

Summer macroalgal biomass in Potter Cove, South Shetland Islands, Antarctica: its production and flux to the ecosystem

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Abstract Summer macroalgal biomass and production were analyzed at Potter Cove, King George Island, Antarctica and the potential carbon transfer of macroalgal production to the coastal ecosystem of the cove was estimated. A total of 38 algal species were found, with *Desmarestia anceps*, *D. menziesii* and *Himantothallus grandifolius* accounting for almost 80% of the biomass. Biomass data and published growth rates were combined to calculate the production of the five most abundant species. The standing stock for each summer month was estimated as the product of the average biomass and the area of the macroalgal stands. The monthly biomass production was calculated for each species by difference between the expected biomass and the observed biomass at the previous month. The macroalgal production showed a decreasing trend during the summer months. The average standing stock in the whole cove was 792.84 MT and the production was 1,401.33 MT during the summer 1994–1995. The flux of biomass to the ecosystem during the summer period was 1,370.61 MT, which is almost as much as the total summer production. The study demonstrates that macroalgae are one of the main energy sources in Potter

Cove, and probably support a large fraction of the secondary production of the benthos.

Keywords Macroalgae · Biomass · Production · Flux · Antarctica

Introduction

The sublittoral rocky shores of the Western Antarctic Peninsula are colonized by extensive populations of macroalgae, with the species of the Order Desmarestiales as the dominant taxonomic groups. One major characteristic of Antarctic regions is the absence of Laminariales (Moe and Silva 1977). In Antarctica, their ecological role is taken over by the perennial, non-acidic members of Desmarestiales (Clayton 1994). *Desmarestia anceps* Montagne, *D. menziesii* J. Agardh and *Himantothallus grandifolius* (Gepp and Gepp) Zinova are the main species, which present the highest macroalgal biomass in Antarctica (Brouwer 1996a).

Macroalgal coastal carbon production seems to be an important food source to the benthic Antarctic communities (Iken et al. 1998). If not grazed, macroalgae die and decompose returning particulate organic matter and mineral nutrients to the system (Hanisak 1992). Zielinski (1981) observed that the seaweed decomposition process depends on the place where it occurs (seawater or seashore), the kind of thalli and the season.

Biomass data of Antarctic macroalgae were published for different localities (DeLaca and Lipps 1976; Miller and Pearse 1991; Amsler et al. 1995; Brouwer et al. 1995; Klöser et al. 1996). Most of this data have been presented only as maximum wet or dry biomass and the comparison with data for other localities is not easy.

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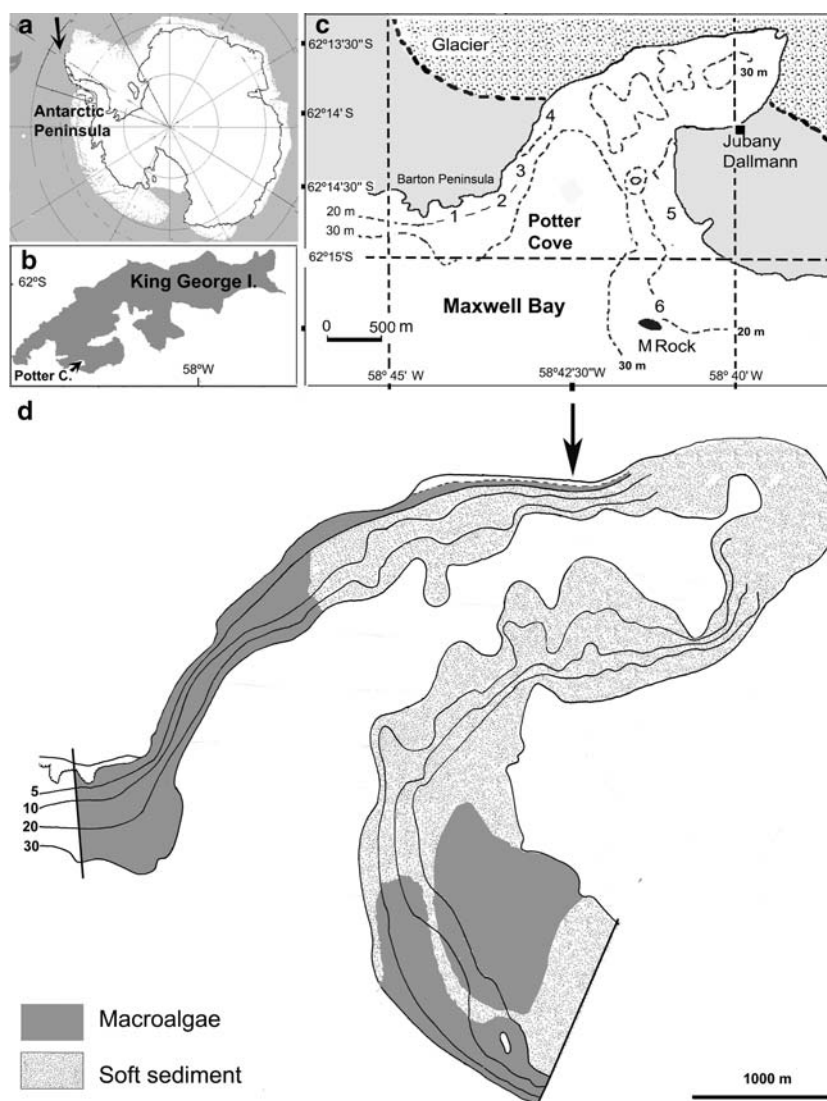
Furthermore, growth rates of selected Antarctic seaweed have been measured in the laboratory by Wiencke (1990a, b) and Gómez and Wiencke (1997). Production in the field can be estimated by differences in standing stocks between successive dates (Bellamy et al. 1973; De Wreede 1985; Israel 1995) or through the product of growth rates and biomass (Mann 1972). The first method underestimates the production because it does not consider how much biomass is lost to the system. The second method can lead to overestimation of the primary production when applied for longer time periods because as it is assumed that biomass accumulates and there are no losses in the system. The biomass production of the most abundant species has not been calculated yet and there is no information available about the biomass production and algal detritus fate of the benthic Antarctic ecosystems. The aim of this study was to determine the relative contribution in biomass of each macroalgae species present in Potter Cove during summer, as well as to assess the summer biomass production of the

most abundant seaweed species and to calculate the biomass flux to the ecosystem. This study is part of a multidisciplinary effort performed during the last 15 years to achieve a deeper knowledge of the benthic system at Potter Cove (King George Island, South Shetland, Antarctica) including studies of the macroalgal community structure (Klöser et al. 1996; Quartino et al. 2005), biomass in the inner side of Potter Cove (Quartino et al. 2001) and benthic Antarctic faunal communities (Iken et al. 1998; Sahade et al. 2004; Tatián et al. 2004).

Materials and methods

Potter Cove ($62^{\circ}14'S$, $58^{\circ}38'W$) is a tributary inlet of Maxwell Bay, one of the two big fjords of the central South Shetland Islands. The study area is situated on the coasts at the mouth of the cove (Fig. 1). The bottom of the outer Potter Cove consists of hard substrate with macroalgal

Fig. 1 Map showing the location **a** South Shetland Islands (arrow). **b** Potter Cove at Isla 25 de Mayo/King George Island (arrow). **c** Sampling sites at Potter Cove (numbers mark the position of the six sites at the Cove). **d** Macroalgae and soft bottoms distribution in Potter Cove



vegetation of variable density (Klöser et al. 1996). Detailed descriptions of Potter Cove have been presented earlier (Quartino et al. 2005).

Sampling was performed by scuba diving at six sites (Fig. 1), from January to March 1994, 1995 and 1996. Three sampling units of 1 m² were placed at 0, 5, 10, 20 and 30 m along 26 transects perpendicular to the shore. The three sampling units at each study site were averaged to obtain 130 biomass data for each species.

All the macroalgae except crustose red algae were removed from the substratum. Voucher specimens of each species were deposited at the Herbarium of the Museo Argentino de Ciencias Naturales B. Rivadavia (BAc). Seaweeds were dried at 60°C and weighed using electronic balances Mettler AJ (0.001–100 g) and Ohaus TP 400 S (0.01–400 g) for biomass (g m⁻²) determinations.

The three most abundant Phaeophyceae species *D. anceps* Montagne, *D. menziesii* J. Agardh and *H. grandifolius* (Gepp and Gepp) Zinova and the two most abundant Rhodophyceae *Gigartina skottsbergii* Setchell and Gardner, *Iridaea cordata* (Turner) were selected to estimate the biomass production of the cove.

Biomass data from two sites (sites 1 and 2, Fig. 1) obtained during two summer seasons 1994–1995 and published growth rates (Wiencke 1990a, b; Gómez and Wiencke 1997) were used to calculate the macroalgal production of the five most abundant species. Published growth rates were determined by exposure of different developmental stages to different photon fluence rates and seasonally fluctuating daylengths mimicking the light conditions on King George Island. The experimental growth rates obtained in laboratory light conditions by Wiencke (1990a, b) and Gómez and Wiencke (1997), which match with the irradiance measures in the field at each depth were selected. Growth rates of *I. cordata* were separated into two categories, one of small first-year plants with fast growth and the other group including bigger second-year plants. For both cases the growth rates of gametophytes cultivated under 46 μmol m⁻² s⁻¹ were

taken. In *G. skottsbergii* growth rates of second-year tetrasporophytes growing at 9 μmol m⁻² s⁻¹ were used. Growth rates of the two morphologically similar species varied between 2 and 4% increase per day under photon fluence rates between 9 and 46 μmol m⁻² s⁻¹. In the case of *D. anceps*, *D. menziesii* and *H. grandifolius* growth rates of the sporophytes growing at 27 μmol m⁻² s⁻¹ were used (Table 1). Growth rates determined under 3–27 μmol m⁻² s⁻¹ in *D. anceps* and *H. grandifolius* were similar with 2–3.5% increase per day (Wiencke 1990a).

The average expected biomass (EB) of each species (*i*) during a month (*j*) was calculated for each depth (*d*) as:

$$EB_{i;j;d} = OB_{i;j-1;d} \cdot e^{rt}$$

where $OB_{i;j-1}$ is the observed average biomass (g m⁻²) for the same depth at the previous month; r (g g⁻¹ day⁻¹) is the daily growth rate and t (days) is the period length.

The monthly average production of species *i* (*P*) (g m⁻²) at each depth in the period between 2 months was calculated as:

$$P_{i;[(j-1);j]} = EB_{i;j} - OB_{i;j-1}$$

where $EB_{i;j}$ is the expected biomass of species *i* (g m⁻²) at month *j* and $OB_{i;j-1}$ is the observed biomass (g m⁻²) at month *j* - 1.

The P_i/B_i ratio was calculated for two sites (sites 1 and 2, Fig. 1) at several depth strata, B_i being the average observed biomass (OB) in the period

$$B_i = (OB_{i;j-1} + OB_{i;j})/2$$

These P_i/B_i ratio values were later used to calculate the production in the whole area of the cove.

Areas covered by macroalgae at different depth strata were calculated using the bathymetric charts of South Shetlands Islands H-137 (1:25,000), H-711 (1:200,000) and Cuarteron Potter Cove (1:10,000) and Potter Cove no. H-711 (1:200,000) with an inset (1:10,000). Areas with soft sediments and without macroalgae were excluded. Depth

Table 1 Growth rate (g g⁻¹ day⁻¹) of macroalgal species

Macroalgae species	Depth (m)	December 1994	January 1995	February 1995	March 1995
<i>I. cordata</i> ^b	0	0.046 ^d	0.036 ^d	0.027 ^d	0.020 ^d
		0.012 ^e	0.006 ^e	0.006 ^e	0.006 ^e
	5	0.046 ^d	0.036 ^d	0.027 ^d	0.020 ^d
		0.012 ^e	0.006 ^e	0.006 ^e	0.006 ^e
<i>G. skottsbergii</i> ^b	10	0.009	0.006	0.006	0.006
<i>D. menziesii</i> ^c	5	0.005	0.003	0.003	0.001
	10	0.005	0.003	0.003	0.001
<i>D. anceps</i> ^a	20	0.003	0.003	0.004	0.004
<i>Hi. grandifolius</i> ^a	20	0.024	0.006	0.005	0.005
	30	0.025	0.023	0.017	0.015

^a Wiencke (1990a)

^b Wiencke (1990b)

^c Gómez and Wiencke (1997)

^d First year growth

^e Second year growth

curves and areas with macroalgae according with Klöser et al. (1996) were drawn on the digitized maps. The areas with macroalgae between Barton Peninsula and M Rock from 0 down to 30 m were calculated using the Color Mapping 1.0 program.

The standing stock for each selected species at each summer month was estimated as the product of the area of the species population (m^2) and its respective monthly average biomass (g m^{-2}).

The monthly production of each species at each depth stratum was estimated as the product of the species standing stock and the production to biomass ratios (P/B) obtained for sites 1 and 2. These ratios were estimated with the average P/B of the depth stratum or, when this was not available, with the value of the nearest depth. The total production of the most abundant species at each depth was calculated as the product of the monthly production of the species and areas with macroalgae (m^2) at their respective depth.

The biomass flux to the ecosystem ($F_{1,2}$) in sites 1 and 2 was calculated for each species (i) for each period ($j - 1, j$) as the difference between observed and expected biomass at the end of the period:

$$F_{1,2[(j-1);j];i} = \text{EB}_{1,2(j;i)} - \text{OB}_{1,2(j;i)}$$

Biomass flux during each period was considered to be proportional to the calculated production in the period and to the net losses observed between the period and the next one. So, the ratio $R_{1,2}$ for each period $j - 1, j$, and each i species was calculated for sites 1 and 2 as

$$R_{1,2} = (P_{1,2} + \delta_{1,2})(F_{1,2})^{-1}$$

where $\delta_{1,2}$ is an adjustment for net loss of biomass, it was considered $\delta = 0$ when the mean biomass in the period increased. If the mean biomass decreased between periods:

$$\delta = \text{SS}_{j-1,j} - \text{SS}_{j,j+1}$$

where SS was the mean standing stock present during each period.

Flux (F) to the ecosystem in the whole cove (F) was calculated as

$$F = R_{1,2}(P + \delta)$$

where P is the production in the whole cove and δ means the same as $\delta_{1,2}$ for the whole cove.

The sum of F for each species, date and depth are considered the total biomass flux to the ecosystem.

Results

A total of 38 species were identified within the sampling units in the study area (Table 2): frequency in the sample

units (%); mean dry biomass in all the samples (MDB1) and mean dry biomass considering only the samples with presence of the species (MDB2), maximum wet biomass (MXWB) and maximum dry biomass (MXDB) values are also shown in Table 2. These values are shown just to allow comparison with other Antarctic areas where only these data are available.

Desmarestia anceps, *D. menziesii* and *H. grandifolius* accounted for almost 80% of the biomass, whereas *I. cordata*, *Ascoseira mirabilis*, *Plocamium cartilagineum*, *G. skottsbergii*, *Curdiea racovitzae*, *D. antarctica*, *Adenocystis utricularis* and *Palmaria decipiens* and the other 27 species observed accounted for only 15 and 5% of the total wet biomass, respectively.

The EB at sites 1 and 2 based on laboratory growth rates of the most abundant species (*D. anceps*, *D. menziesii*, *H. grandifolius*, *G. skottsbergii*, *I. cordata*) is presented in Table 3. In general the EB exceeded the OB at the former month and the production during the period could be estimated. It was also observed that the EB often was higher than the OB at each date and some flux to the ecosystem could be presumed.

The P_i/B_i ratios of the five selected species were calculated to sites 1 and 2 for each monthly period during summer (1994–1995) (Table 4). P/B was higher for *I. cordata* and *H. grandifolius* than for the other species. These ratios were used to calculate the production at the whole cove (Table 5).

The sum of biomass production at all depths of the most abundant species obtained as the product of average biomasses and area data (Table 5) decreased over the summer period (Fig. 2), except for *G. skottsbergii*, which remained almost constant. *I. cordata* presented higher production than *G. skottsbergii* at the beginning of the summer but comparable values in March. The production of the Desmarestiales also decreased with time but less than in the two Gigartinales (Fig. 2).

The standing stock (dry weight) of the most abundant species at each depth stratum is shown in Table 5. The standing stock present at the whole cove during the summer months of 1994 and 1995 was on average 792.84 MT. The macroalgal biomass production of the most abundant species in Potter Cove during the entire summer period 1994–1995 was 1,401.33 MT and the daily production over the whole period was $0.0138 \text{ g g}^{-1} \text{ day}^{-1}$. The flux of biomass to the ecosystem in the period December–March was 1,370.61 MT (Table 5).

A comparison was performed between the standing stock expected at the end of the study according to our calculations and the actual biomass present in the field (Table 6). The difference between the initial standing stock (1) plus the production (2) and the biomass gone to the ecosystem (3) gives an idea of the remaining biomass at the end of the

Table 2 Biomass and abundance of species in Potter Cove

Macroalgae species	F (%)	MDB1	MDB2	MXWB	MXDB	Site number/date
Ulvoephyceae						
<i>Enteromorpha bulbosa</i> (Suhr) Montagne 1946	6.20	0.29 (0.10)	6.61 (1.91)	103.88	16.08	1 December 1994
<i>Lambia antarctica</i> (Skottsberg) Delépine 1967	2.32	0.09 (0.05)	3.76 (1.15)	53.08	5.26	4 February 1994
<i>Monostroma hariotii</i> Gain 1911	17.05	2.95 (0.79)	17.33 (3.17)	480.12	52.16	1 December 1994
Phaeophyceae						
<i>Adenocystis utricularis</i> (Bory) Skottsberg 1907	17.05	4.12 (1.12)	24.37 (4.61)	798.35	81.56	5 February 1995
<i>Ascoseira mirabilis</i> Skottsberg 1907	24.80	8.68 (1.62)	36.39 (3.75)	803.13	80.95	4 February 1995
<i>Cystophaera jacquinotii</i> (Montagne) Skottsberg 1907	3.87	2.50 (1.31)	63.50 (20.94)	1,350.55	131.82	1 February 1995
<i>Desmarestia anceps</i> Montagne 1842	31.78	55.19 (0.40)	170.94 (26.7)	6,043.68	671.52	6 February 1995
<i>Desmarestia antarctica</i> Moe & Silva 1989	7.75	4.40 (1.58)	55.89 (11.66)	1,255.22	125.32	5 January 1996
<i>Desmarestia menziesii</i> J. Agardh 1848	34.88	134.28 (22.2)	378.96 (44.57)	6,737.31	748.59	3 December 1995
<i>Geminocarpus geminatus</i> (Hooker f. & Harvey) Skottsberg 1907	1.55	0.02 (0.015)	1.42 (0.22)	12.06	1.64	5 January 1996
<i>Halopteris obovata</i> (Hooker f. & Harvey) Sauvageau 1904	3.10	0.12 (0.06)	3.80 (0.43)	52.14	5.09	5 December 1995
<i>Himantothallus grandifolius</i> (Gepp & Gepp) Zinova 1959	34.88	145.64 (22.35)	411.70 (40.39)	10,366.20	1,151.80	3 December 1995
<i>Petalonia fascia</i> (Müller) Kuntze 1898	1.55	0.11 (0.075)	6.72 (1.23)	78.50	7.96	5 February 1995
<i>Phaeurus antarcticus</i> Skottsberg 1907	19.37	2.58 (0.56)	13.28 (1.63)	412.03	41.04	1 February 1995
Rhodophyceae						
<i>Ballia callitricha</i> (C. Agardh) Kützing 1843	21.70	0.58 (0.12)	2.64 (0.36)	77.14	7.69	4 January 1995
<i>Callophyllis atrosanguinea</i> (Hooker f. & Harvey) Hariot 1887	2.32	0.26 (0.16)	11.17 (2.51)	146.20	14.37	1 January 1995
<i>Curdia racovitzae</i> Hariot 1900	25.58	4.49 (1.11)	17.27 (3.47)	915.20	91.44	5 December 1994
<i>Delesseria lancifolia</i> (Hooker f.) Agardh 1872	10.85	1.59 (0.71)	14.39 (5.55)	732.18	73.16	1 December 1994
<i>Georgiella confluens</i> (Reinsch) Kylin 1956	13.17	1.50 (0.54)	11.18 (3.27)	595.13	59.25	6 December 1994
<i>Gigartina skottsbergii</i> Setchell & Gardner 1936	24.03	5.98 (1.42)	24.49 (4.49)	946.00	95.08	5 February 1995
<i>Gymnogongrus antarcticus</i> Skottsberg 1953	2.32	0.22 (0.13)	9.12 (2.96)	1,099.70	11.68	3 March 1995
<i>Gymnogongrus turquetii</i> Hariot 1907	8.52	0.99 (0.34)	11.41 (2.41)	189.30	18.92	5 December 1995
<i>Hymenocladopsis crustigena</i> Moe 1986	6.97	0.76 (0.28)	10.79 (2.02)	210.54	19.14	2 January 1996
<i>Iridaea cordata</i> (Turner) Bory 1826	51.93	26.28 (3.96)	50.09 (6.33)	2,554.60	255.36	1 January 1996

Table 2 continued

Macroalgae species	<i>F</i> (%)	MDB1	MDB2	MXWB	MXDB	Site number/date
<i>Kallymenia antarctica</i> Hariot 1907	16.27	1.43 (0.39)	8.65 (1.68)	375.00	37.28	5 December 1995
<i>Myriogramme smithii</i> (Hooker f. & Harvey) Kylin 1924	16.40	0.51 (2.12)	6.24 (4.46)	212.32	20.90	2 December 1995
<i>Nereoginkgo adiantifolia</i>	0.77	0.02 (0.02)	2.07 (0.00)	18.09	2.07	6 January 1996
<i>Neuroglossum ligulatum</i> (Reinsch) Skottsberg 1919	1.55	0.16 (0.12)	10.25 (4.90)	155.14	15.23	1 January 1996
<i>Notophycus fimbriatus</i> Moe 1986	1.55	0.07 (0.05)	4.60 (0.52)	53.21	5.12	1 February 1995
<i>Pachymenia orbicularis</i> (Zanardini) Setchell & Gardner 1934	0.77	0.09 (0.09)	11.52 (0.00)	124.22	11.52	3 January 1996
<i>Palmaria decipiens</i> (Reinsch) Ricker 1987	19.37	4.40 (1.37)	23.11 (5.87)	1,210.06	120.12	5 December 1995
<i>Pantoneura plocamioides</i> Kylin 1919	4.65	0.13 (0.07)	2.83 (1.06)	77.32	7.59	3 December 1995
<i>Phycodrys austrogeorgica</i> Skottsberg 1923	3.10	0.26 (0.17)	8.16 (4.18)	205.43	20.40	2 January 1996
<i>Picconiella plumosa</i> (Kylin) De Toni 1936	4.65	0.08 (0.04)	1.71 (0.54)	42.06	3.89	6 January 1996
<i>Plocamium cartilagineum</i> (Linné) Dixon 1967	39.53	6.79 (1.03)	16.90 (1.81)	1,502.00	148.00	1 December 1995
<i>Porphyra endiviifolium</i> (Gepp & Gepp) Chamberlain 1963	3.10	0.14 (0.10)	6.41 (2.40)	120.54	11.96	5 February 1995
<i>Porphyra plocamiestris</i> Ricker 1987	4.65	0.15 (0.09)	3.24 (1.53)	123.41	10.64	5 January 1995
<i>Sarcodia montagneana</i> (Hooker f. & Harvey) J. Agardh 1852	5.42	0.65 (0.25)	11.77 (1.93)	201.25	19.53	3 January 1996

F frequency (percentage of sample units where the species was presented), *MDB1* mean dry biomass in all the samples (g m^{-2}), *MDB2* mean dry biomass taking into account only the samples with presence of the species (g m^{-2}), *MXWB* maximum wet biomass, *MXDB* maximum dry biomass (g m^{-2})

Site and date are given for maximum biomass. Standard error of the means between brackets

Table 3 Expected dry biomass (g m^{-2}) for each species during the summer months of 1995 in sites 1 and 2

Macroalgae species	Depth (m)	January 1995	February 1995	March 1995	April 1995
<i>I. cordata</i> ^b	0	542.19	315.02	0.00	0.00
	5	0.00	33.25	42.14	31.57
<i>G. skottsbergii</i> ^b	10	28.84	15.60	26.50	0.00
<i>D. menziesii</i> ^c	5	438.95	238.17	122.24	0.00
	10	0.00	289.630	207.630	57.52
<i>D. anceps</i> ^a	20	80.48	48.45	324.10	339.80
<i>H. grandifolius</i> ^a	20	487.05	463.91	347.95	225.45
	30	1,370.06	1,622.60	1,069.15	538.52

References of the growth rates sources: ^aWiencke (1990a), ^bWiencke (1990b), ^cGómez and Wiencke (1997)

3-months studied period (4) (Table 6). The comparison of the values (4) for all the species (672.43 MT), and the respective standing stock (5) observed in March 1995 (672.34 MT) shows a negligible difference (6). Its result is

very low also when it is expressed as percent of the OB (7). This global similarity between expected and observed values is the result of the good adjustment of the five most abundant species, specially *H. grandifolius* and *D. menziesii*.

Table 4 Monthly biomass production (dry weight g m^{-2}) and P/B ratio (in bold) of main red and brown macroalgae, in sites 1 and 2 (summer months 1994–1995)

Macroalgae species	Depth (m)	December–January	January–February	February–March	March–April
<i>I. cordata</i>	0	349 1.98	167 1.30	72 1.32	0 –
	5	0 –	18 0.88	17 0.73	11 0.53
	10	7 0.40	3 0.17	4 0.36	0 –
Biomass production sum (Rhodophyceae)		356	188	93	11
<i>D. menziesii</i>	5	67 0.23	24 0.15	9 0.16	0 –
	10	0 –	29 0.13	14 0.11	2 0.04
	20	7 0.12	198 1.19	35 0.12	39 0.13
<i>H. grandifolius</i>	20	256 0.83	78 0.23	45 0.18	32 0.17
	30	740 1.04	827 1.13	401 0.80	200 0.43
Biomass production sum (Phaeophyceae)		1,070	1,156	504	273
Total biomass production		1,426	1,344	597	284

Table 5 Biomass and production at Potter Cove during the summer months of 1994 and 1995

	Depth (m)	0–5	5–10	10–20	20–30	Sum
	Area (m^2)	1,074,506	437,948	543,435	468,376	2,524,265
<i>I. cordata</i> December–January	MB (g m^{-2})	63.92	13.79	3.13	0.00	
	SS (MT)	68.68	6.04	1.70	0.00	76.42
	MP (MT)	135.99	11.96	3.37	0.00	150.37
	DP ($\text{g g}^{-1} \text{day}^{-1}$)					0.066
	F (MT)					147.69
<i>G. skottsbergii</i> December–January	MB (g m^{-2})	3.35	11.21	8.85	0.00	
	SS (MT)	3.60	4.91	4.81	0.00	13.32
	MP (MT)	1.44	1.96	1.92	0.00	5.33
	DP ($\text{g g}^{-1} \text{day}^{-1}$)					0.013
	F (MT)					12.08
<i>D. menziesii</i> December–January	MB (g m^{-2})	175.48	210.29	86.23	0.00	
	SS (MT)	188.56	92.09	46.86	0.00	327.51
	MP (MT)	43.37	21.18	10.78	0.00	75.38
	DP ($\text{g g}^{-1} \text{day}^{-1}$)					0.008
	F (MT)					182.66
<i>D. anceps</i> December–January	MB (g m^{-2})	34.37	78.09	117.86	77.47	
	SS (MT)	36.93	34.20	64.05	36.29	171.47
	MP (MT)	4.43	4.10	7.69	4.35	20.58
	DP ($\text{g g}^{-1} \text{day}^{-1}$)					0.004
	F (MT)					93.41

Table 5 continued

	Depth (m) Area (m ²)	0–5 1,074,506	5–10 437,948	10–20 543,435	20–30 468,376	Sum 2,524,265
<i>H. grandifolius</i>	MB (g m ⁻²)	0.00	22.78	144.64	440.41	
December–January	SS (MT)	0.00	9.97	78.60	206.28	294.85
	MP (MT)	0.00	8.28	65.24	193.90	267.42
	DP (g g ⁻¹ day ⁻¹)					0.030
	F (MT)					180.37
All species	SS (MT)					883.57
December–January	MP (MT)					519.97
	F (MT)					616.21
<i>I. cordata</i>	MB (g m ⁻²)	65.69	8.84	2.27	0.00	
January–February	SS (MT)	70.58	3.87	1.23	0.00	75.69
	MP (MT)	76.94	3.41	1.09	0.00	81.49
	DP (g g ⁻¹ day ⁻¹)					0.036
	F (MT)					92.40
<i>G. skottsbergii</i>	MB (g m ⁻²)	9.71	11.74	4.42	0.00	
January–February	SS (MT)	10.43	5.14	2.40	0.00	17.98
	MP (MT)	1.77	0.87	0.41	0.00	3.05
	DP (g g ⁻¹ day ⁻¹)					0.006
	F (MT)					0
<i>D. menziesii</i>	MB (g m ⁻²)	154.82	210.02	95.70	0.46	
January–February	SS (MT)	166.36	91.98	52.01	0.22	310.56
	MP (MT)	24.95	12.88	6.76	0.03	44.62
	DP (g g ⁻¹ day ⁻¹)					0.005
	F (MT)					39.63
<i>D. anceps</i>	MB (g m ⁻²)	11.98	9.56	96.67	103.74	
January–February	SS (MT)	12.87	4.19	52.53	48.59	118.18
	MP (MT)	15.32	4.98	62.52	57.82	140.64
	DP (g g ⁻¹ day ⁻¹)					0.040
	F (MT)					0.0
<i>H. grandifolius</i>	MB (g m ⁻²)	0.00	27.98	155.02	386.72	
January–February	SS (MT)	0.00	12.25	84.24	181.13	277.62
	MP (MT)	0.00	2.82	19.38	123.17	145.36
	DP (g g ⁻¹ day ⁻¹)					0.017
	F (MT)					164.20
All species	SS (MT)					800.03
January–February	MP (MT)					415.11
	F (MT)					296.00
<i>I. cordata</i>	MB (g m ⁻²)	40.54	14.19	3.18	0.00	
February–March	SS (MT)	43.56	6.21	1.73	0.00	51.5
	MP (MT)	44.87	4.54	1.26	0.00	50.76
	DP (g g ⁻¹ day ⁻¹)					0.033
	F (MT)					84.6
<i>G. skottsbergii</i>	MB (g m ⁻²)	7.34	9.5	4.54	0.00	
February–March	SS (MT)	7.89	4.16	2.47	0.00	14.52
	MP (MT)	2.84	1.50	0.89	0.00	5.23
	DP (g g ⁻¹ day ⁻¹)					0.012
	F (MT)					29.488

Table 5 continued

	Depth (m)	0–5	5–10	10–20	20–30	Sum
	Area (m ²)	1,074,506	437,948	543,435	468,376	2,524,265
<i>D. menziesii</i>	MB (g m ⁻²)	132.55	206.25	114.21	0.46	
February–March	SS (MT)	142.43	90.33	62.07	0.22	295.04
	MP (MT)	22.79	12.65	6.83	0.02	42.29
	DP (g g ⁻¹ day ⁻¹)					0.005
	F (MT)					55.14
<i>D. anceps</i>	MB (g m ⁻²)	11.98	12.05	121.40	128.75	
February–March	SS (MT)	12.87	5.28	65.97	60.30	144.42
	MP (MT)	1.54	0.63	7.92	7.24	17.33
	DP (g g ⁻¹ day ⁻¹)					0.004
	F (MT)					145.86
<i>H. grandifolius</i>	MB (g m ⁻²)	0.00	5.21	196.95	428.37	
February–March	SS (MT)	0.00	2.28	107.03	200.64	309.95
	MP (MT)	0.00	0.41	19.27	98.31	117.99
	DP (g g ⁻¹ day ⁻¹)					0.013
	F (MT)					143.08
All species	SS (MT)					815.43
February–March	MP (MT)					233.5
	F (MT)					458.17
<i>I. cordata</i>	MB (g m ⁻²)	28.33	15.32	1.82	0.00	
March–April	SS (MT)	30.44	6.71	0.99	0.00	38.14
	MP (MT)	39.57	4.9	0.72	0.00	45.19
	DP (g g ⁻¹ day ⁻¹)					0.039
<i>G. skottsbergii</i>	MB (g m ⁻²)	0.00	3.48	3.48	0.00	
March–April	SS (MT)	0.00	1.52	1.89	0.00	3.42
	MP (MT)	0.00	0.55	0.68	0.00	1.23
	DP (g g ⁻¹ day ⁻¹)					0.012
<i>D. menziesii</i>	MB (g m ⁻²)	62.46	164.62	102.17	0.00	
March–April	SS (MT)	67.11	72.09	55.52	0.00	194.73
	MP (MT)	10.74	7.93	6.11	0.00	24.78
	DP (g g ⁻¹ day ⁻¹)					0.0042
<i>D. anceps</i>	MB (g m ⁻²)	0.00	4.98	80.02	86.24	
March–April	SS (MT)	0.00	2.18	43.49	40.39	86.06
	MP (MT)	0.00	0.26	5.22	4.85	10.33
	DP (g g ⁻¹ day ⁻¹)					0.004
<i>H. grandifolius</i>	MB (g m ⁻²)	0.00	0.00	245.86	461.98	
March–April	SS (MT)	0.00	0.00	133.61	216.38	349.99
	MP (MT)	0.00	0.00	24.05	106.3	130.08
	DP (g g ⁻¹ day ⁻¹)					0.012
All species	SS (TM)					672.34
March–April	MP (MT)					211.61
All species	SS (MT)	Average in December–April				792.84
	MP (MT)	Accumulated in December–April				1,401.33
	MP (MT)	Accumulated in December–March				1,167.83
	F (MT)	Accumulated in December–March				1,370.61

MB mean biomass (g m⁻²), *SS* average standing stock (MT), *MP* monthly production (MT), *DP* daily production (g g⁻¹day⁻¹)
Mean biomass and standing stock are average values for each month and depth. Biomass flux to ecosystem (*F*) (MT)

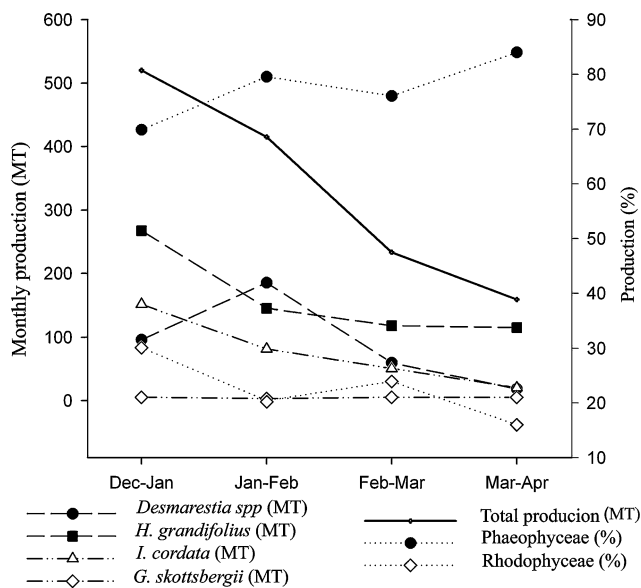


Fig. 2 Monthly biomass production (right) of the most abundant seaweed species (MT). Percentage of Phaeophyceae and Rhodophyceae production (left) during the summer 1994–1995

Discussion

Although macroalgal biomass data from several Antarctic localities have been published, up to now no results on production are available. This is the first estimation of the seaweed production in Antarctica, combining biomass data with experimentally obtained growth rates.

Biomass of Antarctic macroalgae has been usually reported as maximum wet or dry weight (Table 7). This is valuable information to compare different Antarctic seasons and localities. For instance, the maximum wet biomass of *D. anceps*, *D. menziesii* and *H. grandifolius* reported for summer conditions by Brouwer et al. (1995) at Signy Island was 8,800 g m⁻², which is more than four

times the value of 2,050 g m⁻² found by Richardson (1979) in winter at the same locality. These differences could be explained by the life strategies of the Desmarestiales, which start growing in winter and reach maximum biomass in spring–summer (Drew and Hastings 1992). Considering the phenology of some subtidal species Kain (1989) observed that some algae “anticipate” favorable seasons while others “respond” to them. Antarctic season anticipators (*D. anceps*, *D. menziesii* and *H. grandifolius*) starting growth in the winter season. Seasonal growth and reproduction in these species is based on photoperiodism and circannual rhythms and is synchronised by daylength (Wiencke 1996). The macroalgae of the second group (*I. cordata* and *G. skottsbergii*), as season responders start growth in spring and summer (Kirst and Wiencke 1995). In the present study, the macroalgal biomass and also the production of Desmarestiales showed a general decreasing trend during the summer, supporting the view that growth rates of season anticipators are higher in spring than in summer (Wiencke 1996; Wiencke and Clayton 2002).

Our study confirms previous results that *D. anceps*, *D. menziesii* and *H. grandifolius* are the species with the highest biomass in the Antarctic Peninsula. Their mean wet biomass in Potter Cove at 5–30 m depth, ranged from 2,400 to 9,600 g m⁻², which is similar to results from Anvers Island (64°46'S, 64°04'W) (Amsler et al. 1995) (4,500–5,200 g m⁻² at 5–15 m depth). In contrast to our results the macroalgal communities of Ross Sea (74°30'S, 165°42'W; 74°54'S, 163°54'W) are dominated by *I. cordata* and *Phyllophora antarctica* (Cormaci et al. 1996, 1998). The mean wet biomass of *I. cordata* at Potter Cove was 262.9 g m⁻², which is lower than values found in the Ross Sea by Miller and Pearse (1991), who reported 376.2 g m⁻². These values are of the same order of magnitude in spite of the absence of Desmarestiales in the Ross Sea which could act as strong competitors.

Table 6 Summary of results in Potter Cove

	(1)	(2)	(3)	(4)	(5)
<i>I. cordata</i>	76.42	282.62	324.69	34.35	38.14
<i>G. skottsbergii</i>	13.32	13.60	41.56	-14.64	3.42
<i>D. menziesii</i>	320.00	162.29	277.44	204.86	194.73
<i>D. anceps</i>	171.47	178.54	239.27	110.74	86.06
<i>H. grandifolius</i>	294.00	530.78	487.65	337.13	349.99
All species	875.21	1,167.83	1,370.61	672.43	672.34
All species	(6) = (4) - (5) = 0.094				
All species	(7) = (6)/(5) × 100 = 0.0046%				

(1) Average standing stock at the period December 1994 to January 1995. (2) Monthly production during the period December 1994 to March 1995. (3) Biomass flux to ecosystem during the period December 1994 to March 1995. (4) Expected biomass at the end of the study [= (1) + (2) - (3)]. (5) Observed biomass at the end of the summer. (6) Difference between expected and observed biomass at the end of the period December 1994 to March 1995 for all the species. (7) Percentage of the difference between observed and expected remaining biomass for all the species. All the values are in metric tons (MT)

Table 7 Maximum biomass of macroalgae (g m^{-2}) (wet or dry weight), reported by different authors (depths between brackets when provided by the authors)

	Locality	<i>Desmarestia anceps</i>	<i>Desmarestia menziesii</i>	<i>Himantothallus grandifolius</i>	<i>Iridaea cordata</i>	Reference
Wet weight	(1)	–	2,050	–	–	Richardson (1979)
	(2)	5,660 (11 m)	1,850 (11 m)	1,250 (11 m)	–	Brouwer et al. (1995)
	(3)	–	–	–	3,440 (4–5 m)	Cormaci et al. (1996)
	(4)	6,044 (20 m)	6,737 (5 m)	10,336 (20 m)	2,554.60 (0 m)	This study
Dry weight	(5)	–	800 (4 m)	600 (12 m)	–	DeLaca and Lipps (1976)
	(2)	1,000 (11 m)	460 (11 m)	240 (11 m)	–	Brouwer et al. (1995)
		3,300 (5 m)	–	–	–	
	(4)	671 (20 m)	749 (5 m)	1,152 (20 m)	255.36 (0 m)	This study

Localities: (1) Borge Bay, South Orkney Islands (60°43'S, 45°36'W). (2) Signy Island, South Orkney Islands (60°42'S 45°36'W). (3) Ross Sea (74°30'S, 165°30'E). (4) Potter Cove, South Shetland Islands (62°14'S, 58°38'W). (5) Anvers Island (64°46'S, 64°04'W)

Field production or photosynthesis studies are useful to compare the performance of individual species at different times and depths. Brouwer (1996b) found a wide range of variation in the yearly production of *Myriogramme mangini* (0.6–128.1 $\mu\text{mol O}_2 \text{g}^{-1} \text{DW}$). Gómez et al. (1997) studied the metabolic carbon balance under laboratory conditions of five brown and red algal species from different depths at Potter Cove. They observed that the carbon gains are higher in plants growing at 10 and 20 m depth that at 30 m depth the algal exhibited gains lower than 1 mg C $\text{g}^{-1} \text{FW day}^{-1}$. According with our results, biomass accumulation occurs previously during the spring months. This fact strongly supports the view of Gómez et al. (1997) who considered that the light environment in spring provides favorable conditions for macroalgal photosynthesis even at greater depths.

Other phycological studies outside the Antarctic have focused on net production, thallus growth or population dynamics (Silverthorne 1977; De Wreede 1985). Attwood et al. (1991) estimated the production of *Macrocystis laevis* through the thallus growth at Prince Edward Island and Rice and Chapman (1982) calculated net production in *Chordaria flagelliformis* in Nova Scotia through changes in biomass over time. Such studies do not allow to estimate the loss of biomass to the community.

After detached, macroalgae can sink to seabed hollows, be washed ashore or drift in the sea (Klöser et al. 1994). Piles of drifted seaweeds are used as resting places by seal and sea elephants (Brouwer 1996a). The mix of macroalgae, coastal sediments and seals excrements improve the development of the microorganisms, which decompose organic matter and increase remineralization (Zielinski 1981). On the other hand Brouwer (1996a), considered that decomposition of detached *D. anceps* is mainly due to physical agents like waves and currents rather than to microbial action. The excess production of the benthic compartment has two possible fates, to be stored in sediments by burial therein or to be exported to the pelagic compartment (Duarte et al. 2005).

Duarte and Cebrián (1996) reviewed data from the literature about the carbon pathways for several marine primary producers, including macroalgae. They concluded that decomposition within the system is an important process and macrophytes, accounted for more than 40% of the oceanic net primary production. The herbivore pressure on macroalgae and biomass export is significant but storage within the sediments would be negligible for macroalgal communities (Duarte and Cebrian 1996). Furthermore, carbon in the form of dissolved organic material (DOM) lost by seaweed as exudates, mucilage and phenolic or nitrogen compounds may be, according to Khailov and Burlakova (1969) and Sieburth (1969), as high as 30–40% of the net assimilates.

Macroalgal biomass can be available to the benthic fauna through herbivory or by thallus fragmentation followed by bacterial degradation or by spore release. It has been shown that seaweeds are a main source of particulate matter (Fischer and Wiencke 1992), available to filter feeders, and also of dissolved organic carbon (Gutt et al. 1998; Duarte et al. 2005). The extensive community of macroalgae at the outer side of Potter Cove provides habitat, shelter and food to different benthic organisms (Momo et al. 1998; Iken et al. 1998). As Potter Cove is a very low phytoplankton biomass accumulation system (Schloss and Ferreyra 2002), the rich benthic fauna present in the zone must depend on other food sources. This hypothesis is supported by Tatián et al. (2004) who found macroalgal debris in the gut contents of ascidians and other suspension feeders of the benthic community of Potter Cove Corbisier et al. (2004) observed that the soft-bottom community in the shallow zone of Martel Inlet (62°04'S, 58°21'W) was enriched in ^{13}C due to the significant input of carbon from both microphytobenthos and macroalgal fragments. Westermeyer et al. (1992) reported that the algal debris at Bahía Elefante (62°10'S; 58°55'W) was mostly composed of red algae *Palmaria decipiens* (as *Leptosomia simplex*) and *Iridaea cordata* (as *I. obovata*). Additionally, ongoing surveys of the sublittoral benthos in Potter cove by scuba

diving (down to 30 m deep) detected algal debris accumulation, both in crevices and small depressions of the bare plains, devoid of attached macroalgae and colonized by a rich sessile fauna (G. Mercuri, personal communication).

Macroalgae are also a food item in the diet of different herbivorous. According to Iken et al. (1997, 1998) in Potter Cove the limpet *Nacella concinna* feeds mainly on crustose red algae and *A. mirabilis*, while the isopod *Plakarthrium punctatissimum* particularly feeds on *C. racovitzae* and *A. mirabilis*. Other herbivores such as the gastropod *Laevilacunaria antarctica* are generalists and graze on several algal species as *Palmaria decipiens*, *Monostroma hariotii*, *D. menziesii* and *I. cordata*. Recently, studies also showed that the amphipods *Prostebbingia gracilis* and *Gondogeneia antarctica* exhibited their highest consumption rates when grazing on the thalli of the red alga *Palmaria decipiens* (Huang et al. 2006). More recent observations by Barrera Oro and Casaux (1990) and Iken et al. (1997, 1999) concluded that this species ingest macroalgae as proper food items.

The daily production of *D. menziesii* was $0.001 \text{ g g}^{-1} \text{ day}^{-1}$ at the end of summer in Potter Cove. A similar value ($0.0015 \text{ g g}^{-1} \text{ day}^{-1}$) was registered for *Laminaria solidungula* growing in the Arctic at 8 m depth (Chapman and Lindley 1980). In our study the intertidal *I. cordata* presented a daily production of $0.06 \text{ g g}^{-1} \text{ day}^{-1}$ during December–January, almost the same value was observed by Rice and Chapman (1982) who registered $0.06 \text{ g g}^{-1} \text{ day}^{-1}$ for *Chordaria flagelliformis* in the intertidal of Nova Scotia (Canada).

Öberg (2006) used measures through one year of macroalgal coverage, nutrients, temperature and irradiation together with productivity estimates from literature with the aim to calculate seaweed production at a transitional zone between the Baltic Sea and the North Sea. He transformed cover to biomass and calculate the relationship *P/B* from model simulations. To use this interesting approach in Antarctic, more biomass data are required from other seasons of the year and more laboratory production determinations under different nutrient concentrations. Our calculations are rather simple the only theoretical assumption was that of exponential growth between sampling dates. The present data fit well with this assumption except in the case of *D. anceps* between December 1994 and January 1995 in sites 1 and 2. This species presented low biomass in the field during December 1994–January 1995 and the low productivity data available ($0.006 \text{ g g}^{-1} \text{ day}^{-1}$) cannot explain the high biomass present in the next period. The summer production of Potter Cove was 1,401.33 MT, equivalent to 1.76 times the mean biomass present in the cove during the whole study. The daily production of the most abundant macroalgae species was of

$0.01466 \text{ g g}^{-1} \text{ day}^{-1}$. The maximum production was measured at early summer, followed by a trend towards a biomass reduction along the subsequent 3 months.

The calculated flux of biomass to the ecosystem of Potter Cove in the period December–March was 1370.61 (MT). This result shows that during summer the net growth of the thalli is not important compared to the flux to the ecosystem. Summer production and net standing stock losses nearly accounted for biomass flux. This fact supports the assumptions presented in the methodology about the relationships between biomass production and initial biomass in the field within each monthly period. The permanent biomass flux to the ecosystem justifies the application of the exponential growth model proposed in the methods section by keeping the biomass at low levels, and considering competition less important. Under these conditions the growth rate remains constant if related to the biomass quantities present at the start of each monthly period. Nevertheless, the biomass production in the whole cove, or the biomass by square meter, decreased as a result of the continuous losses of growing biomass.

As far as we know this study is the first analysis of macroalgal production in Antarctica in which a relationship between biomass changes observed in the field and growth rates are considered together. If available, field production determinations can also be used in combination with biomass data. We consider that this attempt to relate changes of standing stock in the field and growth rates determined in laboratory to obtain production and flux of biomass to the ecosystem is the first step to a more formal and general model of macroalgal production in Antarctic environments. However, further studies are needed on topics such as size of thalli and population density growth rates at different seasons for a better understanding of the mechanisms involved in these dynamics. Studies about the degradation of tissues to debris of the different macroalgae species, the effects of herbivory and the fate of the different fractions of the biomass flux to the ecosystem are also needed.

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References

- Amsler CD, Rowley RJ, Laur DR, Quentin LB, Ross RM (1995) Vertical distribution of Antarctic peninsular macroalgae: cover, biomass and species composition. *Phycologia* 34:424–430
- Attwood CG, Lucas MI, Probyn TA, McQuaid CD, Fielding PJ (1991) Production and standing stocks of the kelp *Macrocystis*

- laevis Hay at the Prince Edward Islands, Subantarctic. *Polar Biol* 11:129–133
- Barrera Oro ER, Casaux RJ (1990) Feeding selectivity in *Notothenia neglecta* Nybelin, from Potter Cove, South Shetland Islands, Antarctica. *Antarct Sci* 2:207–213
- Bellamy DJ, Wittick A, John DM, Jones DJ (1973) A method for the determination of seaweed production based on biomass estimates. In: A guide to measurement of primary production under some special conditions. Unesco, Monogr Oceanogr Methodol 3 Paris, pp 27–33
- Brouwer PEM (1996a) Decomposition in situ of the sublittoral Antarctic macroalgae *Desmarestia anceps* Montagne. *Polar Biol* 16:129–137
- Brouwer PEM (1996b) In situ photosynthesis and estimated annual production of the red macroalgae *Myriogramme mangini* in relation to underwater irradiance at Signy Island (Antarctica). *Antarct Sci* 8(3):245–253
- Brouwer PEM, Geilen EFM, Gremmen NJM, Van Lent F (1995) Biomass, cover and zonation pattern of sublittoral macroalgae at Signy Island, South Orkney Islands, Antarctica. *Bot Mar* 38:259–270
- Chapman ARO, Lindley JE (1980) Seasonal growth of *Laminaria solidungula* in the Canadian High Arctic in relation to irradiance and dissolved nutrient concentrations. *Mar Biol* 57:1–5
- Clayton MN (1994) Evolution of the Antarctic marine benthic algal flora. *J Phycol* 30:897–904
- Corbisier TN, Petti MAV, Skowronski RSP, Brito TAs (2004) Trophic relationships in the nearshore zone of martel inlet (King George Island, Antarctica): $\delta^{13}C$ stable-isotope analysis. *Polar Biol* 27:75–82. doi:10.1007/s00300-003-0567-z
- Cormaci M, Furnari G, Scammacca B, Alongi G (1996) Summer biomass of a population of *Iridaea cordata* (Gigartinales, Rhodophyta) from Antarctica. *Hydrobiologia* 326/327:267–272
- Cormaci M, Furnari G, Scammacca B, Alongi G, Catra M (1998) Summer biomass of a population of *Phyllophora antarctica* (Phylloporaceae, Rhodophyta) from Antarctica. *Hydrobiologia* 362:85–91
- DeLaca TE, Lipps JH (1976) Shallow-water marine associations, Antarctic Peninsula. *Antarct J US* 11:12–20
- De Wreede RE (1985) Destructive (harvest) sampling. In: Littler MM, Littler DS (eds) Ecological field methods: macroalgae. Handbook of phycological methods. Cambridge University Press, Cambridge, pp 147–160
- Drew EA, Hastings RM (1992) A year-round ecophysiological study of *Himantothallus grandifolius* (Desmarestiales, Phaeophyta) at Signy Island, Antarctica. *Phycologia* 31:262–277
- Duarte CM, Cebrián J (1996) The fate of marine autotrophic production. *Limnol Oceanogr* 41(8):1758–1766
- Duarte CM, Middeburg JJ, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2:1–8. ID:1726-4189/bg/2005-2-1
- Fischer G, Wiencke C (1992) Stable carbon isotope composition, depth distribution and fate of macroalgae from the Antarctic Peninsula Region. *Polar Biol* 12:341–348
- Gómez I, Wiencke C (1997) Seasonal growth and photosynthetic performance of Antarctic macroalgae *Desmarestia menziesii* (Phaeophyceae) cultivated under fluctuating Antarctic day-lengths. *Bot Acta* 110:25–31
- Gómez I, Weykam G, Klöser H, Wiencke C (1997) Photosynthetic light requirements, daily carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica). *Mar Ecol Prog Ser* 148:281–293
- Gutt J, Starmans A, Dieckmann G (1998) Phytodetritus deposited on the Antarctic shelf and upper slope: its relevance for the benthic system. *J Mar Syst* 17:435–444
- Hanisak MD (1992) Nitrogen release from decomposing seaweeds: species and temperature effects. *J Appl Phycol* 5:175–181
- Huang YM, McClintock JB, Amsler CD, Peters KJ, Baker BJ (2006) Feeding rates of common Antarctic gammarid amphipods on ecologically important sympatric macroalgae. *J Exp Mar Biol Ecol* 329:55–65
- Iken K, Barrera-Oro E, Quartino ML, Casaux RJ, Brey T (1997) Grazing by the antarctic fish *Notothenia coriiceps*: evidence for selective feeding on macroalgae. *Antarct Sci* 9(4):386–391
- Iken K, Quartino ML, Barrera Oro E, Palermo J, Wiencke C, Brey T (1998) Trophic relations between macroalgae and herbivores in Potter Cove (King George Island, Antarctica). In: Wiencke C, Ferreyra G, Arntz W, Rinaldi C (eds) The Potter Cove coastal ecosystem, Antarctica. *Rep Polar Res* 299:258–262
- Iken K, Quartino ML, Wiencke C (1999) Histological identification of macroalgae from stomach contents of the Antarctic fish *Notothenia coriiceps* using semi-thin sections. *Mar Ecol* 20(1):11–17
- Israel A (1995) Determinación de la producción primaria en macroalgas marinas. In: Alveal K, Ferrario ME, Oliveira EC, Sar E (eds) Manual de Métodos Ficológicos. Universidad de Concepción, Chile, pp 795–823
- Kain JM (1989) The seasons in the subtidal. *Br Phycol J* 24:203–215
- Khailov KM, Burlakova ZP (1969) Release of dissolved organic matter by marine seaweeds and distribution of their total organic production to inshore communities. *Limnol Oceanogr* 14:521–527
- Kirst GO, Wiencke C (1995) Ecophysiology of polar algae. *J Phycol* 31:181–199
- Klöser H, Mercuri G, Laturnus F, Quartino ML, Wiencke C (1994) On the competitive balance of macroalgae at Potter Cove (King George Island, South Shetlands). *Polar Biol* 14:11–16
- Klöser H, Quartino ML, Wiencke C (1996) Distribution of macroalgae and macroalgal communities in gradients of physical conditions in Potter Cove, King George Island, Antarctica. *Hydrobiologia* 333:1–17
- Mann KH (1972) Ecological energetics of the seaweeds zone in a marine bay on the Atlantic coast of Canada. II Productivity of seaweeds. *Mar Biol* 14:199–209
- Miller KA, Pearse JS (1991) Ecological studies of seaweeds in McMurdo Sound, Antarctica. *Am Zool* 31:35–48
- Moe RL, Silva PC (1977) Antarctic marine flora: uniquely devoid of kelps. *Science* 196:1206–1208
- Momo F, Bogazzi E, Duttweiler F (1998) Amphipods of Potter Cove: community composition, biology and growth. In: Wiencke C, Ferreyra G, Arntz W, Rinaldi C (eds) The Potter Cove coastal ecosystem, Antarctica. *Rep Polar Res* 299:144–149
- Öberg J (2006) Primary production by macroalgae in Kattégat, estimated from monitoring data, seafloor properties and model simulation. *Cont Shelf Res* 26:2415–2432
- Quartino ML, Klöser H, Schloss IR, Wiencke C (2001) Biomass and associations of benthic marine macroalgae from the inner Potter Cove (King George Island, Antarctica) related to depth and substrate. *Polar Biol* 24:349–355. doi:10.1007/s003000000218
- Quartino ML, Boraso de Zaixso AL, Zaixso H (2005) Biological and environmental characterization of marine macroalgal assemblages in Potter Cove, South Shetland Islands, Antarctica. *Bot Mar* 48:187–197. doi:10.1515/BOT.2005.029
- Rice EL, Chapman ARO (1982) Net productivity of two cohorts of *Chordaria flagelliformis* (Phaeophyta) in Nova Scotia, Canada. *Mar Biol* 71:107–111
- Richardson MG (1979) The distribution of Antarctic marine macroalgae related to depth and substrate. *Br Antarct Surv Bull* 49:1–13
- Sahade R, Tatián M, Esnal GB (2004) Reproductive ecology of the ascidian *Cnemidocarpa verrucosa* at Potter Cove, South Shetland Islands, Antarctica. *Mar Ecol Prog Ser* 272:131–140

- Schloss I, Ferreyra GA (2002) Primary production light and vertical mixing in Potter Cove a shallow bay in the maritime Antarctic. *Polar Biol* 25:42–48. doi:[10.1007/s003000100309](https://doi.org/10.1007/s003000100309)
- Sieburth JMcN (1969) Studies on algal substances in the sea. III. Production of extracellular organic matter by littoral marine algae. *J Exp Mar Biol Ecol* 3:290–309
- Silverthorne W (1977) Optimal production from seaweed resource. *Bot Mar* 20:75–98
- Tatián M, Sahade R, Esnal G (2004) Diet components in the food of Antarctic ascidians living at low levels of primary production. *Antarct Sci* 16(2):123–128. doi:[10.1017/s0954102004001890](https://doi.org/10.1017/s0954102004001890)
- Westermeier R, Gómez I, Rivera PJ, Müller DG (1992) Macroalgas marinas antárticas: distribución, abundancia y necromasa en Isla Rey Jorge, Shetland del Sur, Antártida. *Ser Cient INACH* 42:21–34
- Wiencke C (1990a) Seasonality of brown macroalgae from Antarctica a long-term culture study under fluctuating Antarctic daylengths. *Polar Biol* 10:589–600
- Wiencke C (1990b) Seasonality of red and green macroalgae from Antarctica—long-term culture study under fluctuating Antarctic daylengths. *Polar Biol* 10:601–607
- Wiencke C (1996) Recent advances in the investigation of Antarctic macroalgae. *Polar Biol* 16:231–240
- Wiencke C, Clayton MN (2002) Antarctic seaweeds. In: Wägelee JW (eds) *Synopses of the Antarctic benthos*. ARG Ganter Verlag KG Ruggell, Lichtenstein, pp 1–239
- Zielinski K (1981) Benthic macroalgae of Admiralty Bay (King George Island, South Shetland Islands, Antarctica) and circulation of algal matter between the water and the shore. *Polish Polar Res* 2:71–94