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Ecology of periphyton in a meltwater stream ecosystem in the maritime Antarctic

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Abstract: The ecology of two meltwater streams on King George Island, Ornithologists Creek (with penguin rookeries close to its lower reaches) and Petrified Forest Creek (a highly oligotrophic system), was studied during the 1996–97 summer season. To estimate seasonal productivity of the periphyton and to establish which environmental parameters influenced periphyton growth most strongly, two types of artificial substrata (fibreglass nets – ash-free dry weight (AFDW), and microscope slides – Chlorophyll *a* (Chl *a*)) were tested *in situ*. Thus relative periphyton productivity (RPP) reflects algal colonization and growth as well as losses due to cell mortality and abrasive action of moving sediments. The Petrified Forest Creek was more productive (AFDW = 108.63 µg cm^{-2} d^{-1}, Chl *a* = 0.35 µg g cm^{-2} d^{-1}) than the Ornithologists Creek (AFDW = 69.90 µg cm^{-2} d^{-1}, Chl *a* = 0.26 µg cm^{-2} d^{-1}). RPP differed both along the streams, and during the season. Significant positive or negative relationships (generalized linear models) were found between RPP and streamwater 'physico-chemical parameters' and 'geomorphological-geographical characteristics' of the streams' catchments. In addition, in the lower reaches of both streams almost no active colonization or growth was recorded. In the Petrified Forest Creek, the periphyton biomass was so high that mainly passive organic matter deposition occurred. By contrast, in the lower reach of Ornithologists Creek, periphyton colonization and growth was around zero, being negatively influenced by penguin excrement. Ornithologists Creek was richer in nutrients (DIN, DRP), which also fluctuated more widely along its length and throughout the season, than in the Petrified Forest Creek. Parameters associated with the inorganic carbon cycle of the streamwater reflect higher RPP in Petrified Forest Creek. Moreover, RPP was higher in stream reaches with higher amounts of gravel boulders on the bottom.

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Key words: environmental parameters, King George Island, meltwater streams, periphyton productivity, South Shetland Islands

Introduction

Antarctic streams are responsive to climate variations in a similar way to other global aquatic systems. In alpine and polar regions these shifts influence the discharge of melting glaciers and snowmelt run-off within their watersheds. As a result, the stream waters carry disparate loads of silt and nutrients liberated by varied ice and soil melt.

Contrary to expectations, in general, the Antarctic mainland has been demonstrating marked cooling. In McMurdo Dry Valleys the mean temperatures have decreased by 0.7°C over the last 35 years (Doran *et al.* 2002). This change is likely to be regional in extent, as in tandem with the global trends, the sub-Antarctic islands and the Antarctic Peninsula and associated island groups have been undergoing the fastest warming in the Southern Hemisphere (e.g. King 1994, Thomas & Dieckmann 2002). Thus, on Signy Island, South Orkney Islands, a 35% reduction in ice cover has been observed over the last 40 years, which has caused major changes in the island's hydrology (Smith 1990).

Nutrients measured in these glacial- and snowmelt-derived waters, well identifiable with respect to their source, are indicative of the subsequent transfer of mass and energy (Howard-Williams *et al.* 1986). Microbial mats inhabit most of these streambeds where cyanobacteria and eukaryotic algae predominate (Hawes 1989, Hawes & Brazier 1991, Vincent *et al.* 1993a). These mats persist, in spite of highly variable seasonal discharge, temperature and water chemistry, all of which are important factors in determining the type of mats, microbial assemblage and biomass. No substantial grazing of algae has been reported for these streams (Vincent & Howard-Williams 1986, Howard-Williams *et al.* 1989b, Hawes 1989).

The majority of limnological studies of flowing waters in Antarctica have examined species diversity, nutrient dynamics and ecophysiology of the periphyton and have been undertaken in continental Antarctica (e.g. Downes *et al.* 1986, Howard-Williams *et al.* 1989a, Vincent & Howard-Williams 1989, Vincent *et al.* 1993a, 1993b). Lotic systems of maritime Antarctica, as defined by Smith (1990), have received comparatively less attention (Hawes & Brazier 1991, Caulkett & Ellis-Evans 1997, Pizarro &

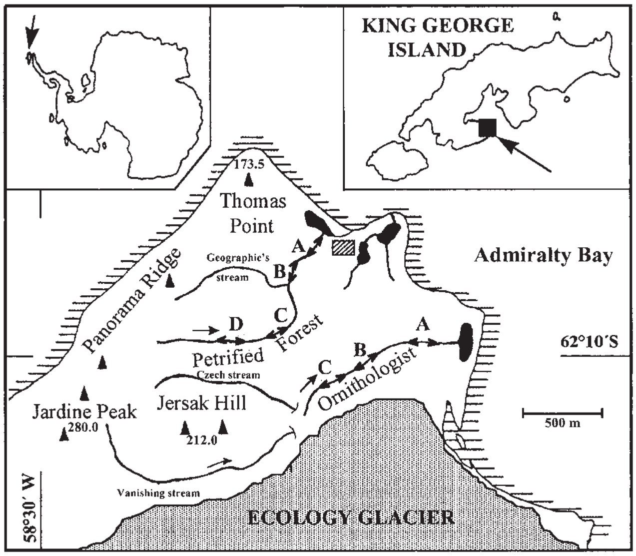

Fig. 1. Map of region near the H. Arctowski Polish Antarctic research station, Admiralty Bay, King George Island. Aquatic habitats of this deglaciated landscape are mainly temporary melt-water streams, and shallow pools and lakes. Two streams, Ornithologists Creek and the Petrified Forest Creek were divided into 3 and 4 reaches (A–C and A–D), respectively for sampling.

Vinocur 2000), with the main objective often focussed on algal diversity (Luscinska & Kyc 1993, Kawecka & Olech 1993, Pizarro *et al.* 1996, Izaguirre & Pizarro 2000).

The Maritime Antarctic experiences a much milder climatic regime in comparison with the continental mainland. At Admiralty Bay, King George Island, the mean annual temperature for 1978–87 was -1.8°C and the mean summer (January) and winter (July) temperatures were +2.3°C and -7.1°C, respectively (Rakusa-Suszczewski 1992). The region is subject to high rain or snowfall with monthly maxima > 145 mm and minima as low as 10.9 mm (Marsz & Rakusa-Suszczewski 1987). Precipitation is abundant mainly in summer (December–April), the winter season (June–August) usually being much drier. However, owing to strong winds, large amounts of snow accumulate in streambeds and depressions. Melt from this provides for a high flow rate in streams running down the deglaciated landscape during the first few weeks of summer. However, they differ markedly in chemistry, periphyton diversity and productivity.

Our knowledge of these maritime Antarctic lotic ecosystems, and their responsiveness to climate variability, is still inadequate. It is anticipated that these streams will provide an indication of the changes that may occur in continental Antarctic streams should the climate become warmer. This paper documents two contrasting meltwater streams at King George Island and reports on their nutrient status and in-stream productivity.

Study area

King George Island is part of the Maritime Antarctic archipelago of the South Shetland Islands with > 90% of its volcanic bedrock covered by ice. In Admiralty Bay, where the H. Arctowski Polish Antarctic station is located (Fig. 1), the aquatic habitats are represented by episodically wet ground adjacent to snow-banks, small to intermediate snow-fed (meltwater) streams, and glacial rivulets which run continuously during the summer season.

The meltwater streams are the most common and diverse of the freshwater ecosystems found there. They are usually less than 1500 m long, 10–300 cm wide and 5–70 cm deep, often forming shallow pools along their course and their beds are lined with gravel and sand. They begin as seepages along a spring thaw-line, 40–60 m a.s.l., descend toward the sea and flow over and under melting snowfields, whilst receiving more water from tributaries.

Barren, deglaciated landscapes form the upper stream catchments. However, at the melting snow front, these rocky slopes already show a sparse moss and lichen cover, but no higher plants. In their lower catchments, streams cascade down the steeper slopes forming chutes and falls. Near the seashore, some streams travel through penguin colonies and these areas are able to support extensive moss carpets and scattered cushions of vascular plants.

The length of streams changes during the summer, and as the snow continues to melt during the season their lengths become shorter. Later, when all the snow has melted, water comes from supra-permafrost sources in the active layer of the soil. The mean seasonal flow rate, measured in the meltwater of 'Vanishing Creek' in the vicinity of Arctowski station was 50 l s^{-1}, range 25–60 l s^{-1} (Kozik 1982). The water was generally clear and the stream-bed supported a rich periphyton growth.

Characteristics of two selected streams

Two visually distinct meltwater streams, Ornithologists Creek with penguin rookeries nearby in its lower part and the highly oligotrophic Petrified Forest Creek, were chosen for the study (Fig. 1) during the 1996–97 summer season. Ornithologists Creek was divided into three reaches and Petrified Forest Creek into four reaches. Physical and chemical characteristics, and relative periphyton productivity were measured in these reaches.

The following measurements of geomorphological and geographical characteristics of the streams and catchments were also made:

angle of valley: 1. 100°–120°, 2. 120°–140°, 3. 140°–160°;

slopes: 1. 0.08°–0.1°, 2. 0.04°–0.08°, 3. 0°–0.04°;

granulation of stream bed: 1. sand and soft gravel, 2. gravel and rocks;

stream slope: 1. 0.08°–0.1°, 2. 0.04°–0.08°, 3. 0°–0.04°;

stream orientation: 1. < 90°, 2. 90°–140°, 3. > 140°;

elevation: 1. > 60 m, 2. 30–59 m, 3. 0–30 m; and

stream bed width: 1. < 1.5 m, 2. > 1.5 m.

They were determined by a theodolite and/or estimated from the map (Fig. 1). Parameters were arranged according to their provision of conditions favourable for periphyton growth; parameters ranked number one are less suitable, while three represents the best conditions for growth. Ornithologists Creek has a more open valley, a lower stream slope, is situated at a lower elevation, and the width of the stream body is greater. In contrast the Petrified Forest Creek has a more granulated stream bottom and is oriented more to the north.

The selection of the reaches was done at the beginning of December 1996 when the sections became free of snow and the stream was already crossing the snowfields. It was done with respect to the reaches' slope, rate of flow and snow cover. Subsequently, all snow patches melted and the length of each stream shortened.

Ornithologists Creek originated from a snow patch spread in a wide valley. It ran through a number of pools and fell into a lake close to the shore of Admiralty Bay. Its reach A was located on a raised beach, B was in a deep valley and C was lying within a wide, open valley. The lower part of Ornithologists Creek traversed a gentoo penguin (*Pygoscelis papua*) colony. Skuas (*Catharacta* spp.) also nested along the stream. In early spring the stream was up to 1120 m long, but during the season it shortened to 720 m. Reach A was 68–94 m distant from the lake's shore, B was 338–353 m, and C was 695–713 m.

Petrified Forest Creek was a small watercourse flowing from several snow patches. Initially, it ran down a wide, open valley over a rugged rocky terrain, then cut into a deeper valley with riffles and falls and finally flowed into another small lake situated close to the shore of Admiralty Bay. Only skuas nested in the stream catchment area. At the beginning of December 1996, the stream was 1330 m long; at mid-season it shortened to 920 m. Reach A was at a distance of 85–106 m, B at 245–263 m, C at 461–476 m, and D at 878–885 m from the lake's shore. From late March to early May this stream dried up and froze. All other streams would dry up and freeze towards the end of the summer.

Field and laboratory procedures

Sampling procedure

Water samples for chemical analyses were collected at the beginning and at the end of periphyton productivity measurement reaches. Samples were collected between 10:00 and 12:00 every ten days from 21 December 1997–3 March 1997 for the Ornithologists Creek, and from 20 December 1996–10 March 1997 for the Petrified Forest Creek.

Two acid-washed polythene bottles (250 ml) were filled with water. One of the two bottles was filtered through a pre-rinsed Whatman GF/C filter paper and then frozen for transportation to the Czech Republic. Water samples in the second bottle were used directly at the field site for measurements of pH, conductivity (Kombibox WTE, Weilheim, CB 570) and alkalinity (titration to endpoint, indicated by Taschiro indicator). The CO_2, HCO_3^-, $CO_3^=$ and total dissolved inorganic carbon concentrations (TDIC) were calculated from the measurements of alkalinity, pH and temperature by using standard equations (Stumm & Morgan 1981). A digital thermometer 'Yokogawa' (accuracy 0.1°C), placed about 5 cm below the water surface, measured stream temperature concurrently with water sampling.

Periphyton productivity

Relative periphyton productivity (RPP), determined as ash-free dry weight (AFDW) along the streams, was measured from 17 December 1996–7 March 1997. The stream reaches were lined with 30 pre-weighed fibreglass net strips, 10 cm x 10 cm, cut from commercial grade window-screen material (mesh size 1 x 1 mm). Each net was fixed to the streambed by two U-shaped wires. After 22, 40, 60 and 80 day periods of exposure (i.e. on 8 January, 26 January, 15 February and 7 March) the nets were collected, and oven dried at 85°C in the field laboratory. The nets, now covered with dry algal biomass and fine mineral sediment, were then weighed and ashed at 550°C in a crucible allowing the AFDW and mineral components to be calculated from the weight differences.

In addition to nets, in each reach 20 rubber 'plugs', holding four microscope slides, were fixed to the stream-bed by a vertical wire. One slide from each plug was collected for Chlorophyll *a* (Chl *a*) measurements after 24, 40, 60 and 80 days. Thirty nets and 80 slides were places in each section, but only 5–12 nets and 8–9 slides were recovered at the sampling days. The erosive force of the stream has damaged the rest of the nets and slides.

The algal biomass was washed off the slides with water, helped by a small brush, into a funnel lined with Whatman GF/C filter paper. Filters with algal suspension were then covered with 90% methanol (Hansson 1988) and ground in a frictional mortar. The extract was transferred into a vial and kept tightly capped in a dark refrigerator overnight. The methanol extraction was then adjusted to a set volume, pooled and centrifuged for 15 min at 6000 RPM to remove fine sediment. Absorbance was measured by a spectrophotometer at 665 and 750 nm before and after acidification with 10^{-3}M HCl for 1 h. Concentrations of

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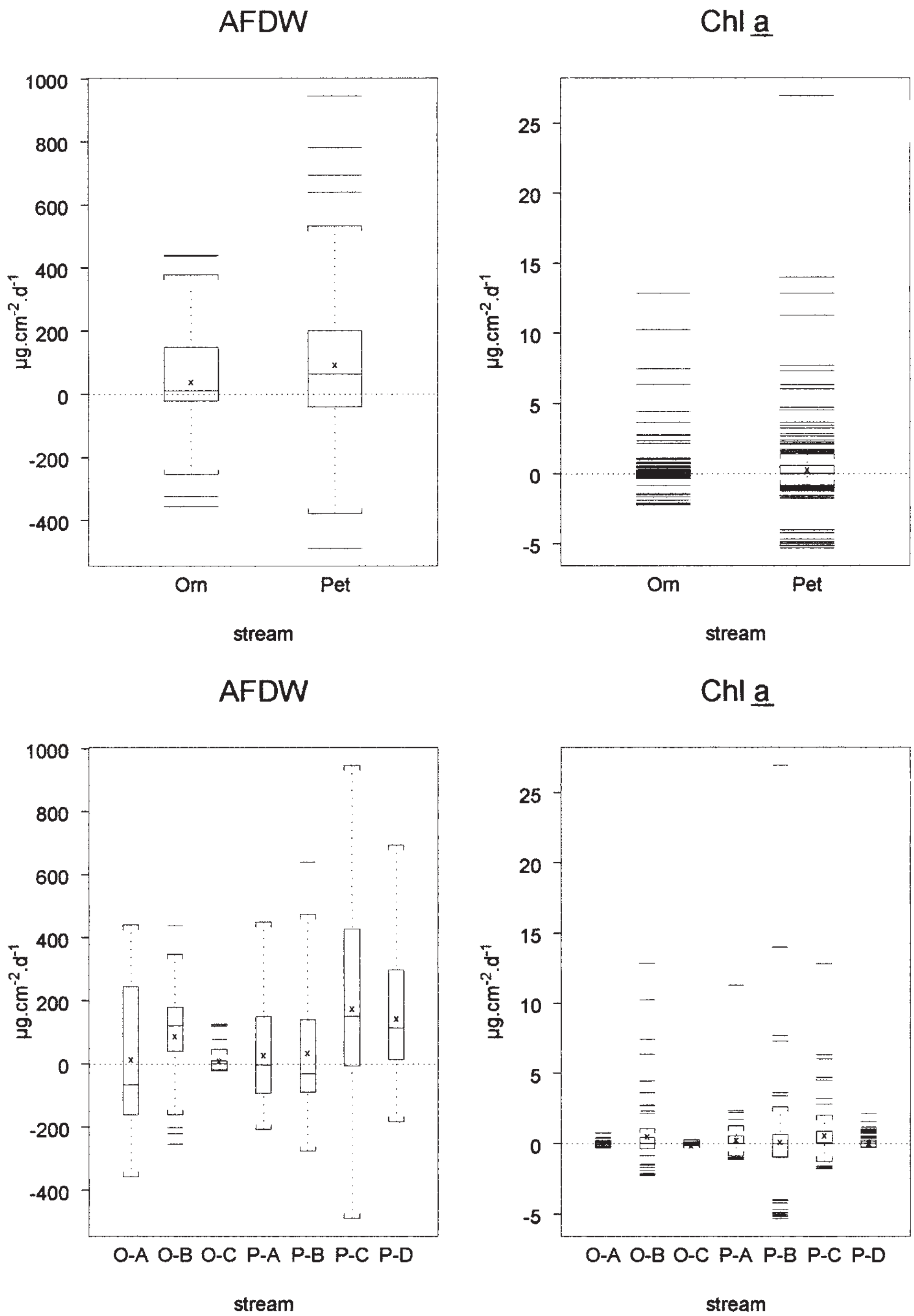

Fig. 2. Seasonal values of relative periphyton productivity, along the Ornithologists Creek (Orn) and its three reaches. O-A: 66–88 m, $n = 25$ and $n = 57$; O-B: 336–358 m, $n = 30$ and $n = 70$; O-C: 695–715 m; $n = 30$ and $n = 66$ and the Petrified Forest Creek (Pet) and its four reaches; P-A: 85–105 m, $n = 28$ and $n = 59$; P-B: 245–265 m, $n = 29$ and $n = 57$; P-C: 461–481 m, $n = 26$ and $n = 69$; P-D: 878–898 m, $n = 26$ and $n = 71$ streams in 1996–97 summer season, measured as AFDW on fibreglass nets ($n = 85$ and $n = 109$, respectively) and as Chl *a* concentration on microscope slides ($n = 193$ and $n = 256$, respectively). Graphs show the upper and lower quartile (box margins), mean value (x), median (black stripe inside the box), upper and lower extreme - nearest values not beyond a standard span (1.5x inter quartile range) from the quartiles (whiskers) and outliers (black lines beyond whiskers).

Chl *a* and phaeophytin were then calculated using standard equations of Marker *et al.* (1980).

RPP (AFDW and Chl *a*) was then calculated as the difference between consecutive measured values, divided by the number of incubation days in the streams. This productivity reflects algal colonisation and growth, as well as losses due to cell mortality and abrasive action of the moving sediments. As expected, there were differences in

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attached biomass per unit area between the fibreglass nets and glass slides. Fibreglass nets trapped the drifting algae, which increased the rate of colonization and growth. Colonization of slides took longer but less dead organic matter and mineral suspension became attached.

Water chemistry

Phosphorus (as dissolved reactive phosphorus, DRP) and nitrogen (as dissolved inorganic nitrogen, DIN) were determined using a Flow Injection Analyser (FIA, Tecator, Sweden; Ruzicka & Hansen 1981). DRP (PO_4–P) was analysed by reaction with ammonium molybdate and reduction by stannous chloride to phosphomolybdenum blue (Proctor & Hood 1954, Application note AN 60/83 Tecator). The detection limit for DRP was 5 µg l^{-1}. Nitrate–nitrogen ($NO_3^{=}$–N) was analysed by reaction with sulphonamide (Application note ASN 62-01/83) and ammonium–nitrogen (NH_4^+–N) by the gas diffusion method (Karlberg & Twengstrom 1983, Application note ASN 50-0187 Tecator). The detection limit for NH_4^+–N was 10 and for $NO_3^{=}$–N was 3 µg l^{-1}. The sum of nitrate- and ammonium–nitrogen gave values of DIN (dissolved inorganic nitrogen).

Statistical analyses

Generalized Linear Models (GLM, McCullagh & Nelder 1989) were used for evaluation of the influence of multiple factors on RPP in both streams together, and separately, using the S-plus software package (Statistical Sciences 1995a, 1995b). Significance of GLM was tested using an F-test (Zar 1984, Sokal & Rohlf 1995). F and P values of all significant predictors originated from basic modelling procedures (models with only one predictor) and also from simplified models (forward stepwise selection of variables). Seasonal curves of RPP productivity were visualised using a robust local smoother (Lowess function) again using the S-plus software package (Statistical Sciences 1995a, 1995b).

Results

Relative Periphyton Productivity

The AFDW and Chl *a* mean seasonal values of the Ornithologists Creek were 69.90 µg cm^{-2} d^{-1} (n = 87) and 0.26 µg cm^{-2} d^{-1} (n = 193), respectively. AFDW values were generally higher and more uniform than those for Chl *a* values, which also fluctuated widely (Fig. 2). The Petrified Forest Creek was more productive than the Ornithologists Creek, with a mean seasonal AFDW 108.63 µg cm^{-2} d^{-1} (n = 112) and Chl *a* value of 0.35 µg cm^{-2} d^{-1} (n = 256).

Figure 2 shows mean seasonal dynamics of RPP measured in each stream reach. In the Ornithologists Creek, the mean reach values were: A = 74.24, B = 104.33 C = 31.14 µg cm^{-2} d^{-1} (for AFDW), and A = 0.04, B = 0.71, C = 0.02 µg cm^{-2} d^{-1} (for Chl *a*), with the AFDW:Chl *a* correlation coefficient r = 0.83. In the Petrified Forest Creek, the sectional values between AFDW and Chl *a* were rather incongruous: A = 70.55, B = 74.90, C = 141.97, D = 147.10 µg cm^{-2} d^{-1} (AFDW), and A= 0.35, B = 0.18, C = 0.70, D = 0.16 µg cm^{-2} d^{-1} (Chl *a*), with r = 0.33.

Seasonal dynamics of RPP (AFDW and Chl *a*) in both stream reaches are also shown in Fig. 3. In the Ornithologists Creek the productivity slightly decreased upstream from reach A to C (AFDW more, and Chl *a* less notably). In the Petrified Forest Creek (Fig. 3b & d) it decreased downstream, from D to A (in AFDW more sharply, in Chl *a* moderately; Fig. 3a & c). In both streams, the biomass harvested on the fibreglass nets was changing rapidly (Fig. 3a & b). As the season progressed, productivity either increased due to periphyton colonisation and its growth, and catching drifting organic matter, or it decreased due to cell mortality and biomass loss by water abrasive action.

The RPP measured on microscope slides also changed during the season in both streams (Fig. 3c & d). Here, however, cell mortality and losses of Chl *a* markedly outweighed the values of colonisation and growth only on 3 March in the Petrified Forest Creek. Incremental colonization and growth continued for almost the whole season.

Figures 3e & f show curves of seasonal ratios of Chl *a*: AFDW in both streams. Because two different methods (µgChl *a*, µgC) were used, these values are only very rough estimates of the proportions between two biomass components; that of the autotrophic periphyton, and that of autotrophic + non-autotrophic attached biomass, i.e. live and dead autotrophic organisms, bacteria, fungi, protozoans, nematodes and rotifers. These proportions change during the season and along the streams. In addition, any estimate of the ratio between autotrophic and autotrophic + non-autotrophic components is also influenced by biomass transport downstream due to variable scouring by changeable discharge. Along the Ornithologists Creek, in the first half of the season, the ratio Chl *a* : AFDW remained close to zero when the upper section C was still mostly covered by snow and penguins were generally present (Fig. 3e). After this snow had melted, the periphyton growth and the trapping of drifting algae in the B reaches increased. Meanwhile, in the lower A reach, close to the penguin rookeries, the proportions matched each other and the ratio remained close to zero. In reach B, the autotrophic build up and trapping of algae prevailed for a short time only, while the non-autotrophic biomass accumulation, again influenced by transport, greatly exceeded the photosynthetic growth.

At the start of the season, large quantities of what was probably the previous year's biomass were being transported down the Petrified Forest Creek. In the lower A

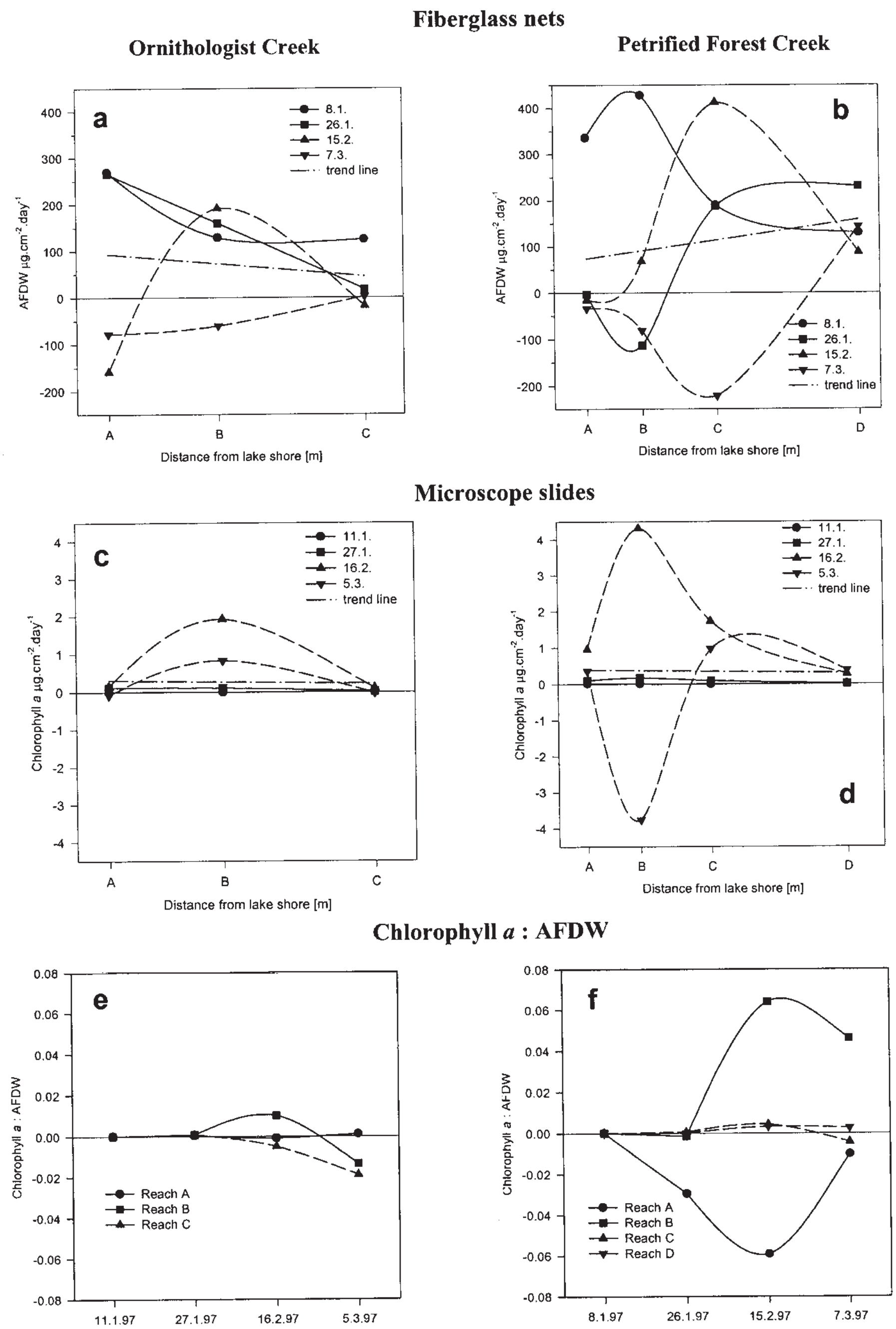

Fig. 3. Seasonal curves of relative periphyton productivity, measured as AFDW on fibreglass nets along **a.** the Ornithologists Creek, and **b.** the Petrified Forest Creek, and as Chl *a* concentration on microscope slides along **c.** the Ornithologists Creek and **d.** the Petrified Forest Creek, and Chl *a*: AFDW ratio along **e.** the Ornithologists Creek and **f.** the Petrified Forest Creek, in 1996–97 summer season. In graphs a, b, c and d legends show date of relative periphyton productivity harvested together with trend line. In graphs e and f legends show studied streams reaches.

reach (Fig. 3f) periphyton and trapped organic debris quickly covered the fibreglass nets. In reach B (245–265 m) and to a lesser extent in reaches C (461–481 m) and D (878–898 m), the highest biomass increase occurred mainly in the second half of the season (i.e. in February and March). Moreover, along the Petrified Forest Creek, the biomass covering the fibreglass nets contains both non-autotrophic and autotrophic components, transported either from the stream catchment or growing actively on the nets. It almost matched the phototrophic production, thus lowering the net production of the new periphyton.

Figure 4 shows the rate of periphyton colonisation,

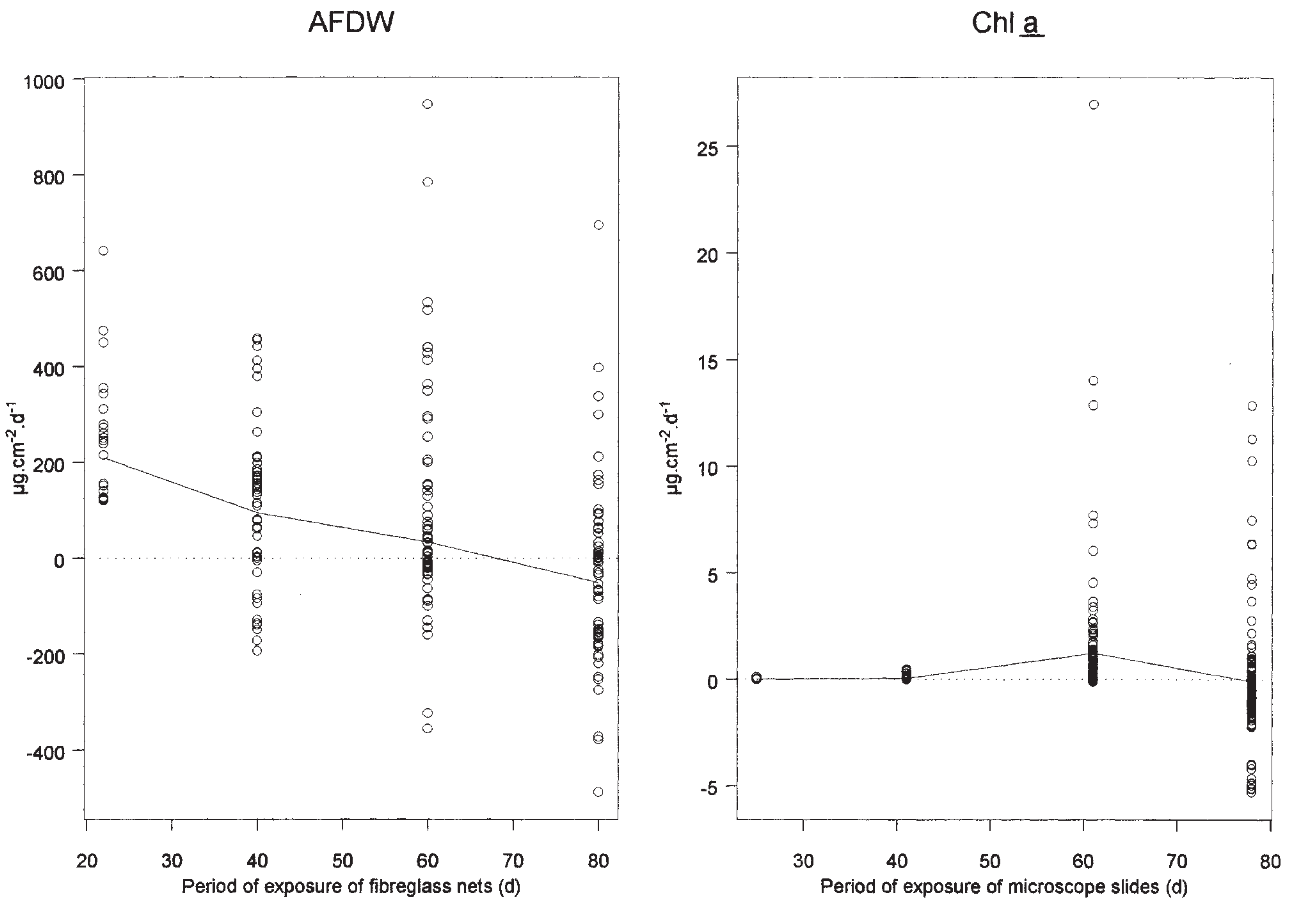

Fig. 4. Changes with time in relative periphyton productivity (colonization/growth and losses/mortality) as measured on fibreglass nets (AFDW) and microscope slides (Chl *a*), along both the Ornithologists Creek ($n = 85$ and $n = 109$) and the Petrified Forest Creek ($n = 193$ and $n = 256$), during 1996–97 summer season. Curves pass through mean values.

growth and passive trapping of drifting organic matter on the fibreglass nets and microscope slides, in both streams. From Fig. 4 - AFDW, it can be seen that the fibreglass nets fixed on the streams' beds were quickly occupied by biomass and periphyton growth was probably limited by a lack of available area at the nets' surface (after about 23 days of exposure in the streams). However, the RPP decreased slowly with time and after about 65 days of exposure, biomass losses due to dieback exceeded productivity (colonization and growth). On the microscope slides (Fig. 4 - Chl *a*), the rate of periphyton colonisation and growth were slower, due to biomass sloughing, and reached their maximum after about 57 days of exposure in the streams. Here, periphyton growth and losses were in balance after 78 days of exposure in both streams.

Physical and chemical parameters of stream water

Seasonal mean values of NH_4^+–N, $NO_3^=$–N, DIN, DRP, DIN : DRP, conductivity, temperature, pH, alkalinity, CO_2, HCO_3^- and $CO_3^=$ for each stream and in individual reaches are shown in Fig. 5. The Ornithologists Creek was richer in nutrients, which also fluctuated more widely along its length and throughout the season, than in the Petrified Forest Creek. Conductivity and temperature values for the Petrified Forest Creek showed slightly higher values compared to the Ornithologists Creek. Values of other measured parameters for the Petrified Forest Creek and the Ornithologists Creek are associated with the inorganic carbon cycle of the stream water, and reflect higher periphyton productivity of the Petrified Forest Creek. Also, the relatively high CO_2 concentration in the Ornithologists Creek in comparison with the Petrified Forest Creek, may reflect the high penguin guano decomposition in reach A of the former. In addition, the pH, CO_2, and $CO_3^=$ concentrations fluctuated widely along the Ornithologists Creek and during the season.

There were interesting differences along each stream (Fig. 5). Concentrations of NH_4^+–N, $NO_3^=$–N and DIN were high in the lowest reach A of the Ornithologists Creek (up to 88 m from the lake's shore). DRP concentration decreased down the Ornithologists Creek. In the Petrified Forest Creek the DRP was slightly higher in reaches A and D. The DIN : DRP ratio was high in the lowest section A of the

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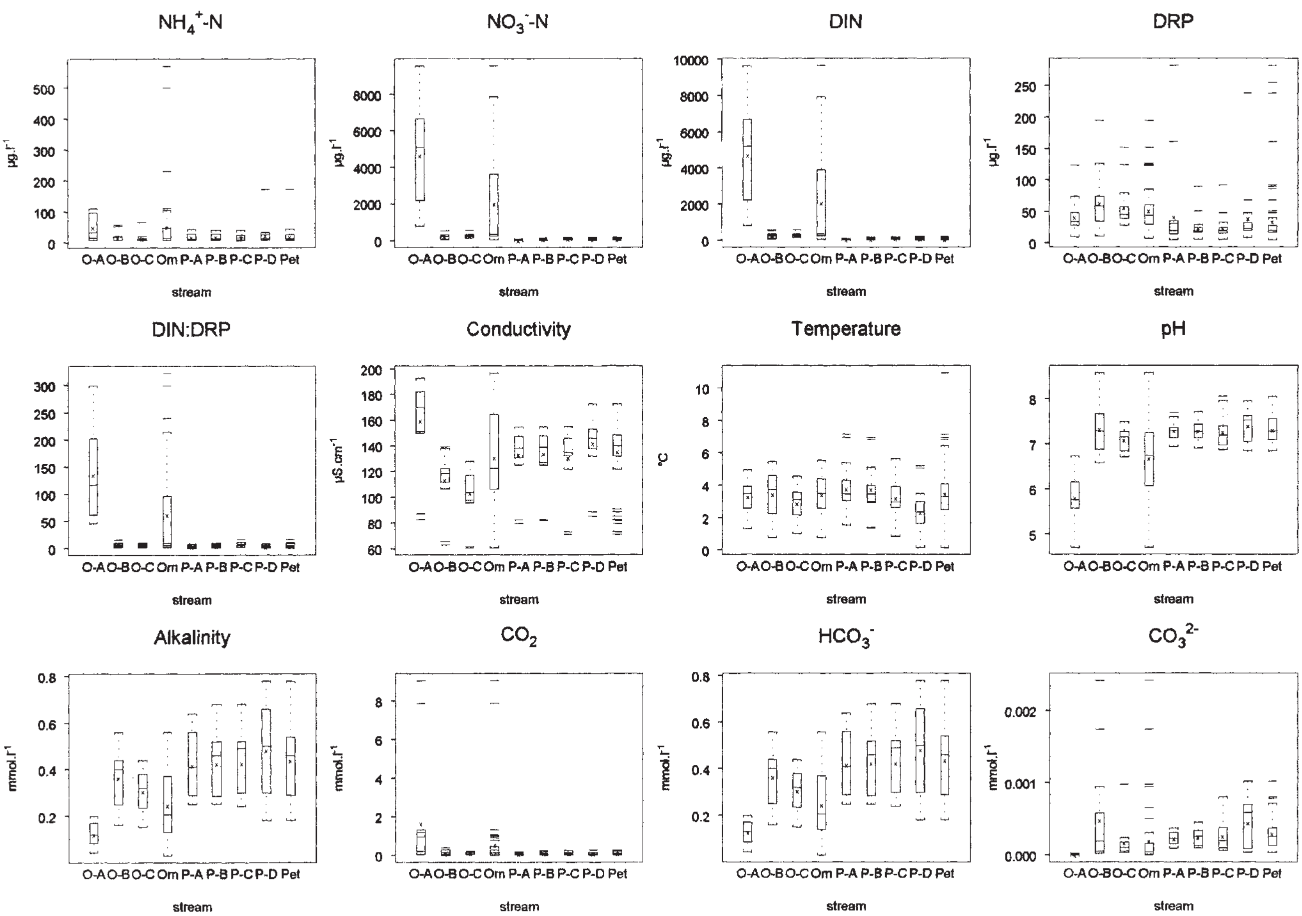

Fig. 5. Seasonal values of physicochemical water parameters of samples along the Ornithologists Creek ($n = 56$) and its individual study reaches (O-A: 66–88 m; O-B: 336–358 m; O-C: 695–715 m; $n = 8$ for each reach) and the Petrified Forest Creek ($n = 81$) and its individual study reaches (P-A: 85–105 m; P-B: 245–265 m; P-C: 461–481 m; P-D: 878–898 m; $n = 9$ for each reach) streams in 1996–97 summer season. Graphs show the upper and lower quartile (box margins), mean value (x), median (black stripe inside the box), upper and lower extreme - nearest values not beyond a standard span (1.5x inter quartile range) from the quartiles (whiskers) and outliers (black lines beyond whiskers).

Ornithologists Creek. Values of conductivity showed an opposite tendency in the two streams. Temperature increased downstream with decreasing elevation. In the lower A reach of Ornithologists Creek, pH, alkalinity, HCO_3^- and $CO_3^=$ were low, while, in contrast, CO_2 concentration in this section was higher. In B and C in Ornithologists Creek, and A, B, C and D in Petrified Forest Creek, higher values of pH, alkalinity, HCO_3^- and $CO_3^=$ were measured.

The influence of multiple factors on RPP

Data analysis shows that (Table I) RPP was limited by lack of space on the net surfaces (Date - time of nets incubation in the streams negatively influenced RRP). In both models, the ‘basic’ and ‘simplified’ variants, the date of measurement had a highly negative influence on productivity. After pooling the data for both streams, and treating the Petrified Forest Creek separately, increasing temperature had a highly negative effect on RPP in both models.

In the basic model, HCO_3^-, alkalinity, $CO_3^=$, TDIC, and CO_2 all show a positive influence on productivity, in pooled data and in the Ornithologists Creek separately. In the Petrified Forest Creek, only TDIC, HCO_3^- and alkalinity showed such influence. In the simplified model, the increasing concentrations of only $CO_3^=$ were highly correlated with the periphyton productivity in the pooled streams and in the Ornithologists Creek data.

In the basic model, NH_4^+–N and DRP in the Ornithologists Creek, and $NO_3^=$–N and DIN in the Petrified Forest Creek, positively correlated with periphyton productivity. However, in the simplified model, only NH_4^+–N was positively associated with productivity in pooled and the Ornithologists Creek data. In the Petrified Forest Creek, $NO_3^=$–N positively influenced productivity in this model. In contrast, DRP and the DIN : DRP ratio were negatively associated with productivity.

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Table I. Two versions of Generalised Linear Models (GLM) for relative periphyton productivity, measured as AFDW for both streams together, and for the Ornithologists Creek and the Petrified Forest Creek separately.

In both streams together Variable (df)	*F*	*P*	Effect	Ornithologist Creek Variable (df)	*F*	*P*	Effect	Petrified Forest Creek Variable (df)	*F*	*P*	Effect
Basic model											
Date (1)	35.22	***	-	Date (1)	29.49	***	-	Temperature (1)	22.31	***	-
HCO_3^- (1)	19.29	***	+	DRP (1)	16.51	***	+	$NO_3^=$–N (1)	21.25	***	+
Alkalinity (1)	18.97	***	+	TDIC (1)	16.41	***	+	DIN (1)	17.45	***	+
$CO_3^=$ (1)	10.92	**	+	HCO_3^- (1)	12.34	***	+	Date (1)	14.02	***	-
TDIC (1)	9.64	**	+	CO_2 (1)	11.95	***	+	Valley (1)	8.97	**	+
Temperature (1)	8.65	**	-	Alkalinity (1)	11.72	***	+	TDIC (1)	8.59	**	+
Site (6)	2.96	**	+	$CO_3^=$ (1)	11.46	**	+	HCO_3^- (1)	7.13	**	+
Altitude (1)	5.29	*	+	NH_4^+–N (1)	8.02	**	+	Alkalinity (1)	7.13	**	+
CO_2 (1)	4.47	*	+	Granulation (1)	4.57	*	+	Altitude (1)	4.54	*	+
								Site (3)	2.95	*	+
								Conductivity (1)	4.46	*	-
Simplified model											
Date (1)	42.73	***	-	Date (1)	43.38	***	-	Temperature (1)	27.59	***	-
$CO_3^=$ (1)	14.67	***	+	$CO_3^=$ (1)	18.34	***	+	$NO_3^=$–N (1)	14.90	***	+
NH_4–N (1)	15.01	***	+	NH_4^+–N (1)	24.19	***	+	DIN:DRP (1)	6.33	*	-
Temperature (1)	8.49	**	-					DRP (1)	7.78	**	-
Wideness (1)	8.05	**	-								

Notes: df = degrees of freedom (in brackets), *F* = F-ratio, *P* = level of importance, Effect = negative (-) or positive (+).

High conductivity had a negative effect on periphyton growth in the Petrified Forest Creek. In the basic model, altitude (in pooled streams), granulation of stream bottom (in Ornithologists Creek) and valley type and altitude (in Petrified Forest Creek) were positively associated with the periphyton growth. Productivity slightly increased with elevation in the Petrified Forest Creek.

Surprisingly, in the simplified model pooled stream width negatively influenced periphyton productivity.

Table II presents factors showing some association with the RPP based on Chl *a* extractions. $CO_3^=$ concentrations (except in the simplified model for Petrified Forest Creek), and pH values (except in the simplified model in pooled streams and the Ornithologists Creek) were positively correlated with productivity. In the Petrified Forest Creek (simplified model), again high conductivity was negatively associated with algal growth. In the Ornithologists Creek (basic model) stream floor granulation was positively associated whilst the valley width was negatively associated with the periphyton growth.

Discussion

Relative Periphyton Productivity

Our data for RPP, determined as AFDW for the Petrified Forest Creek 4.53 µg cm^{-2} h^{-1} and Ornithologists Creek 2.91 µg cm^{-2} h^{-1} fit well within the range of previous measurements of gross periphyton primary production (measured either as oxygen prouction or as ^{14}C uptake). Vincent & Howard-Williams (1986) measured photosynthesis rates from 0.39 to 2.15 µg C cm^{-2} h^{1} in two major types of benthic cyanobacteria in the McMurdo Dry Valleys. Similarly, in various localities around continental Antarctica, measurements of stream periphyton gross productivity per unit area ranged from 0.4 to 4.3 µg C cm^{-2} h^{1} (Hawes & Howard-Williams 1998). A comparable rate (3.0 to 3.6 µg C cm^{-2} h^{1}) was also shown by Hawes (1993) for maritime Antarctic streams.

The Antarctic stream benthos community contains cyanobacteria/algae and associated microorganisms. It has been shown by Howard-Williams *et al.* (1989b) in the ponds of the McMurdo Ice Shelf, that the Chl *a* content was low relative to Carbon (Chl *a*: C < 0.01). Even though our data gives only a very rough estimate, it can be concluded that the ratios of Chl *a* : AFDW (Chl *a* : C) were extremely low for both the Ornithologists Creek and Petrified Forest Creek: -0.002 and 0.001 (µgChl *a*: µgC), respectively. These analyses indicate that the stream periphyton was extremely rich in non-chlorophyll organic carbon.

The overall trends shown in Fig. 3a–d, furthermore, indicate that the relative productivity of periphyton was well-balanced along both streams. The periphyton did not produce single clusters of high biomass along the streams but rather was regularly spread. Unlike the observations recorded by Vincent & Howard-Williams (1986) in the McMurdo Sound region, Antarctica, in our study we did not observe the fibreglass nets or microscope glass slides becoming dammed or overwhelmed by bed-load material. In their study, a thick algal layer dominated by *Phormidium* mat communities predominated. In our two streams different algal communities prevail, composed mainly of small diatoms (Kawecka & Olech 1993) accompanied by *Hydrurus foetidus* (Vill.) Kirchn., *Phormidium pseudopristlei* Anagnostidis et Komárek, which formed a mosaic on the stony bottom with locally dominating *Klebsormidium* sp. and cyanobacteria *Phormidium*

Table II. Two versions of Generalized Linear Models (GLM) for relative periphyton productivity, measured as Chl *a* for both streams together, and for the Ornithologists Creek and the Petrified Forest Creek separately.

In both streams together				Ornithologist Creek				Petrified Forest Creek			
Variable (df)	*F*	*P*	Effect	Variable (df)	*F*	*P*	Effect	Variable (df)	*F*	*P*	Effect
Basic model											
$CO_3^{=}$ (1)	16.02	***	+	$CO_3^{=}$ (1)	20.06	***	+	pH (1)	7.15	**	+
pH (1)	8.2	**	+	Granulation (1)	8.07	**	+	NH_4^{+}–N (1)	5.75	*	-
NH_4–N (1)	4.27	*	-	pH (1)	7.9	**	+	$CO_3^{=}$ (1)	5.61	*	+
				Valley (1)	6.64	*	-				
				Site (2)	4.01	*	+				
Simplified reduced model											
$CO_3^{=}$ (1)	16.02	***	+	$CO_3^{=}$ (1)	20.06	***	+	pH (1)	7.47	**	+
								Conductivity (1)	12.41	***	-

Notes: df = degrees of freedom (in brackets), *F* = F-ratio, *P* = level of importance, Effect = negative (-) or positive (+).

amoenum Kützing ex Anagnostidis et Komárek, *P. pristleyi* Fritsch and *Gloeocapsopsis aurea* Komárek (Komárek & Komárek 2001).

As indicated in Fig. 3e & f, the lower A reach of Petrified Forest Creek had a Chl *a* : AFDW ratio which was negative (except during the first 22 days of incubation on the in-stream artificial substrata); no active colonization or growth was recorded here. Here, benthic biomass was rich in non-chlorophyll organic carbon, probably contained in dead or non photosynthetically active organic matter brought from the upper part of the stream. Similarly, in the lower A reach of Ornithologists Creek, the Chl *a* : AFDW ratio remained around zero for most of the season; here, periphyton colonization and growth may have been negatively influenced by penguin excrement.

The measurements of RPP in the Petrified Forest Creek showed a large inconsistency between AFDW and Chl *a*; the correlation coefficient between AFDW and Chl *a* data was low (0.33). We believe that this difference between measurements, accept two different methods were used as proxies for productivity, has also occurred due to the passive capture of old and dead organic material brought from the stream's upper reaches at the beginning of the season. In the Ornithologists Creek, organic matter from the upper part was washed downstream but this biomass was quickly decomposed by the high bacterial inoculum that probably existed here due to the penguin rookery. This hypothesis is supported by the correlation coefficient between AFDW and Chl *a* being 0.83.

Finally, in the evaluation of the rate of periphyton colonization and/or growth (Fig. 4), extremely high differences were found between nets and slides, and between stream reaches, as well as in time. The ratio between periphyton colonization and growth, and its losses and mortality, is probably also regulated by both environmental conditions, as well as by availability of space on the surfaces of the nets and glass slides. However the results of other studies on gross and net primary production in Antarctica and the Arctic can be noted (Vincent & Howard-Williams 1986, 1989, Peterson *et al.* 1986, Howard-Williams & Vincent 1989, Howard-Williams *et al.* 1989a, 1989b, Vincent *et al.* 1993b, Hawes & Howard-Williams 1998). Generally, these studies show higher respiration rates in thicker benthic communities, resulting in the gross photosynthesis rate being approximately equal to that of respiration. In our study, periphyton on fibreglass nets probably increased their respiration during the period of our productivity measurements, because their biomass was slowly decreasing (Fig. 4).

We conclude that because the Ornithologists Creek drains through a gentoo penguin colony it was a stream where non-autotrophic biological activity prevailed, with the exception of its central section with higher periphyton production. In contrast the Petrified Forest Creek was an autotrophic stream where periphyton production was significant, except for its lower reach where old and dead biomass transported downstream accumulated. However, the relative productivity of both streams was low.

Mineral nutrients and RPP

Several studies in Antarctica (Vincent & Howard-Williams 1986, Howard-Williams & Vincent 1989, Hawes & Brazier 1991, Vincent *et al.* 1993b, Hawes & Howard-Williams 1998), as well as in the Arctic (e.g. Miller *et al.* 1992), have looked at the importance of mineral nutrients (N, P) for stream periphyton. It has been concluded that mineral nutrient limitation appears to have a minor effect on periphyton growth. In our streams, it was frequently found that with increased RPP, as measured by AFDW, the concentrations of NH_4^{+}–N, $NO_3^{=}$–N (DIN) and DRP also increased (Table I). There was a close relationship between the accumulation of biomass and the N and P released from the accumulated biological material. On sites with a small biomass accumulation, N and/or P can be present in very low concentrations and depletion of available mineral nutrients can occur temporarily. The relationships shown in Tables I & II represent such situations. The Petrified Forest Creek water was poor in its DIN concentration and had a low DIN:DRP ratio. Lack of inorganic nitrogen (low

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DIN:DRP ratio) in the Petrified Forest Creek could have negatively influenced periphyton growth. Conversely, in the Ornithologists Creek's lower reach A where penguin excrements fertilized the stream water, periphyton growth was probably negatively influenced by lack of phosphorus (low DRP concentrations and high DIN:DRP ratios (see Fig. 5)). However, it has also been shown (Downes *et al.* 1986, Howard-Williams *et al.* 1989a) that Antarctic stream waters are rich in organic nitrogen (mainly urea) and can partially cover periphyton nitrogen uptake. It has also been shown (Downes *et al.* 1986) that dissolved organic phosphorus levels are generally lower than dissolved organic nitrogen, but can cover the requirements of phosphorus uptake. Nitrogen and phosphorus transport between stream water and periphyton function sufficiently rapidly to cover the periphyton requirements for growth.

Our results for DIN and DRP concentrations in the lower part of the Ornithologists Creek confirm earlier published data by Myrcha *et al.* (1985) from the area of Admiralty Bay. Bacterial, enzymatic and chemical processes mineralize and rapidly transform the penguin guano. About 50% of C and N is volatilized during the first three weeks; most of the NH_4^+–N contained in percolated water is oxidized to $NO_3^=$–N in the subsurface layer of the rookery soil.

The periphyton growth in the stream section through the penguin rookery can be limited by a wide range of factors: lack of dissolved phosphorus, toxic concentrations of ammonium or nitrate nitrogen, or other compounds in penguin excrement, periphyton competition with guano-decomposing bacteria, etc. However, this problem has not yet been studied. Moreover, as has been noted by many authors (Smith 1985, Cocks *et al.* 1998), so-called 'ornithological' mineral nutrients can increase the abundance and productivity of terrestrial ecosystems.

Increased conductivity connected with a decreased rate of flow (~10 µS cm^{-1}) during our measurements was still too small to have a negative effect on periphyton growth. The fact that conductivity showed a negative effect in GLM analysis (Tables I & II) seems to be an artefact.

Water inorganic carbon cycle parameters and temperature

Even though high levels of water turbulence occurred in the streams, and CO_2 exchange between water and air had to be substantial, differences were measured in those parameters connected with the stream water inorganic carbon cycle (pH, alkalinity, CO_2, HCO_3^-, $CO_3^=$, TDIC). Both streams were shallow and the periphyton biomass was high enough to permanently shift the water inorganic carbon balance throughout the season. The Petrified Forest Creek was the more productive system and also had the higher pH and alkalinity, while, simultaneously, the inorganic carbon balance was shifted from CO_2 into HCO_3^- and $CO_3^=$ saturation. In contrast, in the Ornithologists Creek, CO_2 concentration reflected the penguin guano decomposition in its lower reach A.

The shift in inorganic carbon balance from CO_2 to HCO_3^- and $CO_3^=$ was not so marked that it could probably have substantially influenced the composition and growth of the stream periphyton community. However, this suggestion needs to be be tested in future research.

In their overview, Hawes & Howard-Williams (1998) argue that for gross photosynthesis and respiration of stream cyanobacteria-dominated mats in the McMurdo Dry Valleys temperature rather than irradiance may have been the dominant variable determining stream production. Similarly, Vincent & Howard-Williams (1989) reported that benthic cyanobacterial mats at Fryxell Stream, Taylor Valley, Antarctica, showed strongly positive metabolic responses to increases in temperature. In our study, mean seasonal temperature for the more productive Petrified Forest Creek was slightly warmer than the less productive Ornithologists Creek. GLM for RPP (measured as Chl *a* concentration) did not show any relationship between temperature and periphyton productivity (see Table II). The GLM for AFDW showed a negative relationship between RPP and temperature (see Fig. 1); this negative relationship, however, was not generally found in the Petrified Forest Creek. It can be concluded that this negative relationship was probably more connected with water discharge and downstream transportation of old and dead organic matter than with a temperature effect.

Geomorphological and geographical characteristics of the streams and RPP

Our study showed the Ornithologists Creek and Petrified Forest Creek to be different in their geomorphological and geographical characteristics. Moreover, the GLM for Chl *a* and AFDW showed that reachs of the Ornithologists Creek with a higher content of gravel or boulders, had higher periphyton productivity. Periphyton cyanobacteria and algae grow more readily on a stable stream bottom. Howard-Williams *et al.* (1986), Hawes & Howard-Williams (1998), and Kubečkova *et al.* (2001) have stated that the disturbance of periphyton growth by suspended loads of mineral particles, which cause sloughing, scraping and peeling off of the algal biomass, is an important factor limiting periphyton development in polar streams. Analysis of stream elevation introduced the idea that biological material was more easily accumulated at low elevations, rather than that higher periphyton productivity was measured at higher elevations. Frequently there exists a declining downstream gradient in periphyton biomass (Howard-Williams *et al.* 1986, Hawes & Howard-Williams 1998, Elster & Svoboda 1996, Elster *et al.* 1997).

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Periphyton ecology for prediction of climate changes

The detailed knowledge of the maritime Antarctic stream ecosystems and their ecological functioning can be used as an indicator of changes which can be expected in continental Antarctica if the trend of global warming continues. Of course, increase in temperature and consequently liquid water availability is the most important symptom of such changes. Elster (2002) reviewed the distribution of cyanobacteria and algae communities of the terrestrial and hydro-terrestrial (wetlands) polar environment along a water availability gradient. He stated that the species composition of cyanobacteria and algae, their ecological structure and functioning were closely related to the liquid water availability gradient and/or the duration of melt water period. Moreover, periphyton responses to temperature increase, as a single ecological factor, were also evaluated in an *in situ* experiment in the Arctic archipelago of Svalbard, 79°N (Elster *et al.* 2001). In addition a temperature manipulation experiment has shown that the periphyton reacts rapidly to a temperature increase from 4 to 11°C. Dieback of the periphyton community, including its intensive consumption by Chironomid and midge larvae, was recorded as a result of increase.

This study has evaluated the seasonal RPP along two contrasting meltwater streams. The two types of artificial substrata used for RPP measurements provided not only the periphyton carbon uptake, but also include associated processes, such as active or passive downstream transport of biomass and nutrients/energy. This phenomenon is commonly reported under the term "river continuum concept" (Vannote *et al.* 1980). In this respect, the RPP measurements, together with assessments of associated environmental factors, integrate almost all ecological processes commonly occurring in shallow lotic freshwater ecosystems. However, this evaluation of RPP should be complemented by an exact evaluation of the proportions of photosynthetic and non-photosynthetic periphyton components, and an exact description of the species diversity and community structure.

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