CHAPTER 7

NUTRIENT DYNAMICS IN THE VICINITY OF THE PRINCE EDWARD ISLANDS

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Nutrient concentrations in the open waters of the Polar Frontal Zone (PFZ) are highly variable, reflecting the region's complex oceanographic regime. Surface concentrations of nitrate, silicate and phosphate range from 9.5 to 97.5, from 0.2 to 16.5 and from < 0.1 to 16.6 mmol m⁻³, respectively (Allanson *et al.* 1985; Duncombe Rae 1989; Ismail 1990; Balarin 2000). Changes in nutrient concentrations coincide with the intrusion of Antarctic surface water from the south and sub-Antarctic surface water from the north (Ansorge *et al.* 1999; Froneman *et al.* 1999). Mesoscale features such as far field eddies or the eddies generated by the interaction between the Antarctic Circumpolar Current (ACC) and the South-West Indian Ridge further contribute to the heterogeneity in nutrient concentrations within the surface waters of the PFZ (Ansorge & Lutjeharms 2002, 2003; Ansorge *et al.* 2004).

Terrestrial nutrient dynamics on the Prince Edward Islands are strongly affected by the marine environment, through nutrients in aerosols blown in from the sea and brought in by seabirds and seals. In turn, the islands significantly influence nutrient composition of the surrounding ocean. Here we describe the dynamics of these land-sea nutrient interactions and provide a scenario of how the present warming being experienced by the islands and surrounding ocean (le Roux 2008) might influence these dynamics.

7.1   Oceanic inputs of nutrients to the Marion Island terrestrial system

7.1.1   Rainwater input

The ocean overwhelmingly dominates the chemical composition of rainwater at the island, so that the rainwater is simply a very dilute solution of seawater, with the same ionic concentration order ($Cl^->Na^+>SO_4^{2-}>Mg^{2+}>Ca^{2+}\approx K^+$) as seawater and an Oceanic Origin Number of 103% (seawater has an O.O.N. of 100%; Grobbelaar 1978). Total ionic concentration ($Cl^- + Na^+ + SO_4^{2-} + Mg^{2+} + Ca^{2+} + K^+$) in the rainwater decreases from 400 to 700 mg l^{-1} about 15 m from the shore to 100 to 200 mg l^{-1} 800 m from the shore and does not decline appreciably further inland (Grobbelaar 1974, 1978).

Appreciable concentrations of NH_4-N (up to 0.3 mg l^{-1}) and NO_3-N (up to 0.1 mg l^{-1}) occurred in 88 rainwater samples collected over a one year period about 450 m inland on the eastern part of the island; the NH_4-N probably originated as ammonia volatilised from penguin colonies on the coast and the NO_3-N as aerosols of seawater (Smith 1987). No PO_4-P has ever been detected in the island's rainwater, which is surprising since appreciable levels of PO_4-P (up to 0.03 mg l^{-1}) are found in the surrounding ocean. In total, about 0.21 g N m^{-2} y^{-1} is deposited through precipitation 450 m inland on the eastern part of the island (Smith 1987), a small fraction of the amount contained in the soil or taken up annually by the vegetation (Smith 2008), but probably sufficient to compensate for losses of N from the area through leaching and wind removal of plant litter (Smith 1988). Estimated deposition rates for other nutrients at the same locality were 10.4 g Na m^{-2} y^{-1}, 1.2 g Mg m^{-2} y^{-1}, 0.4 g K m^{-2} y^{-1}, 0.4 g Ca m^{-2} y^{-1}, 16.4 g Cl m^{-2} y^{-1} and 2.1 g S m^{-2} y^{-1}. In total, 31 g m^{-2} y^{-1} of these elements were added to the site through rainwater, which agrees well with the input of 35 g m^{-2} y^{-1} at the nearby meteorological station (computed from data in Grobbelaar 1974).

7.1.2   Bird and seal input

Table 7.1 provides an estimate of the amounts of nutrients brought in through the guano of surface nesting birds in the mid 1970s and in 2002/03 and the excreta of Elephant Seals in 1980/81. Table 7.2 gives the amounts of nutrient input as moulted feathers and Elephant Seal fur. Elephant seal inputs are from Panagis (1984). The 1970 values for the avian inputs are from a reanalysis of guano nutrient inputs given by Burger *et al.* (1978) and of feather nutrient input by Williams & Berruti (1978), the reanalysis being based on more accurate census data for the period (Cooper & Brown 1990; Huyser *et al.* 2000; Crawford *et al.* 2003), a refinement of feather production at moult for the two most abundant species (Brown 1985) and a more comprehensive data base on guano nutrient composition (unpublished data; Smith 1976; Lindeboom 1979). The 2002/03 estimates of nutrient input through guano and feathers are based on bird census data in Crawford *et al.* (2003), assuming that the proportion of non-breeders to breeders, the amounts of guano and feathers produced per

bird, the number of days spent ashore and the nutrient composition of the guano and feathers were the same in 2002/03 as in 1974/75.

Burrowing bird species have been shown to markedly enhance the nutrient status of plants and soils at the island (Smith 1976), but hitherto a lack of information on the population sizes of burrowing birds made it impossible to estimate the quantity of nutrients they bring to the island. Ryan and Bester (2008) give body masses and population sizes of the various burrowing species. These were used to estimate the amounts of nutrients input by each species, from feather mass and feather nutrient concentration data in Williams (1978), and published (Fugler 1985) and unpublished nutrient composition data for the guano of burrowing species. Daily guano production of adult burrowers was estimated from body mass using the body mass:guano production relationship for the smaller surface nesters (Lesser Sheathbill, Kelp Gull, sub-Antarctic Skua and Crozet Shag). It was assumed that the adults of all of the burrowing species spend 150 days at the island. Guano production of the chicks of burrowing species was obtained from Fugler (1985).

In total, the 2002/03 population of seabirds brought in 4 279 tons of guano per year to the island (Table 7.1), containing 640 t N, 106 t P and 222 t Ca, amounts that represented a substantial proportion of the annual uptake of nutrients by the island's vegetation (c.37% of N, 67% of P and 31% of Ca uptake). However, most guano is produced in a very narrow shore-zone strip; King Penguins, Macaroni Penguins and Rockhopper Penguins account for 76% of all guano, most of which is deposited on bare ground and washes down to the sea or (or in the case of N) is volatilised. This has a considerable local effect since the surrounding vegetation around colonies has a much enhanced nutrient status (Smith 1978), forming what Lindeboom (1984) termed an "ammonia shadow" around the island's penguin colonies. However, on a whole island basis, it is not known to what extent the nutrients deposited in penguin colonies affect the vegetation inland. There has been one study of the fate of guano N in the penguin colony, at Kildalkey Bay on the island's south east coast (Lindeboom 1979, 1984). There, in the mid 1970s 350 000 Macaroni Penguins and 150 000 King Penguins daily produced 2 900 kg of guano containing 600 kg N, about 80% as uric acid and the rest as proteins, NH_4-N and NO_3-N. Uric acid N and protein N are rapidly transformed to NH_4-N ammonia, but about 24 kg is washed down to the sea in small streams that flow through the colony. About 11 kg of the NH_4-N is nitrified (and then probably denitrified) and about 10 kg is washed to the sea. Most (about 430 kg N) volatilises, about 370 kg of which is blown out to sea and about 60 kg blown inland. An unknown amount of the latter is deposited inland through rain and dry deposition. About 16 kg N day^{-1} is deposited directly on the vegetation near the colony, mainly by non-breeding King Penguins. This, with the ammonia blown inland (and assuming all that ammonia is deposited somewhere on the island), means that only about 12% of the penguin guano N produced at Kildalkey Bay influences the island's soils and vegetation. A similar situation

Table 7.1 Annual input of nutrients (kg per annum) in excreta of seabirds and seals.

Species	1974/75				2002/03			
	Guano production (tons y⁻¹)	N	P	Ca	Guano production (tons y⁻¹)	N	P	Ca
King Penguin	2 182	23 666	61 320	136 169	2 210	239 700	62 108	137 919
Gentoo Penguin	46	5 531	1 541	2 640	27	3 315	924	1 582
Macaroni Penguin	1 145	225 644	27 031	34 591	930	183 151	21 941	28 077
Rockhopper Penguin	179	35 641	4 227	5 409	129	25 598	3 036	3 885
Sub-Antarctic Skua	14	1 716	147	559	6	745	64	243
Lesser Sheathbill	22	1 645	279	940	17	1 332	226	761
Crozet Shag	12	866	55	1 870	6	439	28	949
Kelp Gull	6.1	446	29	963	0.8	56	4	120
Wandering Albatross	5.3	810	58	25	4.6	696	50	21
Grey-headed Albatross	2.1	319	23	10	2.1	317	23	10
Sooty Albatross	0.9	129	9	3.9	0.3	45	3	1.4
Light-mantled Sooty Albatross	0.08	12.2	0.9	0.4	0.05	7.7	0.5	0.2
Northern Giant Petrel	0.13	26.7	1.2	1.1	0.08	16.6	0.7	0.7
Southern Giant Petrel	0.92	188	8	8	0.56	114	5	5

Table 7.1   Continued.

Species	1974/75				2002/03			
	Guano production (tons y⁻¹)	N	P	Ca	Guano production (tons y⁻¹)	N	P	Ca
Fairy Prion					4	877	78	220
Salvin's Prion					456	91 214	8 152	22 851
Blue Petrel					234	43 535	4 876	14 395
Great-winged Petrel					64	11 537	730	1 620
Grey Petrel					8	1 889	113	258
Soft-plumaged Petrel					26	5 411	462	2 370
Kerguelen Petrel					54	10 856	970	2 720
White-chinned Petrel					96	18 983	2 471	3 943
South Georgian Diving Petrel					2	426	38	107
Shore	3 519	498 939	92 643	178 042	3 275	448 934	87 116	170 830
Inland	95	10 694	2 087	5 149	59	6 600	1 296	2 743
Burrows	-	-	-	-	945	184 728	17 891	48 483
Total birds					4 279	640 262	106 303	222 056
Elephant Seal excreta (1980/81)		6 683.0	387.3	57.5				

probably occurs at the island's other large penguin colonies, since the prevailing wind is westerly and all of them are on the island's north, south and east coasts.

In contrast to the large inputs of nutrients in the shore-zone, much smaller amounts are brought in by surface nesting birds inland. However, the nutrients deposited inland very markedly influence the stature, vitality and nutrient status of the vegetation surrounding the nests (Smith 1978). For instance, the yearly deposition of guano N around a single occupied Wandering Albatross nest is about 720 g N, all of which is rapidly transformed to NH_4-N and NO_3-N (Lindeboom 1979) and, since low soil pH prevents volatilisation of ammonia, is available for uptake by the vegetation. In addition to the local effect around the nest, down-slope leaching of nutrients improves soil fertility of a large area away from the nest. A similar situation applies for other inland surface nesting species, such as the Grey-headed Albatross, Giant Petrel, Kelp Gull, Skua and Light-mantled Sooty Albatross.

Moulted feathers represent another important avian input of nutrients to the island, in 2002/03 bringing in 54 t N, 214 kg P and 670 kg Ca (Table 7.2). Again, penguins on the shore zone account for most (88% to 98%) of the feather input of nutrients and it is not known how much of the nutrients become incorporated into the soils and vegetation.

With the exception of the King Penguin and Grey-headed Albatross, populations of the surface nesting species have declined since the mid 1970s (Crawford *et al.* 2003), for reasons suggested by Ryan and Bester (2008). The biggest decrease in absolute numbers has been for Macaroni Penguins (83 000 breeding pairs) and Rockhopper Penguins (26 000 pairs), but relative to population size the largest declines (40% to 88%) have been for Gentoo Penguins, Crozet Shags, Skuas, Sooty Albatrosses and Kelp Gulls. These declines have lead to a significant lowering of the annual input of nutrients to the island via guano or feathers, and the most marked effect has been inland. For instance, between the mid 1970s and 2002 the input of N, P and Ca through guano of the surface nesters declined by 4% to 10% in the shore zone and by 38% to 47% inland. N, P and Ca input through moulted feathers declined by 15% to 18% in the shore zone and by 22% to 24% inland. These changes refer to nutrient inputs by the surface nesters only. It is not known exactly how the populations of burrowing species have changed during the period, but it is likely that such changes have been notable, with marked effects on nutrient dynamics (Gremmen & Smith 2008).

Elephant seals excreta represent an annual input of 6 683 kg N, 387 kg P and 57 kg Ca to the island (Table 7.1). Moulted Elephant Seal fur represents an input of 699 kg N, 5 kg P and 4 kg Ca (Table 7.2). In total, Elephant Seal excreta and fur inputs of N and P are about two orders of magnitudes less than the inputs via bird excreta or feathers. Elephant Seals input three orders of magnitude less Ca than do birds. The input of nutrients to the island by sub-Antarctic Fur Seals and Antarctic Fur Seals, which together have a

Table 7.2   Annual input of nutrients (kg per annum) through moulted feathers and fur by seabirds and seals.

Species	1974/75				2002/03			
	Feather production	N	P	Ca	Feather production	N	P	Ca
King Penguin	154 380	13 365	52	119	156 363	13 536	53	120
Gentoo Penguin	1 095	108	0.13	1.6	656	65	0.08	1.0
Macaroni Penguin	398 045	42 997	151	458	323 086	34 900	123	372
Rockhopper Penguin	71 406	5 872	17	220	51 286	4 217	12	158
Sub-Antarctic Skua	269	31	0.07	0.4	117	14	0.03	0.2
Lesser Sheathbill	232	24	0.12	0.6	188	19	0.09	0.5
Crozet Shag	131	13.4	0.1	0.4	67	7	0.03	0.2
Kelp Gull	79	9.2	0.02	0.1	10	1	0.00	0.01
Wandering Albatross	878	101.9	0.23	1.1	756	88	0.20	1.0
Grey-headed Albatross	1 685	195	0.44	2.2	1 675	194	0.43	2.2
Sooty Albatross	549	63.7	0.14	0.7	193	22	0.05	0.3
Light-mantled Sooty Albatross	57	6.6	0.01	0.07	36	4	0.01	0.05
Northern Giant Petrel	110	13	0.03	0.14	68	8	0.02	0.09
Southern Giant Petrel	1 076	125	0.3	1.4	655	76	0.2	0.9

Table 7.2   Continued.

Species	1974/75				2002/03			
	Feather production	N	P	Ca	Feather production	N	P	Ca
Fairy Prion					15	2	0.04	0.02
Salvin's Prion					2 460	299	6.2	2.1
Blue Petrel					1 570	161	8.3	6.7
Great-winged Petrel					904	97	1.4	1.0
Soft-plumaged Petrel					209	30	0.5	0.7
Kerguelen Petrel					584	53	1.9	0.9
Grey Petrel					156	22	3.5	0.1
White-chinned Petrel					1 644	176	2.5	1.9
South Georgian Diving Petrel					7	1	0.02	0.06
Shore	624 511	62 310	221.1	797.6	530 994	52 683	188	650
Inland	5482	613	1.3	8.3	4 160	468	1	6
Burrows	-	-	-	-	7 549	841	24	14
Total birds					542 703	53 992	213	670
Elephant seal fur (1980/81)		699.2	5.4	3.9				

population size nearly two orders of magnitude higher than that of elephant seals, is presently unknown. However, given the large numbers of Fur seals it is likely that their contribution to the nutrient dynamics of the island's terrestrial ecosystem will be substantial.

Nutrients brought in by seabirds and seals influence terrestrial ecosystem function at the island beyond the direct effect of vegetation production through enhanced soil nutrient concentrations. Various studies (discussed by Smith 2008) have shown that seabird and seal manuring, by providing readily oxidisable organic substrates and inorganic nutrients, is the principal determinant (even more so than temperature or moisture content) of other components of ecosystem energetics and nutrient cycling on the island, especially at the decomposition level. These include the size and activity of soil microorganism populations, soil heterotrophic activity, soil respiration and cellulose decomposition, and the numbers and diversity of microbivores.

7.2   Terrestrial/pelagic coupling

Macronutrient concentrations in the ocean in the immediate vicinity of the islands are largely determined by the interaction between the oceanographic environment and the activity of seabirds and seals (Lindeboom 1984; Allanson *et al.* 1985; Duncombe Rae 1989; Ismail 1990; Balarin 2000). In the shallow shelf waters between the two islands, concentrations of macronutrients, particularly reduced nitrogen (ammonia and urea) and phosphate are elevated compared to the open waters of the PFZ (Fig. 7.1) (Pakhomov & Froneman 1999; Pakhomov & Chown 2003). These elevated nutrient concentrations are largely derived from the guano of sea going animals, dung, urine and animal remains which are carried off the islands to the shelf waters via freshwater runoff (Allanson *et al.* 1985; Duncombe Rae 1989). Indeed, good correlations are found between the concentrations of the nutrients between the two islands and water column stability generated by freshwater runoff from the islands (Allanson *et al.* 1985; Duncombe Rae 1989). Maximum concentrations of phosphate derived from the mineralization of feathers are recorded from April to May in the shallow shelf waters of the islands whereas the peak in guano production occurs from December to February (Pakhomov & Froneman 1999). Temporal variation in the main sources of reduced nitrogen and phosphate culminates in a highly variable N:P ratio in the shallow shelf waters of the islands, which may range from 6.5:1 to 38:1 (Pakhomov & Froneman 1999). The elevated concentrations of nutrients derived from the land are not restricted to the immediate vicinity of the island. Elevated concentrations of ammonia and urea have been detected up to 80 km offshore (Pakhomov & Froneman 1999). Perissinotto *et al.* (1990a) attribute this to the advection of shelf waters downstream of the islands.
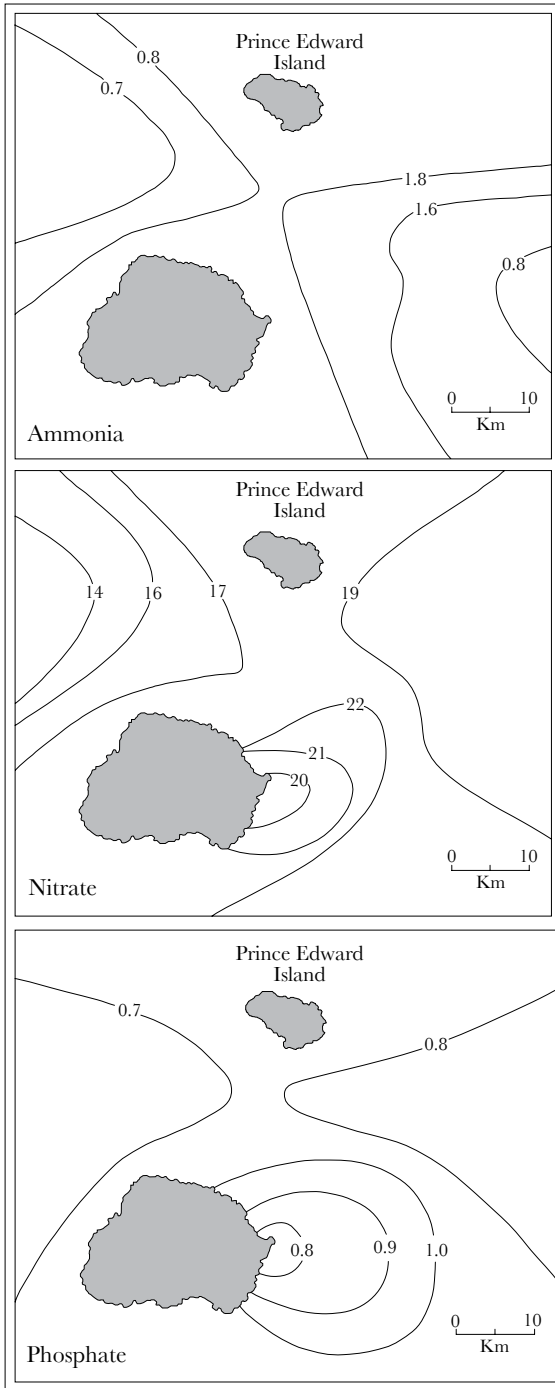
Figure 7.1   Surface concentrations (μmol l^{-1}) of selected nutrients in the vicinity of the Prince Edward Islands during austral autumn 1998. Data are from Balarin (2000).

Although activities of the seals and seabirds on the islands contribute to the nutrient levels in the waters surrounding the islands, oceanic phenomena are largely responsible for the build up of nutrient concentrations in the shallow shelf waters. The Antarctic Circumpolar Current (ACC) shows highest flow rates near the fronts that delimit it (Pakhomov *et al.* 2000a; Ansorge & Lutjeharms 2002) and under conditions when the SAF lies far to the north of the islands, current speeds past the islands are comparatively low (Ansorge & Lutjeharms 2002). This results in a weak interaction between the ACC and the archipelago and this in turn allows the retention of waters on the inter-island shelf (Pakhomov & Chown 2003). By contrast, when the SAF lies in close proximity to the islands, advection forces prevail and a flow through-flow system is established between the islands (Perissinotto & Duncombe Rae 1990; Pakhomov *et al.* 2000b). The retention of waters over the shallow island shelf when eddies are trapped between the islands contributes to the build-up of nutrient concentrations derived from the freshwater runoff from the islands within the inter-island region (Allanson *et al.* 1985). These elevated nutrient concentrations coupled with the increased water column stability derived from the freshwater runoff from the islands generates periodic phytoplankton blooms between the two islands; a phenomenon known as the, "island mass effect" (Allanson *et al.* 1985; Boden 1985; Pakhomov & Froneman 1999; Perissinotto *et al.* 1990a, ; Pakhomov & Chown 2003; McQuaid & Froneman 2004). Conversely, when the flow through prevails, concentrations of nutrients in the shelf waters are in the range of the open waters of the PFZ, due to a strong dilution effect (Balarin 2000).

Although large-scale hydrodynamic processes are largely responsible for determining nutrient concentrations in the waters between the islands, recent work suggests that smaller scale processes may also contribute to the build up of nutrient concentrations in the vicinity of the archipelago. The kelp *Macrocystis laevis* forms extensive beds in shallow waters close to shore and in relatively deep water (60 m) over the Natal Bank. It grows to nearly 30 m and forms a dense surface canopy that visibly subdues swell and retains freshwater run-off from the islands (Pakhomov *et al.* 2002). If this freshwater is nutrient-rich there will be a build up of nutrient concentrations in and around the kelp beds. The biological consequences of this process are as yet not known.

7.3 Impact of global climate change on nutrient dynamics of the Prince Edward Islands ecosystem

Although evidence of climate change (especially warming) in the sub-Antarctic is now well documented (Adamson *et al.* 1988; Jacka & Budd 1998; Smith 2002; Mélice *et al.* 2003) and some of the consequences on the terrestrial ecosystem of the Prince Edward Islands have been described (Smith & Steenkamp 1990; Chown & Smith 1993; Smith 2002), the effect of global climate change on the nutrient dynamics of the ocean around the Prince Edward Islands has received little attention.

The strongest evidence of change in the marine ecosystem is the southward shift, since the 1970s, in the average meridian position of the SAF (Hunt *et al.* 2001). While there is considerable inter-annual (and shorter-term) variability in the position of the front, it is currently *c.*1 degree farther south than in the 1970s. The shift in the position of the front can be linked to large-scale changes in atmospheric circulation patterns resulting from global climate change. Alterations in the ocean circulation patterns will in all probability be associated with changes in food availability and the foraging behaviour of the top predators, particularly flying seabirds on the two islands (Pakhomov & Chown 2003; Ryan & Bester 2008). These factors combined may result in changes in the populations of top predators on the islands, with subsequent decrease in the input of nutrients by these organisms. Clearly any decrease in the populations of the top predators on the islands coupled with the expected decrease in rainfall resulting from global climate change will alter the delivery of nutrients from the terrestrial to the marine environment.

7.4   References

Adamson, D.A., Whetton, P. & Selkirk, P.M. 1988. An analysis of air temperature records for Macquarie Island: Decadal warming, ENSO cooling and Southern Hemisphere circulation patterns. *Papers and Proceedings of the Royal Society of Tasmania* **122**, 107-112.

Allanson, B.R., Boden, B.P., Paker, L. & Duncombe Rae, C. 1985. A contribution to the oceanology of the Prince Edward Islands. In: Siegfied, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 38-45.

Ansorge, I.J., Froneman, P.W., Lutjeharms, J.R.E., Bernard, K.S., Bernard, A., Lange, L., *et al.* 2004. An interdisciplinary cruise dedicated to understanding eddies upstream of the Prince Edward Islands. *South African Journal of Science* **100**, 319-323.

Ansorge, I., Froneman, P.W., Pakhomov, E.A., Lutjeharms, J.R.E., Van Ballegooyen, R. & Perissinotto, R. 1999. Physical-biological coupling in the waters surrounding the Prince Edward Islands (Southern Ocean) *Polar Biology* **21**, 135-145.

Ansorge, I.J. & Lutjeharms, J.R.E. 2002. The hydrography and dynamics of the ocean environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* **37**, 107-127.

Ansorge, I.J. & Lutjeharms, J.R.E. 2003. Eddies originating at the South-west Indian ridge. *Journal of Marine Systems* **39**, 1-18.

Balarin, M.G. 2000. *Size fractionated phytoplankton biomass and primary production in the Southern Ocean*. M.Sc. Thesis, Rhodes University, South Africa.

Boden, B.P. 1985. Observations of the island mass effect in the Prince Edward archipelago. *Polar Biology* **5**, 81-93.

Brown, C.R. 1985. Energetic cost of moult in Macaroni penguins (*Eudyptes crysolophus*) and Rockhopper penguins (*E. chrysocome*). *Journal of Comparative Physiology B* **155**, 515-520.

Burger, A.E., Lindeboom, H.J. & Williams, A.J. 1978. The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 59-70.

Chown, S.L. & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the Sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508-516.

Cooper, J.C. & Brown, C.R. 1990. Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. *South African Journal of Antarctic Research* **20**, 40-57.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Ryan, P.G., *et al*. 2003. Populations of surface nesting seabirds at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 427-440.

Duncombe Rae, C.M. 1989. Data report of the first cruise of the Marion Off-shore Ecological study (MOES-1). *South African National Science Progress Report* **159**, 384 pp.

Froneman, P.W., Ansorge, I., Pakhomov, E.A. & Lutjeharms, J.R.E. 1999. Plankton communities and the physical environment in the waters surrounding the Prince Edward Islands in late austral summer 1997. *Polar Biology* **22**, 145-155.

Fugler, S.R. 1985. Chemical composition of guano of burrowing petrel chicks (Procellariidae) at Marion Island. In: Siegfied, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 169-172.

Gremmen, N.J.M. & Smith, V.R. 2008. Terrestrial vegetation dynamics. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 215-244.

Grobbelaar, J.U. 1974. *A contribution to the limnology of the sub-Antarctic island Marion*. D.Sc. Thesis, University of the Free State, South Africa.

Grobbelaar, J.U. 1978. Mechanisms controlling the composition of freshwaters on the sub-Antarctic island Marion. *Archiv für Hydrobiologie* **83**, 145-157.

Hunt, B.P.V., Pakhomov, E.A. & McQuaid, C.D. 2001. Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology* **138**, 369-381.

Huyser, O., Ryan, P.G. & Cooper, J. 2000. Changes in population size, habitat use and breeding biology of Lesser Sheathbills at Marion Island: Impact of cats, mice and climate change? *Biological Conservation* **92**, 299-310.

Ismail, H.E. 1990. Surface nutrients in the vicinity of the Prince Edward Islands during April/May 1989. *South African Journal of Antarctic Research* **2**, 33-36.

Jacka, T.H. & Budd, W.F. 1998. Detection of temperature and sea ice extent changes in the Antarctic and the Southern Ocean. *Annals of Glaciology* **27**, 553-559.

le Roux, P.C. 2008. Climate and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 39-64.

Lindeboom, H.J. 1979. *Chemical and microbial aspects of the nitrogen cycle of the nitrogen cycle on Marion Island*. Ph.D. Thesis, Groningen University, Holland.

Lindeboom, H.J. 1984. The nitrogen pathway in a penguin rookery. *Ecology* **65**, 269-27.

McQuaid, C.D. & Froneman, P.W. 2004. Rhodes southern Ocean Group: scientific findings from seventeen years of biological oceanography in the South African National Antarctic Programme. *South African Journal of Science* **100**, 571-577.

Mélice, J-L., Lutjeharms, J.R.E., Rouault, M. & Ansorge, I.J. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* **99**, 363-366.

Pakhomov, E.A., Ansorge, I.J. & Froneman, P.W. 2000a. Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean). *Polar Biology* **23**, 593-603.

Pakhomov, E.A., Ansorge, I.J., Kaehler, S., Vumazonke, L.U., Gulekana, K., Bushula, T., *et al.* 2003. Studying the impact of ocean eddies on the ecosystem of the Prince Edward Islands: DEIMEC II: research in action. *South African Journal of Science* **6**, 187-190.

Pakhomov, E.A. & Chown, S.L. 2003. The Prince Edward Islands: Southern Ocean Oasis. *Ocean Yearbook* **17**, 348-379.

Pakhomov, E.A. & Froneman, P.W. 1999. The Prince Edward Islands pelagic ecosystem: a review of achievements 1976-1990. *Journal of Marine Systems* **18**, 297-310.

Pakhomov, E.A., Froneman, P.W., Ansorge, I.J. & Lutjeharms, J.R.E. 2000b. Temporal variability in the physico-biological environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* **26**, 75-95.

Pakhomov, E.A., Kaehler, S. & McQuaid, C.D. 2002. Zooplankton community structure in the kelp beds of the Sub-Antarctic Prince Edward Archipelago: are they a refuge for larval stages? *Polar Biology* **25**, 778-788.

Panagis, K. 1984. *The influence of Southern elephant Seals* Mirounga leonina *(Linnaeus) on the coastal terrestrial ecology of Marion Island*. M.Sc. Thesis, University of Pretoria, South Africa.

Perissinotto, R., Allanson, B.R. & Boden, B.P. 1990a. Trophic relations within the island seas of the Prince Edward Archipelago, Southern Ocean. In: Barnes, M. & Gibson, R.N. (Eds.). *Trophic Relationships in the Marine Environment*. Aberdeen University Press, Aberdeen, pp. 296–314.

Perissinotto, R. & Duncombe Rae, C.M. 1990. Occurrence of anticyclonic eddies on the Prince Edward Plateau (Southern Ocean): effects on phyto-plankton biomass and production. *Deep-Sea Research I* **37**, 777-793.

Perissinotto, R., Duncombe Rae, C.M., Boden, B.P. & Allanson, B.R. 1990b. Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series* **60**, 205-209.

Ryan, P.G. & Bester, M.N. 2008. Pelagic predators. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 121-164.

Smith, V.R. 1976. The effect of burrowing species of Procellariidae on the nutrient status of inland tussock grasslands on Marion Island. *South African Journal of Botany* **42**, 265-272.

Smith, V.R. 1978. Animal-plant-soil nutrient relationships on Marion Island (sub-Antarctic). *Oecologia* **32**, 239-253.

Smith, V.R. 1987. Chemical composition of precipitation at Marion Island (sub-Antarctic). *Atmospheric Environment* **21**, 1159-1165.

Smith, V.R. 1988. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 5. Nutrient budgets and turnover times for mire-grasslands, fjaeldmark and fernbrakes. *Polar Biology* **8**, 255-269.

Smith, V.R. 2002. Climatic change in the Sub-Antarctic: an illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. 2008. Terrestrial and freshwater primary production and nutrient cycling. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 181-214.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a sub-Antarctic Island. *Oecologia* **85**, 14-24.

Williams, A.J. 1978. Mineral and energy contributions of petrels (Procellariiformes) killed by cats, to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 49-53.

Williams, A.J. & Berruti, A. 1978. Mineral and energy contributions of feathers moulted by penguins, gulls and cormorants to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 71-74.