve et al. 1998). This suggests that microzooplankton were potentially the most important food source for the >200 µm zooplankton in early winter and spring in these water types and hence form the key link between the microbial food web and higher trophic levels.

The food web structure and phytoplankton composition of the 3 water masses in the STC region east of New Zealand can be summarised as follows: In SA waters in both seasons picophytoplankton dominated both phytoplankton biomass and primary production with bacterial biomass dominating planktonic biomass in winter with similar biomass of bacteria and phytoplankton in spring. In ST waters in winter both biomass and primary production were dominated by phytoplankton >20 µm but in spring were dominated by the <20 µm fraction. The bacterial/phytoplankton carbon ratio was low in winter and variable between stations in spring with bacteria clearly dominating at one station. In the STC in both winter and spring phytoplankton biomass was dominated by the >20 µm fraction, with the <20 µm fraction dominating primary production in winter but not in spring. The bacterial/phytoplankton carbon ratios were consistently low.

Therefore in ST waters in spring and SA waters in both seasons, the microbial food web dominated the food web structure. The major carbon flow was through the microbial food web to the microzooplankton with a very high proportion of the primary production being consumed by the microzooplankton. These results are to be expected for a potentially macronutrient-limited system in ST waters in spring and a potentially micronutrient-limited system in the SA waters (Bradford-Grieve et al. 1997). The structure of the food web in ST waters in winter and the STC in both seasons suggests that the microbial food web was not a dominant feature of these systems and it would be expected that larger zooplankton grazers would be the dominant consumers of phytoplankton biomass. Yet mesozooplankton were apparently consuming a very small proportion of the phytoplankton (Bradford-Grieve et al. 1998). In contrast microzooplankton were shown to be

consistently consuming over 100% of the primary production when not exposed to predation. This suggests that the microzooplankton population can play a pivotal role in food web structure not only in systems where the microbial food web dominates but also in systems where the larger phytoplankton dominate biomass and in some cases primary production. The dominance of the microzooplankton grazing pathway in these systems is supported by findings of Bradford-Grieve et al. (1997), who showed the basic metabolic needs of the mesozooplankton were not being met by grazing on phytoplankton.

The food web structure and size composition of the components has been shown to alter the magnitude of particle flux, and hence carbon, to the deep ocean (Michaels & Silver 1988). It has been suggested that in systems where the microbial food web dominates the system the export fluxes to the deep ocean from the upper surface mixed layer will be low due to the extensive recycling of both nutrients and carbon in the upper mixed layer. This is a result of the primary grazers being microzooplankton, which have small diffuse faecal pellets that are generally recycled in the upper mixed layer, and the dominant phytoplankton population being dominated by groups that have low sinking rates. These factors reduce the export of phytoplankton material from the upper mixed layer. This is consistent with the export fluxes measured in the SA waters in both seasons and the ST waters in spring by Nodder & Alexander (1998) during this study.

In systems where the phytoplankton population is dominated by the larger size fractions, the phytoplankton export fluxes from the upper mixed layer are generally higher (Legendre 1990, Boyd & Newton 1995) for 2 reasons. First, the larger phytoplankton sink directly out of the upper mixed layer, and second, the primary grazers are the mesozooplankton which produce faecal pellets that sink rapidly. This is what would have been expected in the STC in both seasons and ST waters in winter. However the dominance of the grazing by the microzooplankton population in these water types at the times sampled, even when the larger phytoplankton size fractions dominated, probably meant that the phytoplankton export fluxes were reduced. This is consistent with the contemporaneous pigment export fluxes reported by Nodder & Gall (1998), who showed that the pigment fluxes were less than 4% of primary production for all water types.

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LITERATURE CITED

Atkinson A (1996) Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. Mar Ecol Prog Ser 130: 85–96

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257–263

Azam F, Smith DC, Hollibaugh JT (1991) The role of the microbial loop in Antarctic pelagic ecosystems. Polar Res 10:239–243

Banse K (1996) Low seasonality of low concentrations of surface chlorophyll in the Subantarctic water ring: underwater irradiance, iron, or grazing? Prog Oceanogr 37:241–291

Billen G, Servais P, Becquevort S (1990) Dynamics of bacterioplankton in oligotrophic and autrophic aquatic environments: bottom-up or top-down control? Hydrobiologia 207: 37–42

Bloem J, Bar-Gilissen MB, Cappenberg TE (1986) Fixation counting and manipulation of heterotrophic nanoflagellates. Appl Environ Microbiol 52:1266–1272

Boehme J, Friseher ME, Hang SC, Kellogg CA, Pichard S, Rose JB, Steinway C, Paul JH (1993) Viruses, bacterioplankton, and phytoplankton in the south-eastern Gulf of Mexico: distribution and contribution to oceanic DNA pools. Mar Ecol Prog Ser 97:1–10

Boyd P, Newton P (1995) Evidence of the potential influence of planktonic community structure on the interannual variability of particulate organic carbon flux. Deep-Sea Res 42:619–639

Boyd PW, Strom S, Whitney FA, Doherty S, Wen ME, Harrison PJ, Wong CS, Varela DE (1995a) The NE subarctic Pacific in winter. I. Biological standing stocks. Mar Ecol Prog Ser 128:11–24

Boyd PW, Whitney FA, Harrison PJ, Wong CS (1995b) The NE subarctic Pacific in winter. II. Biological rate processes. Mar Ecol Prog Ser 128:25–34

Bradford-Grieve JM, Chang FH, Gall M, Pickmere S, Richards F (1997) Size-fractionated phytoplankton standing stocks and primary production during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. NZ J Mar Freshwat Res 31:201–224

Bradford-Grieve J, Murdoch R, James M, Oliver M, McLeod J (1998) Mesozooplankton biomass, composition, and potential grazing pressure on phytoplankton during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. Deep-Sea Res 45:1709–1737

Burkill PH, Edwards ES, Sleigh MA (1995) Microzooplankton and their role in controlling phytoplankton growth in the marginal ice zone of the Bellingshausen Sea. Deep-Sea Res 42:1277–1290

Caron DA (1983) Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy and comparison with other procedures. Appl Environ Microbiol 46:491–498

Chang FH (1988) Distribution, abundance and size composition of phytoplankton off Westland, New Zealand; February 1982. NZ J Mar Freshwat Res 22:345–367

Chang FH, Gall M (1998) Phytoplankton assemblages and photosynthetic pigments in winter and spring the subtrop-

ical convergence region near New Zealand. NZ J Mar Freshwat Res 32:515–530
Cho BC, Azam F (1990) Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. Mar Ecol Prog Ser 63:253–259
Crooke WM, Simpson WR (1971) Determinations of ammonium in Kjeldahl digest of crops by an automated procedure. J Sci Food Agric 22:9–10
Currie KI, Hunter KA (1998) Surface water carbon dioxide in the waters associated with the Subtropical Convergence, east of New Zealand. Deep-Sea Res 45:1765–1777
Cushing DH (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. J Plankton Res 11:1–13
Ducklow HW (1992) Factors regulating bottom up control of bacterial biomass in open ocean plankton communities. Arch Hydrobiol Beih Ergebn Limnol 37:207–217
Dufour PH, Torreton JP (1996) Bottom-up and top-down control of bacterioplankton from eutrophic to oligotrophic sites in the tropical northeastern Atlantic Ocean. Deep-Sea Res 43:1305–1320
Eppley RW, Peterson BJ (1979) Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282:677–680
Fortier L, Le Fevre J, Legendre L (1994) Export of bionic carbon to fish and to the deep ocean: the role of large planktonic microphages. J Plankton Res 16:809–839
Froneman PW, Perissinotto R (1996a) Microzooplankton grazing and protoplankton community structure in the South Atlantic and in the Atlantic sector of the Southern Ocean. Deep-Sea Res 43:703–721
Froneman PW, Perissinotto R (1996b) Structure and grazing of the microzooplankton communities of the Subtropical Convergence and a warm-core eddy in the Atlantic sector of the Southern Ocean. Mar Ecol Prog Ser 135:237–245
Frost BW (1991) The role of grazing in nutrient-rich areas of the open sea. Limnol Oceanogr 6:1616–1630
Fuhrman JA, Azam F (1982) Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. Mar Biol 66:109–120
Fuhrman JA, Sleeter TD, Carlson CA, Proctor LM (1989) Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. Mar Ecol Prog Ser 57:207–217
Gonzalez HE, Gonzalez SR, Brummer GJA (1994) Short-term sedimentation pattern of zooplankton, faeces and microplankton at a permanent station in the Bjoernafjorden (Norway) during April-May 1992. Mar Ecol Prog Ser 105: 31–45
Hall JA (1991) Long-term preservation of picophytoplankton for counting by fluorescence microscopy. Br Phycol J 26: 169–174
Hall JA, Vincent WF (1990) Vertical and horizontal strucutre in the picoplankton communities of a coastal upwelling system. Mar Biol 106:251–261
Hawes I, Gall M, Weatherhead M (1997) Photosynthetic parameters in water masses in the vicinity of the Chatham Rise, South Pacific Ocean, during late summer. NZ J Mar Freshwat Res 31:25–38
Hobbie JE, Daily RJ, Jasper S (1977) Use of nuclepore filters for counting bacteria by fluorescence microscopy. Appl Environ Microbiol 33:1225–1228
James MR, Hall JA (1998) Microzooplankton grazing in different water masses associated with the subtropical convergence round the South Island, New Zealand. Deep-Sea Res 45:1689–1707
James MR, Hall JA, Barrett DP (1996) Grazing by protozoa in marine coastal and oceanic ecosystems off New Zealand. NZ J Mar Freshwat Res 30:313–324
Joint IR (1986) Physiological ecology of picoplankton in various oceanographic provinces. Can Bull Fish Aquat Sci 214: 287–309
Landry MR, Hassett RP (1982) Estimating the grazing impact of marine microzooplankton. Mar Biol 67:283–288
Lee S, Fuhrman JA (1987) Relationships between biovolume and biomass of naturally derived marine bacterioplankton. Appl Environ Microbiol 53:1298–1303
Legendre L (1990) The significance of microalgal blooms for fisheries and for the export of particulate carbon in oceans. J Plankton Res 12:681–699
Legendre L, Rassoulzadegan F (1995) Plankton and nutrient dynamics in marine waters. Ophelia 41:153–172
Li WKW, Dickie PM, Irwin BD, Wood AM (1992) Biomass of bacteria, cyanobacteria, prochlorophyte and photosynthetic eukaryotes in the Sargasso Sea. Deep-Sea Res 39: 501–519
Lochte K, Bjørnsen PK, Giesenhagen H, Weber A (1996) Bacterial standing stock and production and their relation to phytoplankton in the Southern Ocean. Deep-Sea Res 44: 321–340
Longhurst A (1995) Seasonal cycles of pelagic production and consumption. Prog Oceanogr 36:77–167
Michaels AF, Silver MW (1988) Primary production, sinking fluxes and the microbial food web. Deep-Sea Res 35: 473–490
Miller CB, Frost BW, Wheeler PA, Landry MR, Welschmeyer N, Powell TM (1991) Ecological dynamics in the subarctic Pacific, a possibly iron-limited ecosystem. Limnol Oceanogr 36:1600–1615
Murphy PP, Peely RA, Gammon RH, Harrison DE, Kimberly CK, Waterman LS (1991) Assessment of air-sea exchange of CO_2 in the South Pacific during austral autumn. J Geophys Res 96:20455–20465
Nodder SD, Alexander BL (1998) Sources of variability in geographical and seasonal differences in particulate fluxes from short-term sediment trap deployments, east of New Zealand. Deep-Sea Res 45:1739–1764
Nodder SD, Gall M (1998) Pigment fluxes within the subtropical convergence region east of New Zealand: relationships to planktonic community structure. NZ J Mar Freshwat Res 32:441–465
Nydahl F (1976) On the optimum conditions for the reduction of nitrate to nitrite by cadmium. Talanta 23:349–357
Putt M, Stoecker DK (1989) An experimentally determined carbon: volume ratio for marine (oligotrichous) from estuarine and coastal waters. Limnol Oceangr 34:1097–1103
Robarts RD, Wicks RJ, Sephton LM (1986) Spatial and temporal variations in bacterial macromolecule labelling with [methyl-^{3}H] thymidine in a hypertrophic lake. Appl Environ Microbiol 52:1368–1373
Robarts RD, Zohary T, Waiser J, Yacobi YZ (1996) Bacterial abundance, biomass, and production in relation to phytoplankton biomass in the Levantine Basin of the southeastern Mediterranean Sea. Mar Ecol Prog Ser 137:273–281
Safi K, Hall JA (1997) Factors influencing autotrophic and heterotrophic nanoflagellate abundance in five water masses surrounding New Zealand. NZ J Mar Freshwat Res 31:51–60
Sanders RW, Porter KG, Bennett SI, De Biase AE (1989) Seasonal patterns of bacterivory by flagellates, ciliates, rotifers and cladocerans in a freshwater planktonic community. Limnol Oceanogr 34:673–687
Sanders RW, Caron DA, Berninger VG (1992) Relationships between bacteria and heterotrophic nanoplankton in

marine and freshwaters: an inter-ecosystem comparison. Mar Ecol Prog Ser 86:1-14
Sedwick PN, Edwards PR, Mackey DJ, Griffiths FB, Parslow JS (1997) Iron and manganese in surface waters of the Australian subantarctic region. Deep-Sea Res 44:1239–1253
Sherr EB, Sherr BF (1983) Double staining epifluorescence technique to assess frequency of dividing cells and bacterivory in natural populations of heterotrophic microprotozoa. Appl Environ Microbiol 46:1388–1393
Small LFS, Fowler SW, Unlu MY (1979) Sinking rates of natural copepods faecal pellets. Mar Biol 51:233–241
Smith JD, Milne PJ (1981) Spectrophotometric determination of silicate in natural waters by formation of a-molybdosilic acid and reduction with a tin(IV)-ascorbic acid-oxalic acid mixture. Anal Chim Acta 123:263–270
Smith R, Hall J (1997) Bacterial abundance and production in different water masses around South Island, New Zealand. NZ J Mar Freshwat Res 31:515–524
Søndergaard M, Jensen LM, Ærtejerg G (1991) Picoalgae in Danish coastal waters during summer stratification. Mar Ecol Prog Ser 79:139–149
Strickland JD, Parsons TR (1972) A practical handbook of seawater analysis. Bull Fish Res Board Can 167
Strom SL, Strom MW (1996) Microplankton growth, grazing and community structure in the northern Gulf of Mexico. Mar Ecol Prog Ser 130:229–240
Takahaski T, Azevedo AEG (1982) The ocean as a CO_2 reservoir In: Reck RS, Hummel JR (eds) Interpretation of climate and photochemical models, ozone and temperature measurements. American Institute of Physics, New York, p 83–109
Verity PG, Stoecker DK, Sieracki ME, Nelson JR (1993) Grazing, growth and mortality of microzooplankton during the 1989 North Atlantic spring bloom at 47 degree N, 18 degree W. Deep-Sea Res 40:1793–1814
Vincent WF, Howard-Williams C, Tildesley P, Butler E (1991) Distribution and biological properties of oceanic water masses around the South Island of New Zealand. NZ J Mar Freshwat Res 25:21–42
Wicks RJ, Robarts RD (1987) The extraction and purification of DNA labelled with [methy-^{3}H] thymidine in aquatic bacteria] production studies. J Plankton Res 9:1167–1181

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