

Marine productivity enhancement around Bouvet and the South Sandwich Islands (Southern Ocean)

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ABSTRACT: Selected physico-chemical and biological properties were compared between shelf and deep oceanic waters in the vicinity of Bouvet and the South Sandwich Islands during the austral summers of 1982–1983 and 1990–1991. On 3 of these occasions circuminsular chlorophyll *a* levels were 3 to 7 mg chl *a* m⁻³, an increase of 3 to 4 times over off-shore stations. At South Sandwich in 1990–1991 high phaeopigment levels indicated senescence of the phytoplankton bloom and primary production on this occasion was not markedly greater than in off-shore waters. On 2 occasions (Bouvet 1990–1991, South Sandwich 1982–1983) high chlorophyll concentrations were associated with a marked increase in production (up to ca 280 mg C m⁻² h⁻¹ in 1982–1983 and ca 1.5 mg C m⁻³ h⁻¹ in 1990–1991). This combination of high chl *a* and production levels was associated with depletion of dissolved nutrients. Size fractionation during summer 1990–1991 indicated dominance (ca 70 % of total chl) by netphytoplankton (20 to 200 µm) at Bouvet and by nanoplankton (1 to 20 µm, 70 % of total chl) at South Sandwich. Sharp drops in temperature and salinity over the island shelves, and spatial covariance between upper mixed layer depth and chl *a* concentration, suggest that stabilisation by meltwater may be the main cause of phytoplankton bloom formation. The present and published data suggest a longitudinal trend of decreasing phytoplankton production from Antarctic Peninsula archipelagos to islands in the Indian Ocean sector of the Southern Ocean. This may have implications for the estimation of total carbon flux in Antarctic waters.

INTRODUCTION

Southern Ocean waters generally exhibit low phytoplankton production and standing stock despite uniquely high nutrient content (El Sayed 1988, Jacques 1989, de Baar et al. 1990), a phenomenon known as the Antarctic Paradox (Treguer & Jacques 1986). There are, however, regions where elevated levels of productivity are repeatedly found during the austral spring and summer. These are mainly at oceanic fronts (Fukuchi 1980, Lutjeharms et al. 1985, Bidigare et al. 1986), in the marginal ice zone (Smith & Nelson 1985, 1990), in the neritic waters of the Antarctic Peninsula (El Sayed 1968, 1988, Holm-Hansen & Mitchell 1991) and in the vicinity of oceanic islands (Horne et al. 1969, El Sayed & Jitts 1973, El Sayed et al. 1979, Boden 1988, Perissinotto & Duncombe Rae 1990).

Southern Ocean islands have a particular ecological importance as they support enormous populations of seabirds and mammals. The deep water region of the Southern Ocean extends from 35 to 70° S, and breeding of these land-based predators is largely restricted to 23 small island groups. Their impact on marine food resources is expected to be greatest in these localized

areas, but it is not known whether their food requirements can generally be met entirely by the ecosystem of the island seas (Croxall 1984, Siegfried 1985).

Islands in general may exhibit a marked increase in the biological productivity of circuminsular waters, compared to the surrounding open ocean; the 'Island Mass Effect' or IME (Doty & Oguri 1956, Heywood et al. 1990). In the Southern Ocean this effect has been associated with 2 main causes: (1) micronutrient (iron) availability (Martin 1990, Martin et al. 1990) and (2) dynamic interactions between oceanic circulation and shelf topography (Allanson et al. 1985, Heywood & Priddle 1987, Perissinotto & Duncombe Rae 1990).

Enhanced biological productivity around several Southern Ocean islands, especially in the sub-Antarctic and the Scotia Sea, is now well documented (Planke 1977, El Sayed & Turner 1978, Allanson et al. 1985, Priddle et al. 1986, von Bodungen 1986, Perissinotto & Duncombe Rae 1990). However, for many Antarctic islands available data are very limited and it is unclear how widespread this effect is. In most cases, the hypothesised occurrence of an island mass effect has not been demonstrated (Lutjeharms et al. 1985, Bidigare et al. 1986).

During the annual relief voyage of the SA 'Agulhas' to the South African Antarctic base of SANAE, an investigation in the vicinity of Bouvet and the South Sandwich Islands was carried out to compare phytoplankton biomass and productivity in shelf and open ocean waters. These 2 island systems are among the most remote and southerly of all the Antarctic islands (Fig. 1), being located ca 200 km south of the Antarctic Polar Front (APF) and thus permanently within the domain of the Antarctic Surface Water (ASW) mass.

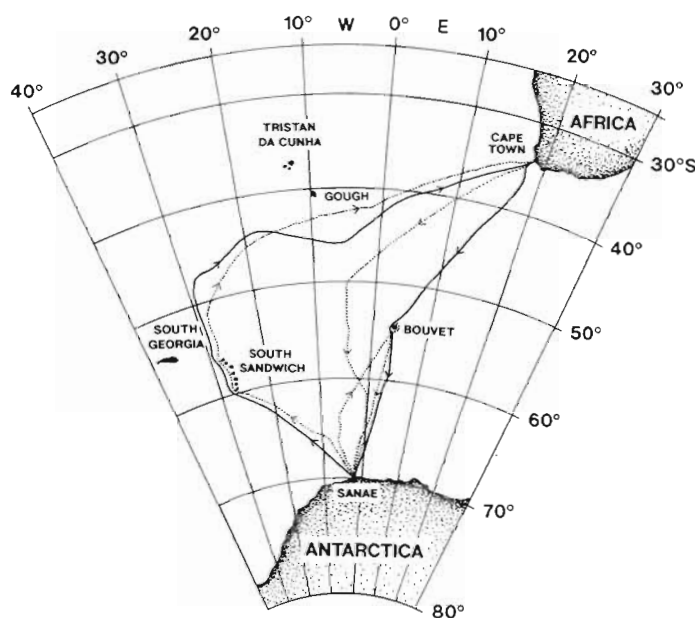


Fig. 1 Position of the South Sandwich and Bouvet Islands in the Southern Ocean and cruise tracks during summer 1982–1983 (—) and 1990–1991 (---).

MATERIALS AND METHODS

Data were collected during the austral summer on 2 cruises, December 1982 through January 1983 and December 1990 through February 1991. Continuous underway records of sea surface temperature and acoustic backscattering were obtained with the ship's temperature probe and an NEC, NS-74 Deep-Sea echosounder (max. penetration depth ca 6000 m) operated at 12 kHz. Calibration of the temperature probe was made by regular measurements with a Crawford Bucket (Crawford 1972). During the 1982–1983 cruise, vertical profiles of temperature to a depth of 450 m were obtained using expendable bathythermographs (XBTs) along a transect from SANAE to the South Sandwich Archipelago. XBTs were launched at regular intervals of ca 30' to 1° latitude. Surface salinity data were also collected during this cruise. Along each entire cruise track (Fig. 1), water samples were collected at regular inter-

vals of ca 20' latitude for analysis of nutrients and pigments. In 1990–1991, samples for the estimation of phytoplankton cell concentration were also taken with the same frequency. In the vicinity of Bouvet and the South Sandwich Islands, the sampling frequency was increased to a station every 5 to 10' latitude. A shipboard pump (Iwaki Magnet Pump), fabricated from polyvinylidene fluoride and ceramic materials, and operated at a flow rate of ca 4 l min⁻¹, was used to collect the water samples. The pump inlet was positioned ca 5 m below sea level and seawater was supplied to the laboratory through PVC piping. Details on the suitability of this method of pump sampling are described by Allanson et al. (1981). For the taxonomic analysis of net-phytoplankton standing stock, a 20 µm mesh filtration unit (Berman & Kimor 1983) was connected to the pump outlet and a constant volume of 25 l of seawater was filtered at each station. The major phytoplankton taxa in aliquots retained by the filter were then counted using an inverted microscope, after sedimentation in 10 ml chambers (Hasle 1978).

During the summer of 1982–1983, spectrophotometric determination of chl *a* concentration was made following the SCOR/UNESCO WG 17(1966) method. In 1990–1991 both chl *a* and phaeopigment levels were calculated from the fluorescence readings of a Turner Model 111 fluorometer (Strickland & Parsons 1968). Prior to pigment analysis, phytoplankton were separated into 3 size-classes by multiple serial filtration. These included net- (200–20 µm), nano- (20–1.0 µm) and picoplankton (1.0–0.2 µm). Phytoplankton production was measured at selected stations during both cruises. In 1982–1983, integrated primary production, $\Sigma P = P_{\max} \times Z_{0.1}$ (where P_{\max} = maximum photosynthetic rate and $Z_{0.1}$ = measured 10 % light depth), was estimated from ¹⁴C uptake rates obtained with the on-board incubation technique of Gargas et al. (1976). This method, described in detail by Allanson et al. (1981), required low specific activities of ca 0.04 µCi ml⁻¹ and involved an incubation period of 4 h. The light regime included no light, full incident radiation (Phillips Daylight fluorescent tubes) and 4 levels determined by an array of neutral density filters with transmission values of 50, 25, 10 and 5 % of the incident light. During summer 1990–1991, a small-volume, rapid incubation (20 min) technique based on the photosynthetron of Lewis & Smith (1983) was used to estimate surface production rates. In this case, the ¹⁴C specific activity was ca 5 µCi ml⁻¹. A 2000 W tungsten halogen lamp was used as a light source and a wide range of neutral density filters provided 36 different irradiance levels. At each production station, measurements of photosynthetically available radiation (PAR, µE m⁻² s⁻¹) in the euphotic layer were obtained with a Li-Cor 192S quantum sensor (1982–1983) or with a Biospherical Instruments, QSP 170B, irradiance meter (1990–1991).

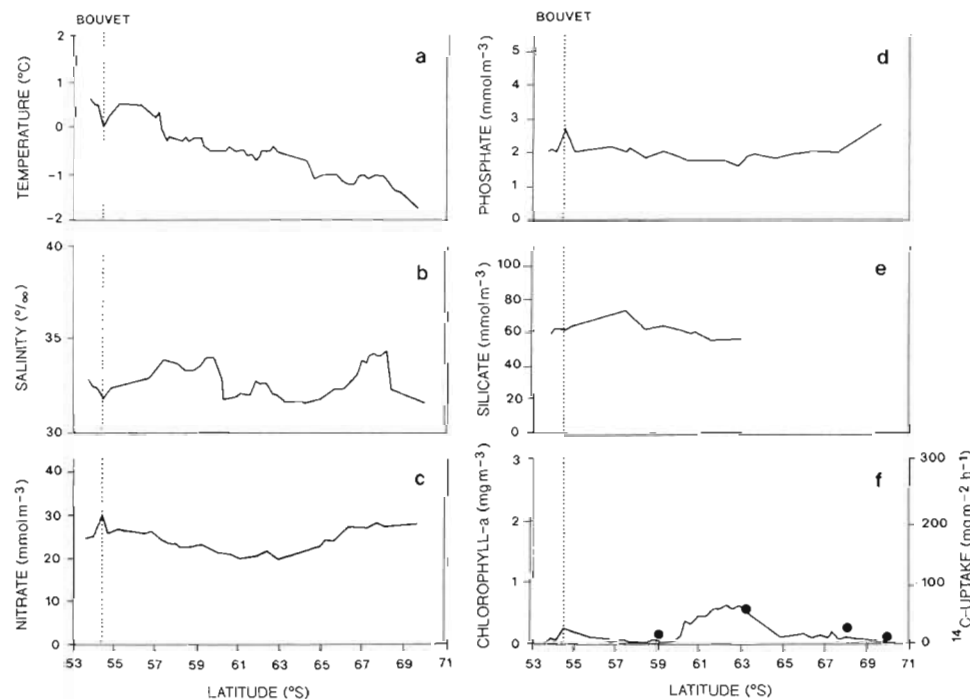


Fig. 2. Latitudinal profiles of the physical, chemical and biological parameters measured along the Bouvet-SANAE transect in 1982–1983. (●) Rates of phytoplankton ^{14}C -uptake. Dotted lines indicate position of island shelf edge

For the on-board chemical analysis of the major inorganic nutrients (silicate, nitrate, nitrite and phosphate) a Technicon AA-II Autoanalyser system was used according to Strickland & Parsons (1968) and Mostert (1983). In addition, measurements of ammonia concentrations were made during the 1990–1991 cruise following the method of Koroleff (1983), scaled down to 5 ml samples (Probyn & Painting 1985).

RESULTS

Horizontal profiles of temperature and salinity for summer 1982–1983 indicate a consistent drop in both parameters as the 2 island systems were approached (Figs. 2a, b & 3a, b). These halothermic depressions were similar in magnitude to those recorded at receding ice-edges and ranged between 0.5 to 1.5 °C

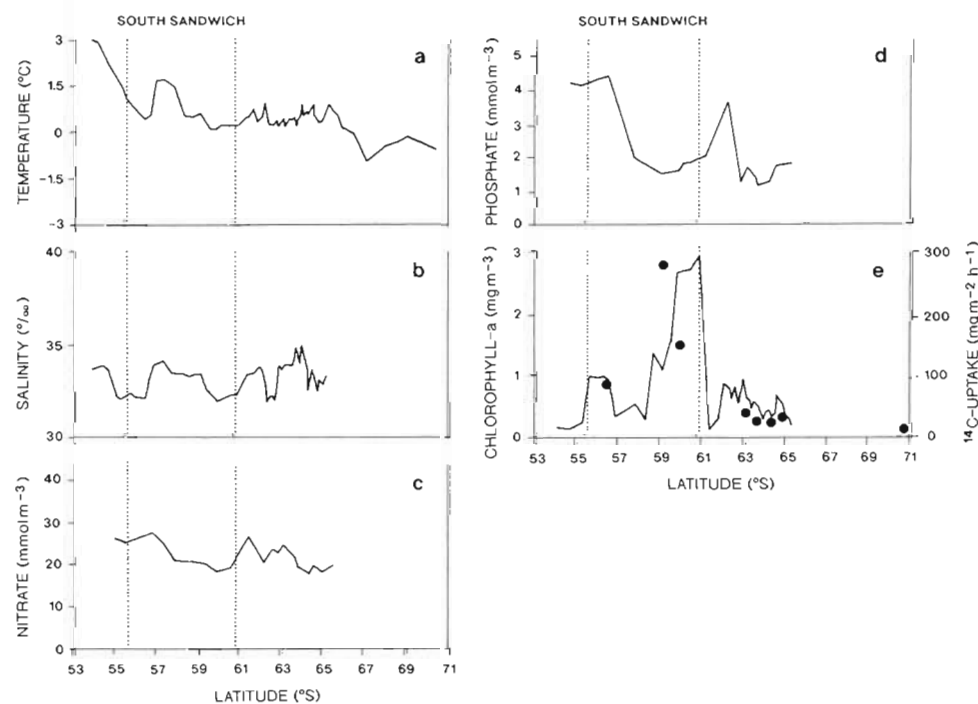


Fig. 3. As in Fig. 2 but for the SANAE-South Sandwich transect

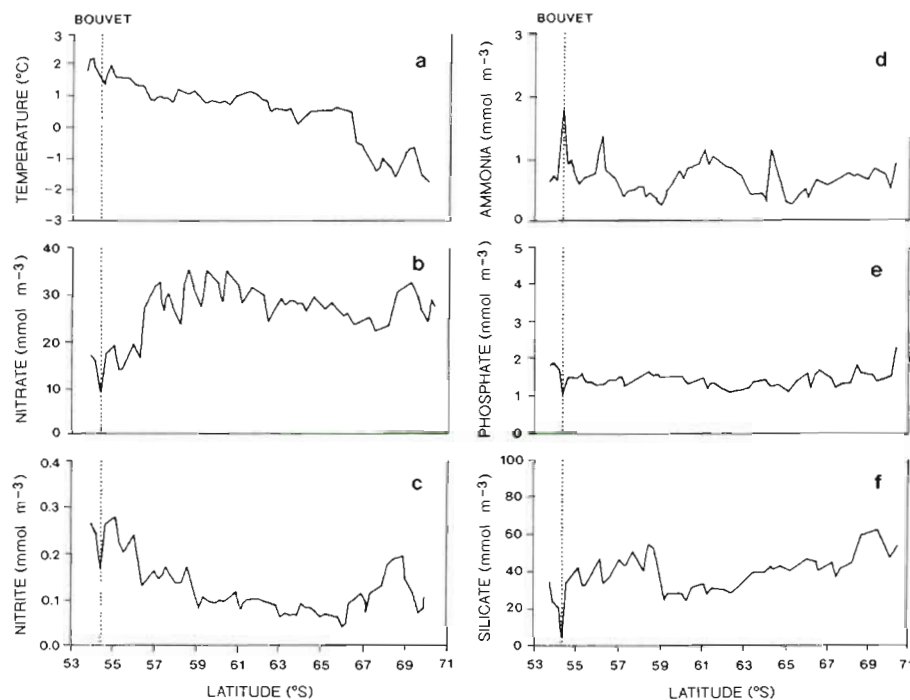


Fig. 4. Latitudinal profiles of surface temperature and nutrient levels along the SANA-E-Bouvet transect during summer 1990–1991. Dotted lines indicate position of island shelf edge

and 1 to 3 ‰. However, unlike the surface waters of the ice-edge, surface temperature values at the islands were never below zero. The same basic thermal structure was observed in the proximity of the islands during summer 1990–1991, although in this case temperature values were markedly higher than during the previous occasion (ranges: 1 to 2 °C in 1990–1991 vs 0 to 1 °C in 1982–1983; Figs. 2a, 3a, 4a & 5a).

Surface macronutrient concentrations frequently showed marked changes in the transition from deep to shelf waters. They also showed some differences between the 2 island systems and varied considerably from year to year. On the Bouvet shelf, levels of dissolved nutrients measured on both cruises were much lower during 1990–1991 than in 1982–1983. During the first cruise, values over the shelf were

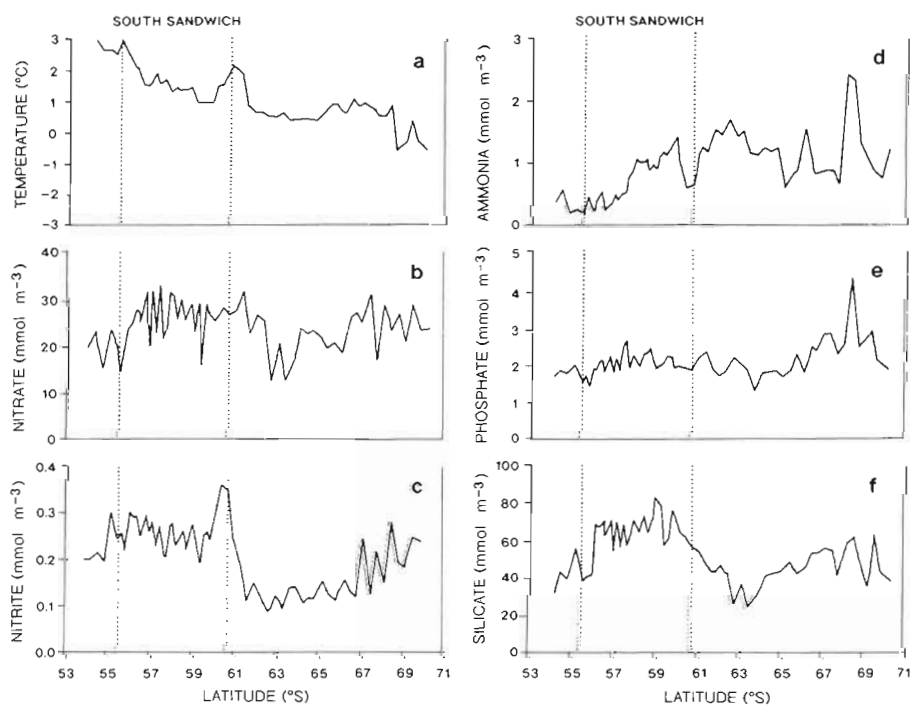


Fig. 5. As in Fig. 4 but for the SANA-E-South Sandwich transect

ca 30, 2.8, and 60 mmol m⁻³ for NO₃, PO₄ and SiO₂ respectively (Fig. 2), but in 1990–1991 they were 11, 1.1 and 7 mmol m⁻³ (Fig. 4). The decrease in nutrient levels over the shelf in 1990–1991 was also evident in a comparison with the surrounding open ocean during the same period. With the exception of ammonia, (up to ca 1.6 mmol m⁻³ in shelf waters) nutrient levels off-shore of Bouvet were generally 1.5 to 5 times higher than over the island shelf (Fig. 4). A sharp drop in nitrate and phosphate levels over the shelf of the South Sandwich Islands was also found in 1982–1983 (Fig. 3c, d) although this was not obvious in 1990–1991 (Fig. 5). On the latter cruise, there was some depletion over the northern edge of the islands' shelf (ca 56° S) but off-shore concentrations never exceeded 2 times those over the shelf (Fig. 5). For nitrite and silicate values increased sharply over the shelf but again with localised depletion around 56° S (Fig. 5c, f).

All 4 data sets (2 island groups, 2 years) showed higher phytoplankton pigment levels over the island shelves than in the surrounding ocean (Figs. 2 to 5). At Bouvet in 1982–1983 the effect was mild, but very conspicuous on the other 3 occasions. High pigment levels were associated with an increase in primary production rates on 2 occasions (Figs. 2, 3, 6 & 7). On the shelf of Bouvet Island, bloom levels of chl *a* were found only in 1990–1991 (>7 mg chl *a* m⁻³; Fig. 6) when production (ca 1.04 mg C m⁻³ h⁻¹; Fig. 6) was 6 to 7 times greater than in off-shore waters. Production values over the shelf were not available for 1982–1983 when chlorophyll levels, while still higher than away from the shelf, were relatively low (ca 0.16 mg chl m⁻³; Fig. 2).

Chlorophyll *a* enhancement over the South Sandwich shelves was marked on both cruises and, during 1982–1983, levels were higher even than at the Marginal Ice Zone, Weddell-Scotia Confluence and Antarctic Polar Front (Table 1). Primary production was an order of magnitude greater than in these areas or in off-shore waters around the islands (Fig. 3e).

While bloom formation occurred in the northern part of the archipelago (ca 56° S) in 1990–1991, phaeopigment levels were also high (ca 9.0 mg m⁻³; Fig. 7) indicating that the bloom was senescent. Production levels were not clearly greater than away from the islands, nor correlated with chlorophyll levels (Fig. 6d, e).

The composition of the phytoplankton communities at both islands was studied in 1990–1991. Around Bouvet Island, ca 70 % of chl *a* was in the net-size plankton (Fig. 6). The nano- and picoplankton constituted ca 28 and 2 %, respectively. This pattern was almost reversed at the South Sandwich Islands. Here, the nano-size class dominated (ca 70 % of the total) followed by the net- (ca 25 %) and picoplankton (ca 5 %; Fig. 7).

Diatoms contributed over 80 % of the total net-phytoplankton crop at all stations (Table 2). Highest cell concentrations occurred over the shelf of Bouvet Island (average >9 × 10⁴ cells l⁻¹, maximum ca 1.8 × 10⁵ cells l⁻¹) where the diatom community was dominated by the chain-forming *Nitzschia kerguelensis* and *Nitzschia* sp. (>60 % of the total crop). Netphytoplankton densities to the south of Bouvet were only ca 1.2 × 10⁴ cells l⁻¹ (Table 2) and were not strongly dominated by any one species. *N. kerguelensis* and *Rhizosolenia hebetata* f. *semispina* were the most abundant taxa but formed only ca 23 and 29 % respectively of the total (Table 2). The diatom community around the South Sandwich Islands was very different. The shelf area had maximum concentrations of ca 8.5 × 10⁴ cells l⁻¹ and species composition was very similar to that in off-shore waters north of the archipelago (Table 2). In both areas, the 3 taxa *R. hebetata* f. *semispina*, *N. kerguelensis* and *Thalassiothrix* sp. accounted for about half of the total cell number, although none of them was in bloom stage. As with Bouvet, diatom communities south of the archipelago were less dense (average ca 2.0 × 10⁴ cells l⁻¹), but dominated by *N. kerguelensis* (>65 % of the total crop; Table 2).

Table 1. Maximum values of chl *a* concentration (mg chl *a* m⁻³) and ¹⁴C uptake rate (mg C m⁻³ h⁻¹) at the most productive areas of the Southern Ocean encountered during 2 cruises of the SA 'Agulhas'

Area	1982–1983		1990–1991	
	Max. [chl <i>a</i>]	Max. prod.	Max. [chl <i>a</i>]	Max. prod.
Subtropical Front	1.65	1.04	3.12	6.33
Subantarctic Front	0.55	1.37	2.74	0.91
Antarctic Polar Front	0.31	1.38	5.32	1.87
Weddell-Scotia Confluence	0.46	0.58	3.06	3.05
Marginal Ice Zone	0.96	2.33	5.97	1.42
Bouvet Island	0.16	–	7.33	1.04
South Sandwich Islands	2.98	23.2	6.53	1.42

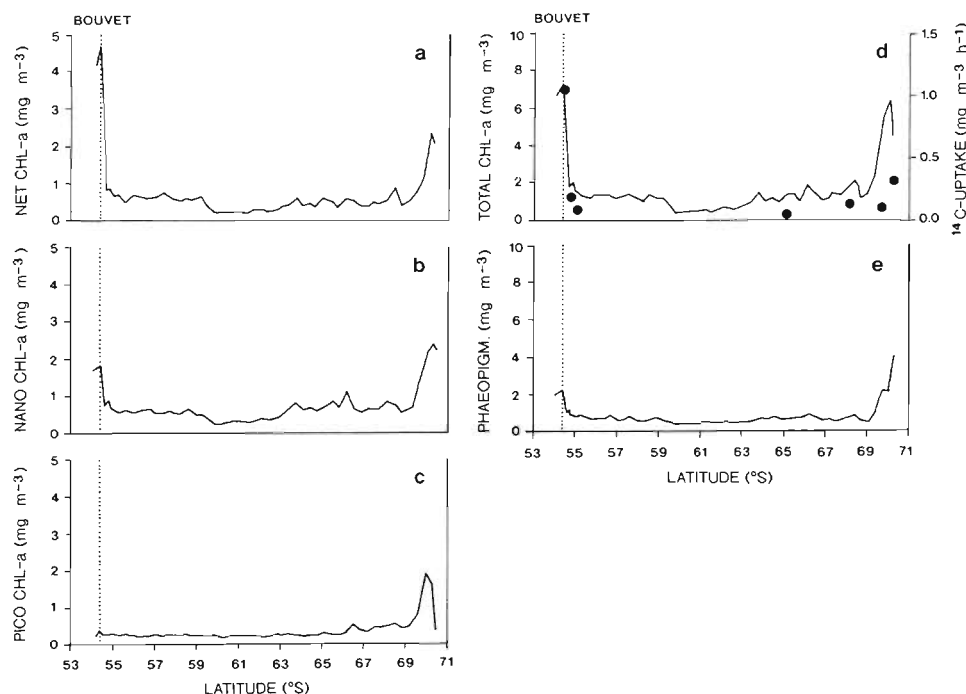


Fig. 6. Latitudinal profiles of chl *a*, phaeopigments and primary production (● in panel d) levels along the SANA-E-Bouvet transect during summer 1990–1991. Dotted lines indicate position of island shelf

The waters in the vicinity of the islands exhibited a strong intensification in acoustic backscattering at 12 kHz. South of Bouvet Island, a deep scattering layer (DSL, at 350 m at night and 450 m in the day) extended for ca 400 km from the island (Fig. 8). The densest scatterers were, however, recorded within <100 km from the island in slope waters, where the DSL split into 2 distinct layers, 150 to 200 m apart in

depth (Fig. 8). No 12 kHz scatterers were detected over the shallow shelf area. Similarly, a strong DSL at 250 to 350 m was observed over the entire South Sandwich Ridge (Fig. 8). These scatterers extended <100 km north and south of the archipelago. Again, backscattering was most intense in slope waters and faded dramatically over the shallow island shelves (Fig. 8).

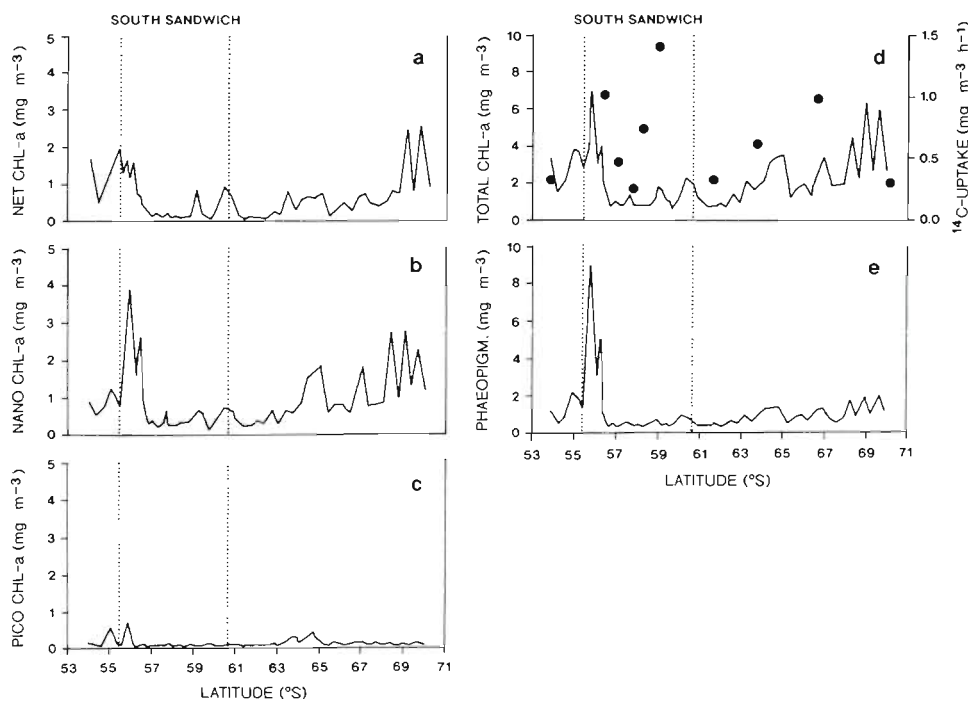


Fig. 7. As in Fig. 6 but for the SANA-E-South Sandwich transect

Table 2. Mean concentrations (cells l⁻¹), 95 % confidence limits and percentage contribution of netphytoplankton at South Sandwich (SSI) and Bouvet Islands during summer 1990–1991. $X = \bar{x} \pm SE$ ($I_{0.05}$)

	South of Bouvet X ($n = 6$)	Bouvet shelf X ($n = 4$)	South of SSI X ($n = 6$)	SSI shelf X ($n = 4$)	North of SSI X ($n = 6$)
	%	%	%	%	%
<i>Thalassiosira</i> sp.	–	337 ± 405	2 ± 3	2294 ± 3115	–
<i>T. antarctica</i>	276 ± 312	4235 ± 4034	65 ± 44	724 ± 751	228 ± 48
<i>Coscinodiscus</i> sp.	85 ± 83	852 ± 933	227 ± 272	321 ± 454	253 ± 411
<i>C. marginatus</i>	48 ± 45	469 ± 409	27 ± 12	197 ± 231	19 ± 17
<i>C. oculus-iridis</i>	14 ± 17	–	22 ± 29	93 ± 207	–
<i>Actinocyclus</i> sp.	–	141 ± 224	–	8 ± 15	–
<i>Asteromphalus</i> sp.	6 ± 9	–	19 ± 31	16 ± 30	12 ± 21
<i>A. heptactis</i>	22 ± 39	384 ± 404	12 ± 20	33 ± 28	–
<i>A. hookeri</i>	23 ± 9	441 ± 84	157 ± 104	25 ± 29	33 ± 44
<i>A. hookeri</i>	34 ± 44	465 ± 644	22 ± 18	83 ± 78	48 ± 27
<i>A. hyalina</i>	74 ± 25	–	427 ± 602	412 ± 358	19 ± 32
<i>Dactylosolen antarcticus</i>	696 ± 968	3065 ± 913	106 ± 158	191 ± 178	283 ± 98
<i>Rhizosolenia</i> sp.	39 ± 47	1106 ± 1297	47 ± 57	42 ± 76	616 ± 819
<i>R. alata</i>	79 ± 17	–	34 ± 29	254 ± 352	29 ± 28
<i>R. alata f. inermis</i>	86 ± 75	–	2 ± 2	348 ± 747	12 ± 21
<i>R. alata f. indica</i>	6 ± 10	–	3 ± 5	–	25 ± 43
<i>R. chunii</i>	117 ± 188	1445 ± 418	–	1266 ± 2380	211 ± 302
<i>R. delicatula</i>	111 ± 193	–	–	29 ± 63	148 ± 255
<i>R. hebelata f. hiemalis</i>	17 ± 31	–	–	30 ± 45	284 ± 422
<i>R. hebelata f. semispina</i>	3557 ± 3323	258 ± 263	38 ± 39	8323 ± 12176	5196 ± 2844
<i>R. simplex</i>	23 ± 20	180 ± 92	–	824 ± 1517	265 ± 443
<i>R. styliformis</i>	–	–	–	42 ± 94	–
<i>Eucampia antarctica v. recta</i>	62 ± 86	7940 ± 12285	3 ± 4	2640 ± 5522	261 ± 136
<i>Chaetoceros</i> sp.	923 ± 1430	1582 ± 1212	59 ± 35	463 ± 376	476 ± 410
<i>C. atlanticus</i>	–	1222 ± 1038	–	170 ± 380	128 ± 131
<i>C. criophilum</i>	251 ± 216	31 ± 53	282 ± 427	727 ± 618	166 ± 144
<i>C. dichæta</i>	33 ± 58	–	291 ± 351	29 ± 54	50 ± 86
<i>C. pendulus</i>	–	–	2 ± 4	–	–
<i>C. peruvianus</i>	–	–	3 ± 5	–	–
<i>C. neogracile</i>	–	–	–	506 ± 1131	–
<i>Odontella weissflogii</i>	–	–	–	337 ± 753	–
<i>Grammatophora marina</i>	–	–	–	7 ± 15	–
<i>Thalassionema</i> sp.	–	3666 ± 6230	–	–	–
<i>Thalassiothrix</i> sp.	198 ± 236	672 ± 812	78 ± 101	3125 ± 5409	815 ± 927
<i>T. heteromorphia</i>	3 ± 5	23 ± 39	–	296 ± 441	227 ± 350
<i>T. longissima</i>	22 ± 39	356 ± 506	61 ± 82	–	96 ± 83
<i>T. longissima v. antarctica</i>	33 ± 58	426 ± 471	284 ± 473	12 ± 28	100 ± 172
<i>Pleurosigma directum</i>	6 ± 9	53 ± 72	14 ± 23	4 ± 5	6 ± 9
<i>Nitzschia</i> sp.	–	359 ± 154	24 ± 14	52 ± 42	37 ± 10
<i>Nitzschia</i> sp. (chain-form.)	1583 ± 1101	20891 ± 14372	4282 ± 1739	815 ± 492	594 ± 468
<i>N. closterium</i>	11 ± 19	19 ± 33	78 ± 76	53 ± 66	–
<i>N. kerguelensis</i>	2871 ± 1995	38047 ± 26394	13573 ± 5532	3264 ± 1734	1913 ± 1485
<i>N. lineata</i>	17 ± 29	68 ± 60	64 ± 56	30 ± 66	–
<i>N. seriata</i> (complex)	178 ± 308	1054 ± 954	141 ± 117	88 ± 93	473 ± 770
<i>Distephanus speculum</i>	497 ± 584	682 ± 599	60 ± 23	679 ± 768	363 ± 336
Dinoflagellates	92 ± 57	385 ± 360	15 ± 15	1026 ± 1366	595 ± 977
Round bodies	205 ± 250	1783 ± 1952	80 ± 55	1404 ± 1174	973 ± 981
Unidentified cells	–	379 ± 95	64 ± 76	45 ± 65	136 ± 84
TOTAL	12299 ± 6053	90926 ± 77506	20669 ± 7489	30678 ± 31920	14972 ± 6692

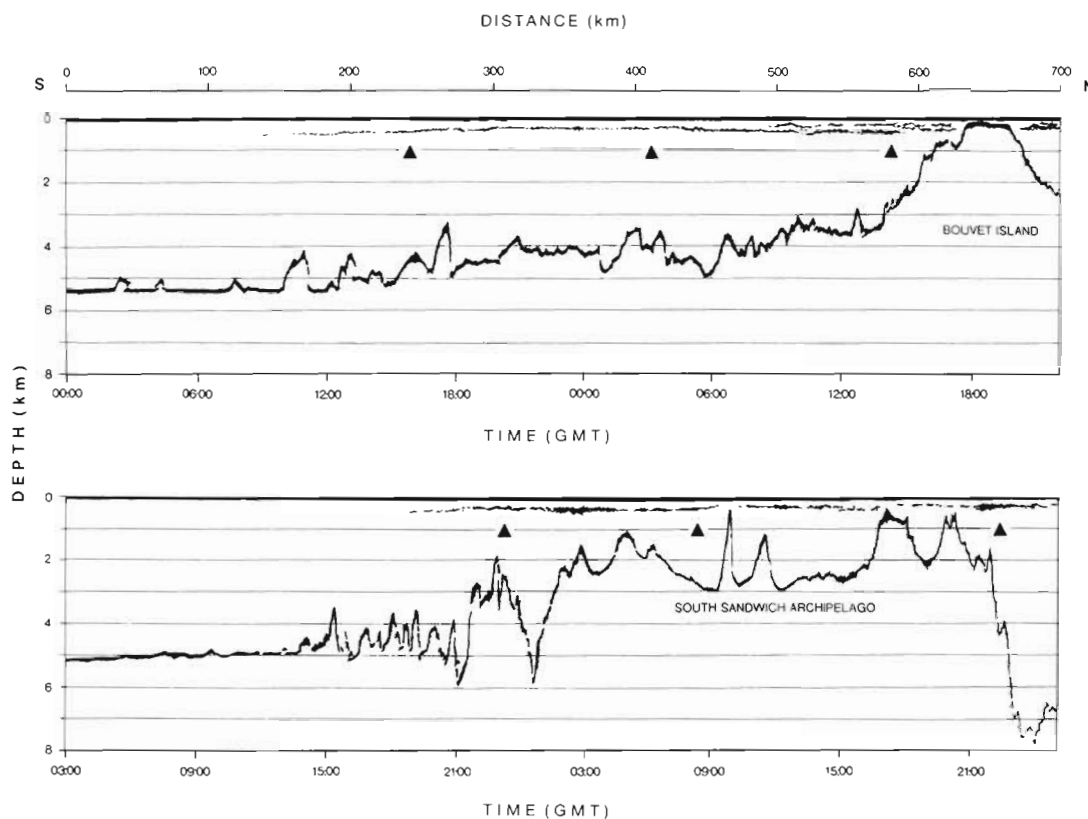


Fig. 8. 12 kHz acoustic echogram recorded over the shelves and in the oceanic area around Bouvet and South Sandwich Islands. Arrows indicate the presence of a deep scattering layer (DSL)

DISCUSSION

The results obtained indicate an increase in chl *a* levels in the vicinity of Bouvet and the South Sandwich Islands on both cruises. The increase was modest at Bouvet in 1982–1983, but otherwise involved an enhancement of 3 to 4 times the chlorophyll concentration of adjacent off-shore waters. Phytoplankton production was also markedly greater (by an order of magnitude at Bouvet in 1990–1991) on 2 of the 3 occasions when it was measured. On the third occasion (South Sandwich 1990–1991) high chlorophyll levels were apparently associated with a senescent bloom (Fig. 6d, e) and production over the shelf area was not clearly raised. Where chlorophyll concentration and production rates were both high (Bouvet 1990–1991, South Sandwich 1982–1983), circum-insular chlorophyll peaks were clearly associated with depletion of dissolved nutrients (Figs. 3 & 4), an indirect indication of high uptake (Jennings et al. 1984). The situation was less clear at the South Sandwich Islands in 1990–1991 where a low productivity, senescent bloom (ca 56° S) was nevertheless associated with some depletion of nutrients (Fig. 5). At Bouvet in 1982–1983, when chlorophyll enhancement

was very mild, nitrate and phosphate levels were in fact raised (Fig. 2).

Chlorophyll and production values obtained are among the highest recorded in Antarctic waters, and of the same magnitude as those observed at marginal ice zones (Smith & Nelson 1985, Nelson et al. 1989), frontal systems (Allanson et al. 1981, Lutjeharms et al. 1985, Jacques & Panouse 1991) and on the shelves around the Antarctic Peninsula (El Sayed 1988, Holm-Hansen & Mitchell 1991).

Utilization of phytoplankton by higher trophic levels was not directly examined in this study but the dense 12 kHz scatterers around the islands suggest a general enhancement of the local food web, based on raised stocks of primary producers. Sound scattering at this resonant frequency is normally due to aggregations of vertically-migrating myctophid fishes (Farquhar 1977, Greenlaw & Percy 1985, Perissinotto & McQuaid 1992) which form a staple item in the diet of most top predators, including seabirds and pinnipeds (Øritsland 1970, Brown et al. 1990). Myctophids typically feed on meso- and macrozooplankton (Sameoto 1989, Hulley 1990) and zooplankton such as krill and copepods in turn feed extensively on *Nitzschia* spp. diatoms (Fryxell & Kendrick 1991)

which dominated the netphytoplankton at both islands in 1990–1991.

Cell size-distribution (measured only in 1990–1991) showed a remarkable difference between the 2 island systems. Netphytoplankton formed ca 70 % of the chl *a* measured at Bouvet Island. This is typical in Southern Ocean waters where high phytoplankton biomass (>1.5 to $2 \text{ mg chl } a \text{ m}^{-3}$) is usually associated with net-size cells (i.e. diatoms), whereas low biomass waters are dominated by nanophytoplankton (Holm-Hansen & Mitchell 1991, Jacques & Panouse 1991). The situation at the South Sandwich Archipelago ran contrary to this pattern. In spite of high biomass levels ($>6 \text{ mg chl } a \text{ m}^{-3}$) the nano size-class accounted for most of the chl *a* (ca 70 %; Fig. 7) and netphytoplankton formed

only ca 25 % of the total. We did not examine cell composition of the nanoplankton. However, phaeopigment levels were particularly high on this occasion, up to 95 % of phaeopigments occurring in the nanoplankton size-class, and damaged or empty diatom frustules were common in the samples collected. The coincidence of both chl *a* and phaeopigment peaks with silicate depletion (Fig. 5) suggest that diatom populations had been previously high. It is possible that free-floating chloroplasts from disrupted diatom cells contributed to the nanophytoplankton chlorophyll fraction (Gieskes & Elbrächter 1986).

The increase in marine productivity around these 2 Antarctic island groups confirms the general validity of an island mass effect in the Southern Ocean (Planke

Table 3. Maximum values of phytoplankton biomass ($\text{mg chl } a \text{ m}^{-3}$), production ($\text{mg C m}^{-3} \text{ h}^{-1}$) and species composition at different island groups in the Indian and Atlantic sectors of the Southern Ocean. All records are limited to the austral summer season (December to February)

Area	Max. [chl]	Max prod.	Dominant taxa	Source
Palmer Archipelago, Brabant	25.0	7.74	<i>Phaeocystis pouchetii</i> (50 %)	Burkholder & Sieburth (1961), Holm-Hansen & Mitchell (1991)
Palmer Archipelago, Anvers	26.8	–	<i>Phaeocystis pouchetii</i> (60–95 %)	Burkholder & Sieburth (1961), Kopczynska & Ligowski (1982)
South Shetland, Deception	25.0	62.5	<i>Trichotoxon</i> (<i>Synedra</i>) <i>reinboldii</i> (50 %)	Burkholder & Sieburth (1961), Mandelli & Burkholder (1966)
South Shetland, King George	19.0	–	<i>Odontella weissflogii</i> , <i>Chaetoceros curvisetum</i> , <i>Thalassiosira tumida</i>	Heywood & Priddle (1987)
D'Urville Island	2.91	2.45	–	Weber & El Sayed (1987)
Joinville Island	5.42	7.72	<i>Chaetoceros socialis</i> , <i>Thalassiosira antarctica</i> , <i>Porosira</i> sp.	von Bodungen (1986)
South Orkney, Signy	42.5	37.4	<i>Biddulphia striata</i> , <i>Thalassiosira antarctica</i> , <i>Corethron criophilum</i>	Horne et al. (1969), Whitaker (1982)
South Georgia Island	3.60	–	<i>Chaetoceros socialis</i> , <i>Thalassiosira scotia</i> , <i>Corethron criophilum</i>	Priddle et al. (1986)
South Sandwich Islands	6.53	23.2	<i>Rhizosolenia hebetata</i> f. <i>semispina</i> (27 %), <i>Nitzschia kerguelensis</i> (11 %), <i>Thalassiotrix</i> (10 %)	This study
Bouvet Island	7.33	1.42	<i>Nitzschia kerguelensis</i> (42 %), <i>Nitzschia</i> sp. (23 %)	This study
Prince Edward Islands	2.58	9.10	<i>Chaetoceros radicans</i> (96 %), <i>Rhizosolenia curvata</i> , <i>Dictyocha speculum</i>	Boden (1988), Perissinotto & Duncombe Rae (1990)
Crozet Islands, Possession	2.03	1.73	<i>Nitzschia turgidula</i> (13 %), <i>N. heimii</i> (10 %), <i>N. kerguelensis</i> (6 %), <i>Dictyocha speculum</i> (6 %)	Planke (1977), El Sayed et al. (1979)
Kerguelen Archipelago	2.50	1.11	<i>Chaetoceros concavicornis</i> (20 %), <i>Thalassionema nitzschioides</i> (21 %), <i>Navicula</i> sp. (11 %)	Planke (1977), El Sayed et al. (1979), Treguer (1987)
Heard Island	1.13	0.72	–	El Sayed & Jitts (1973), El Sayed & Turner (1978)

1977, Nast & Gieskes 1986, Boden 1988, El Sayed 1988). This effect has now been described for several islands both to the south and to the north of the Antarctic Polar Front (Table 3).

Biological enhancement around islands elsewhere is related to hydrographic mechanisms providing pulses of nutrient input into a generally oligotrophic euphotic zone, thereby increasing phytoplankton new production (Doty & Oguri 1956, Heywood et al. 1990). The Southern Ocean, however, is unusual as macronutrients are always present in excess of phytoplankton requirements (Sakshaug & Holm-Hansen 1984, El Sayed 1984, Priddle et al. 1986). Martin (1990) and Martin et al. (1990) account for neritic phytoplankton blooms by greater availability of iron in shallow coastal waters. However, the very low Fe requirements of deep water species (Sunda et al. 1991) and low algal production in the Southern Ocean during the last glaciation, despite an increase in iron supply (Mortlock et al. 1991), fail to support the 'Antarctic Iron Hypothesis'. Furthermore, plankton blooms are repeatedly observed near major frontal systems (Allanson et al. 1981, El Sayed & Weber 1982, Yamaguchi & Shibata 1982, Bidigare et al. 1986, El Sayed 1988, R. K. Laubscher, R. Perissinotto & C. D. McQuaid unpubl.), where Fe supplies are supposedly limited (Martin 1990).

There is increasing evidence that bloom development is triggered by stabilization of the water column (Smith & Nelson 1985, El Sayed 1988, Perissinotto et al. 1990, Holm-Hansen & Mitchell 1991; Mitchell & Holm-Hansen 1991). With a shallow mixed layer the ratio of carbon fixation to respiratory losses improves (Tilzer & Dubinsky 1987). Near islands, increased buoyancy in the surface layer caused by glacial meltwater (south of the APF) or rainwater run-off (north of the APF) can enhance stratification, causing a shoaling of the upper mixed layer.

During both cruises surface temperature and salinity declined on approaching the 2 island groups (Figs. 2a, b, 3a, b, 4a & 5a). These halothermic transitions may represent a front of glacial meltwater spreading from the islands. Both groups have permanent snow and ice coverings. Warm summer temperatures and insolation induce massive ice-melting, as in the seasonal marginal ice zone, and consequent density stratification (Smith & Nelson 1985, Mitchell & Holm-Hansen 1991). This is shown clearly at the South Sandwich Archipelago in 1982–1983. Chl *a* distribution was highest in the southern nearshore (60 to 61° S) where the thermocline was closest to the surface (Figs. 3e & 9). The upper mixed layer depth was significantly related to chlorophyll concentration (\log_{10} -transformed data. F -ratio = 11.5, p = 0.004) and accounted for ca 43 % of its total variance.

Although re-suspension of resting spores may be important in the initiation of diatom blooms over shal-

low waters (Garrison 1981, Hargraves & French 1983, von Bodungen et al. 1986), spore forming taxa constituted only 14 and 23 % of the total diatom crop at Bouvet and South Sandwich respectively (Table 2).

Bloom generation requires favourable environments, such as a stable mixed layer, to persist long enough for the accumulation of excess biomass. Depending upon the growth rate (0.4 to 0.8 doublings d^{-1}), a bloom takes a minimum of 8 to 16 d to develop from ca 0.1 to 10 $mg\ chl\ m^{-3}$, once favourable environmental conditions have been established. Spatial covariance between environmental factors must be maintained throughout this period, both in the vertical and horizontal scales. In the vertical, deep mixing can be minimized around islands where storms are moderated, particularly in their lee (Clarke 1988, Mitchell & Holm-Hansen 1991). The horizontal dimension largely controls the residence time of both phytoplankton cells and freshwater spreading from land (Perissinotto & Duncombe Rae 1990). Under normal flow conditions, and with an average surface speed for the Antarctic Circumpolar Current (ACC) of ca 0.31 $m\ s^{-1}$ (Hofmann 1985), growing cells and stabilizing freshwater would be continuously dissipated downstream of island shelves within the advection time scale (< 1 d in most cases). Some mechanism of horizontal recirculation must prolong the residence time of waters in island seas to periods of at least 1 to 2 wk. In the areas most intensively studied (South Shetland Islands, Bransfield/Gerlache Straits and Prince Edward Archipelago) it has been found that topographically-generated eddies (often associated with Taylor Columns and Rossby Wakes) are responsible for medium-term retention of water masses around island and bank systems (Grelowsky & Pastuszak 1983, Heywood & Priddle 1987, Perissinotto & Duncombe Rae 1990, Lanin 1991, R. C. van Ballegooyen, J. R. E. Lutjeharms & R. Perissinotto unpubl.). This retention mechanism may occur regularly in the Southern Ocean (McCartney 1976, Gordon et al. 1978), thus playing a major role in the development of island blooms.

Finally, there is a longitudinal trend in the magnitude of island blooms. The density of the summer phytoplankton crop found at Bouvet and South Sandwich was intermediate between that of the Antarctic Peninsula archipelagos and that of islands located in the southwest Indian Ocean sector (Table 3). Since all records are representative of the same period of the year (austral summer), this pattern is unlikely to be due to seasonal variability. We offer no explanation for this apparent production gradient but, given the enormous potential contribution of this ocean for the global carbon cycle, this aspect may deserve special attention.

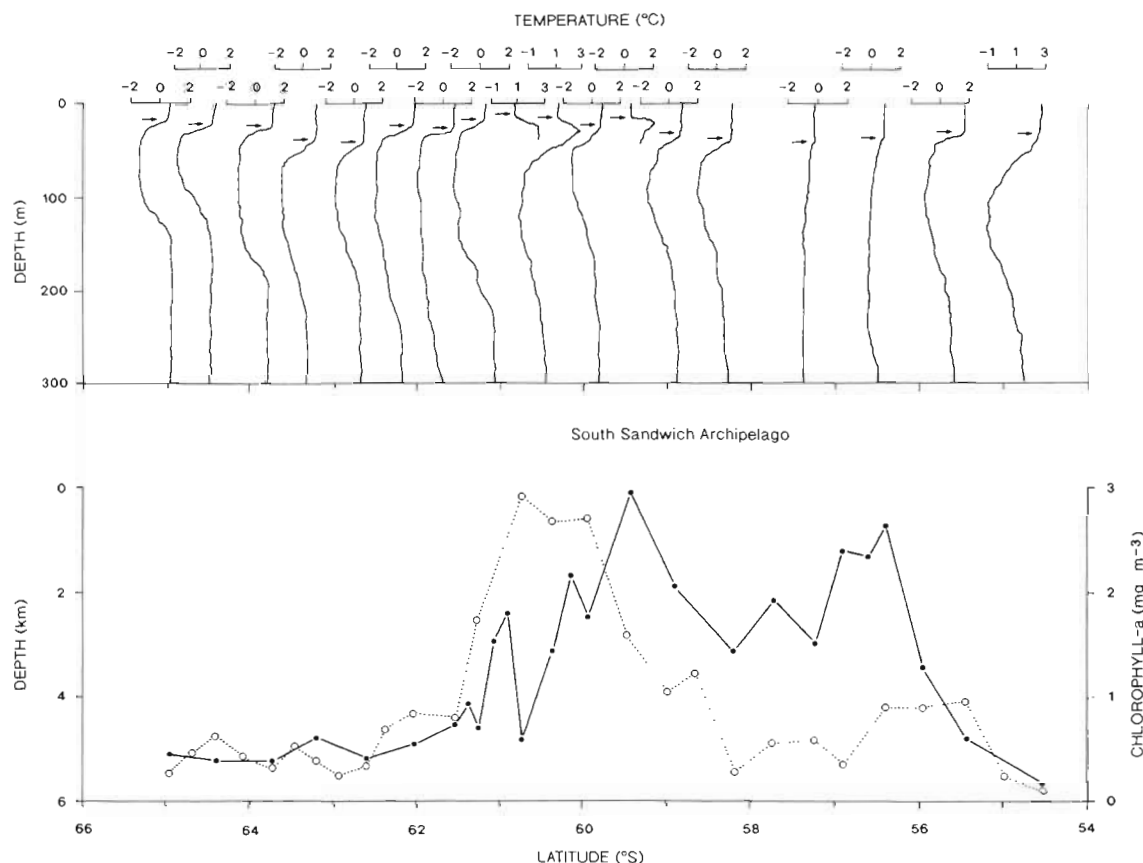


Fig. 9. Spatial covariance between XBT temperature profiles (upper panel), surface chl *a* (---) and bottom topography (—●—) in the South Sandwich Islands region during summer 1982–1983. Arrows in the upper panel indicate the lower depth of the upper mixed layer (UML)

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