The Southern Ocean Group at Rhodes University: seventeen years of biological oceanography in the Southern Ocean reviewed

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This paper reviews the main findings of the Southern Ocean Group at Rhodes University over the last 17 years. A primary contribution has been the development of conceptual models of the physical-biological driving mechanisms that support enormous seasonal populations of land-based top predators at the Prince Edward Islands. Collectively, these models are referred to as the life-support system of the islands. Near-shore subcomponents of the ecosystem, including inshore feeding predators, are largely supported by autochthonous primary production of kelps and localized diatom blooms. These energy sources feed indirectly into top predator populations via the benthic communities. A crucial link is formed by the bottom-dwelling shrimp, *Nauticaris marionis*, which feeds largely on benthic species and detritus and is eaten by a number of diving seabirds. The frontal systems that lie north and south of the islands are important feeding grounds for offshore feeding birds. A decadal-scale southward shift in the position of the Sub-antarctic Front towards the islands is reflected in increases in populations of these species.

Introduction

In 323 BC, Alexander the Great died in Babylon, probably of malaria. He left behind a vast empire that was dismembered among a group of his generals collectively known as the Diodochi, or Successors. They included Ptolemy, who founded the Ptolemaic dynasty that governed Egypt. Even today the last of that dynasty is famous; Cleopatra, Queen of Egypt, was of Macedonian descent. Over three thousand years later, in AD 1988, Brian Allanson, professor of zoology and head of the Department of Zoology and Entomology at Rhodes University, retired. As with Alexander, it took more than one man to pick up his burden. Randall Hepburn was appointed head of the department that has remained since then the most prolific in publications at Rhodes. Jay O'Keeffe became director of the Institute for Freshwater Studies, now the Institute for Water Research and one of the most influential organizations in freshwater research in South Africa. Christopher McQuaid was appointed director of the Southern Ocean Group (SOG), which Allanson had founded in 1981.

Founding this group was a bold, even visionary, perhaps foolhardy step as Allanson's research expertise was in limnology and he had no experience of oceanography. Despite this, he quite rightly persuaded the South African National Antarctic Programme (SANAP) that a programme in biological oceanography should be developed to complement the existing work in physical oceanography.

Allanson led the first research cruise from Cape Town to Antarctica himself and, in retrospect, his pioneering effort led to developments that put South African biological oceanography firmly on the world map. This first cruise produced novel observations of chlorophyll enhancement at the frontal systems south of Africa[1] and this was the focus of considerable subsequent research.[2–4]

The early work also established a hallmark of later research by the group: the integration of physical, chemical and biological oceanography to give a multidisciplinary understanding of complex ecosystems. This article provides a broad overview of the principal concepts developed and contributions made by the Southern Ocean Group over the 17 years following Allanson's retirement. Since 1988, the SOG has completed four major programmes, and participated in a large number of national and international oceanographic cruises, cooperating extensively with local and overseas collaborators.

The main programmes

During the late 1980s–1990s, the Marion Offshore Ecosystem Study (MOES) developed the concept of the life-support system, responsible for supporting enormous populations of land-based predators (birds and seals) at the Prince Edward Islands, in an area where primary production rates are insufficient to cover the energetic needs of these predators.

In the early-mid 1990s, the Antarctic Marine Ecosystem and Global Climate Change project contributed to two major international programmes: the World Ocean Circulation Experiment and the Joint Global Ocean Flux Study. The work of the SOG highlighted the importance of seasonal and spatial variability in the size structure of primary producers to the efficiency of the biological pump and of frontal systems as biogeographical boundaries for phytoplankton and, to a lesser extent, zooplankton.

In the late 1990s–2000, the Prince Edward Islands Life Support System project re-examined and refined the life-support system concept, emphasizing the importance of oceanic fronts as feeding grounds, including the consequences of rising sea temperatures and long-term meridional shifts in frontal positions to seabird populations.

From 2001 to the present, the Marion Offshore Variability Ecosystem Study has used stable-isotope techniques to identify the relative importance of allochthonous and autochthonous sources of energy to the benthic and pelagic food webs. In addition, mesoscale anomalies generated upstream of the islands have been identified as areas of enhanced productivity transported towards the islands, though their fate and biological effects are still unclear.

The Marion Offshore Ecosystem Study

The Prince Edward Islands form an archipelago of just two small islands, representing deep-sea volcanoes rising abruptly from the seabed at approximately 3000 m. They are 16 km apart and are separated by a shallow water shelf, or plateau, about

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200 m deep. The islands lie approximately half-way between Africa and Antarctica in the path of the Antarctic Circumpolar Current, with fast flowing frontal systems to the north (the Sub-antarctic Front, SAF) and the south[5] (the Antarctic Polar Front, APF; see Fig. 1). This effectively gives the islands an upstream (west-facing)–downstream (east-facing) axis. A major biological feature of the islands is that they support great numbers of land-based predators, animals that breed ashore, but feed at sea. Approximately 5 million pinnipeds and birds come to the islands in summer to breed and, in the case of the birds, to moult.[6,7]

Moulting and feeding of young place huge energetic demands on these animals and initially it appeared that satisfying these demands was linked to a distinct island mass effect. Chlorophyll levels in the vicinity of the islands are generally much higher than at comparable latitudes away from the influence of the islands,[8] and dense blooms of diatoms, dominated by *Chaetoceros radicans,* form frequently during summer.[9] It was postulated that phytoplankton blooms were made possible by the supply of reduced nitrogen, in the form of guano and feather run-off from penguin rookeries, and the retention of water over the inter-island plateau by a Taylor column effect.[8,10–12] These periodic blooms were thought to be a primary source of food for the land-based predators. These ideas were later abandoned when it was found that diatom blooms suffer little zooplankton grazing[13] and that their contribution to energy flow through the system is indirect. Senescence and sinking-out of diatoms provides food for a benthos, dominated by bryozoans, that supports dense populations of the swimming shrimp, *Nauticaris marionis. Nauticaris* in turn is a staple in the diets of birds that feed close to the islands, such as rockhopper penguins and imperial cormorants[14,15] (Fig. 2A).

Birds feeding close to the islands also exert enormous predation pressure on prey that are carried over the shallow waters of the island plateau by the Antarctic Circumpolar Current (ACC). This current carries great quantities of zooplankton and myctophid fish towards the island and, while these prey can sink below the foraging depth of air-breathing predators in deeper waters, they are trapped by the shallow water topography of the islands (Fig. 2B). The result is a distinct scarcity of zooplankton over the plateau and immediately downstream of the islands,[16,17] though this is not always true (see below).

These initial concepts were only a first approximation, as they did not allow for differences in feeding biology of the predators. While some birds feed close to the islands, others feed elsewhere and have completely different diets. One problem with the idea of prey advection to the islands is that this supplies sufficient crustacean prey for the predators' needs, but not enough fish.[17] Species that require a high proportion of fish in their diets, and command long foraging ranges and deep diving depths, such as king penguins, appear to feed primarily at oceanic features such as fronts. Together these two components represent what came to be called the 'life-support system' of the islands, the means by which near-shore and offshore feeding predators are supplied with energy.[7] This is a circumstance in which biology and the physical oceanic environment are particularly tightly linked.

The Antarctic Marine Ecosystem and Global Climate project

It is by now common knowledge that human activities have contributed to a considerable increase in atmospheric levels of the so-called greenhouse gases, especially carbon dioxide, that are believed to be linked to a rise in global temperatures.[18] The oceans play a central role in the control of greenhouse gases as they store over 50 times more carbon than the atmosphere and

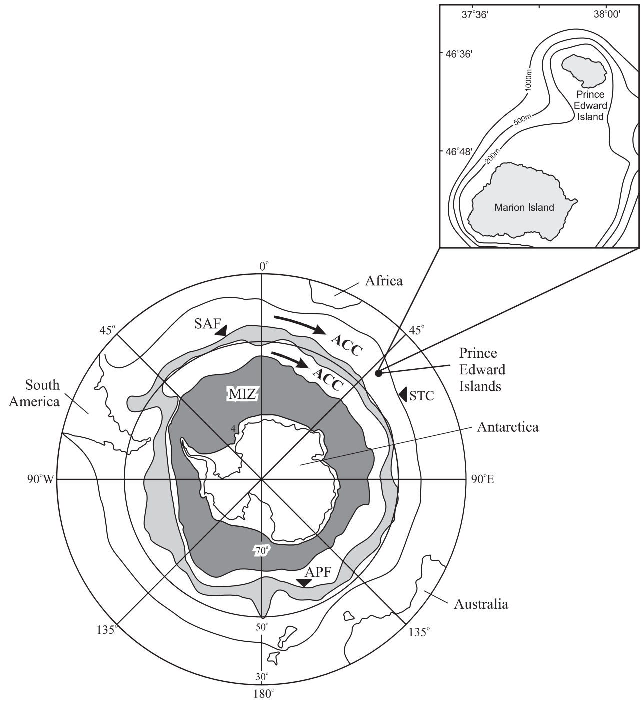

Fig. 1. Map of the Southern Ocean, positions of major frontal systems and the Prince Edward Islands. ACC, Antarctic Circumpolar Current; STC, Subtropical Convergence; SAF, Sub-antarctic Front; APF, Antarctic Polar Front; MIZ, Marginal Ice Zone.

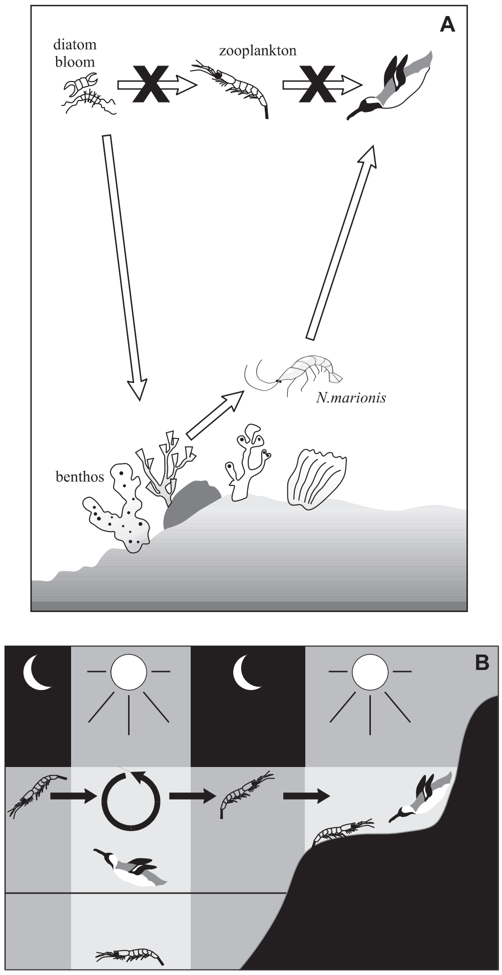

Fig. 2. **A**, Conceptual model of trophic links between local diatom blooms and land-based, inshore feeding predators in the shallow shelf waters around the Prince Edward Islands; **B**, conceptual model of prey trapping by the shallow topography of the Prince Edward Island plateau.

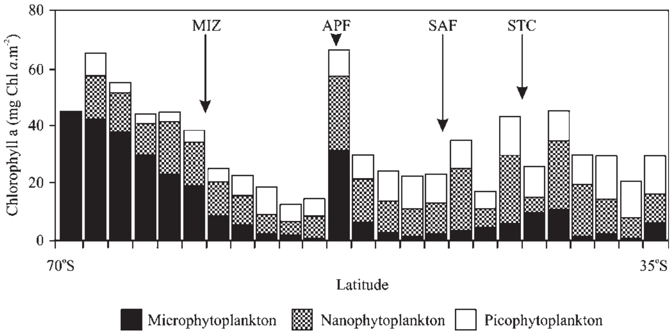

Fig. 3. Size-fractionated chlorophyll-*a* concentration along a transect between Cape Town and Antarctica. STC, Subtropical Convergence; SAF, Sub-antarctic Front; APF, Antarctic Polar Front; MIZ, Marginal Ice Zone.

20 times more than the terrestrial ecosystem.[19] The ocean acts as a carbon pump, extracting carbon dioxide from the atmosphere both physically and biologically through phytoplankton photosynthesis and the export of senescent cells and zooplankton faeces to depth.[20–22] The biological processes that extract carbon from the atmosphere are known as the biological pump and, while biogenic carbon removal does not sequester a significant proportion of anthropogenic carbon releases,[23] there are parts of the ocean where the efficiency of the biological pump could increase dramatically. The most important such area is the Southern Ocean, where nutrient levels are high, yet phytoplankton production is much lower than expected. This is the Antarctic Paradox.[24]

A primary aim of this project was to examine the efficiency of the biological pump in the Southern Ocean.

Oceanic fronts have important effects on primary productivity (see below) and we expect them to have a profoundly important influence on the distribution of Southern Ocean organisms. This seems to be true for some taxa, but not all. The distribution of diatoms is strongly affected by frontal systems, with different species assemblages associated with different water masses.[25–27] The same is true for zooplankton, but not seabirds.[28] More important in this context, there is a definite north–south shift in the size composition of the phytoplankton that is focused on the frontal regions (Fig. 3). Phytoplankton communities to the north of the Antarctic Polar Front (APF) tend to be dominated by smaller organisms (the nano- and picophytoplankton), while the diatom-dominated microphytoplankton becomes increasingly important farther south.[25,26,29–32] Seasonality has a similar effect, with smaller phytoplankton cells predominating in winter. These spatial and temporal effects have extremely important implications for rates of carbon flux and the efficiency of the biological pump.[22,33,34]

Understanding carbon flux requires knowledge of not only primary production and its apportionment among phytoplankton size classes, but also of grazing rates and the length of grazing food webs. Simplistically, large phytoplankton cells are eaten by large zooplankton that produce large, fast sinking faeces and often exhibit diel vertical migrations in the water column, so that they feed near the surface at night and defecate at depth during the day. The result is relatively efficient export of photosynthetically fixed carbon to depth, that is, an efficient biological pump. Smaller phytoplankton are eaten by smaller zooplankton, including microzooplankton. Such organisms are themselves light and release very light micro-faeces that remain in surface waters, where they are degraded by bacteria. These small organisms are in turn eaten by larger zooplankton, resulting in a longer food chain with respiratory losses of carbon at each step. This all results in a much less efficient biological pump, with more of the phytoplankton-fixed carbon being re-released to the atmosphere.

During this programme, microzooplankton were repeatedly found to consume a high proportion of daily primary production in places where small phytoplankton cells predominated.[31,34,35] However, repeated grid and drogue studies at the ice front in the high Antarctic demonstrated that microzooplankton cannot control primary production where it is dominated by the large microphytoplankton; such production is either lost through sedimentation, or grazed by large zooplankton.[31,34–36] Furthermore, feeding studies indicated that heterotrophic carbon, especially microzooplankton, forms a much higher proportion of the diet of macro- and mesozooplankton organisms than previously assumed. This is true for a range of krill species (four around the Prince Edward Islands plus the Antarctic krill, *Euphausia superba,* and *Thysanoessa macrura* in the Antarctic Polar Front and Marginal Ice zones), as well as mesozooplanktonic copepods in the Atlantic sector of the Southern Ocean.[37–39]

The overall conclusion was that short food webs and an efficient biological pump occur only during the seasonal retreat of the sea ice during the Antarctic summer, in the waters close to sub-Antarctic islands and in the vicinity of oceanic fronts.[34,40] Elsewhere, small phytoplankton dominate primary production, leading to long food chains and inefficient carbon sequestration.[36]

This programme also addressed the crucial question of interactions between two Southern Ocean organisms that can dominate biomass within the community and are often super-abundant locally: Antarctic krill and the gelatinous protochordates called salps. Salps and krill generally do not co-exist at high densities, but exhibit spatial segregation at all spatial scales, usually living in different water masses separated by frontal features.[41] Salps are especially efficient filter-feeders, able to retain extremely small particles and may greatly enhance the efficiency of the biological pump in areas where small cells predominate.[41,42] The abundance and distribution of salps have increased considerably for over a decade, while the krill biotope has shrunk. Interaction between the two appears to be indirect.[41] Measurements of salp consumption rates indicate that they are capable of exerting enormous grazing pressure because they can filter particles as small as 2 μm with 100% efficiency, and can attain high densities through asexual reproduction. The low abundances of krill (and other zooplankton) associated with salp swarms has been thought to be due to predation of eggs and larvae by filter-feeding salps, but our studies suggest the effect is probably due to the hyper-efficient, competitive removal of food by salps.[41]

The Prince Edward Islands Life Support System project

This programme refined the life-support system concept, emphasizing the importance of variability in food supply to the ecosystem, and examined the biology of a key species in the system, the shrimp, *Nauticaris marionis.*

It quickly became clear that the Prince Edward Islands lie in a region of high disturbance in the flow of the Antarctic Circumpolar Current, and that physical disturbances in water flow are linked to heterogeneity in the planktonic community. Particularly important is the speed with which the ACC approaches the islands and this in turn reflects the proximity of the Sub-antarctic Front that lies to the north of the islands. When the SAF lies close to the islands, water flows past and around them, with little retention over the inter-island plateau. This is described as a 'flow-through' system[43–46] and is a situation that favours predators feeding away from the islands. Offshore feeders tend to focus on the vicinity of the fronts and a southward shift of the SAF means that their feeding grounds effectively approach the islands, reducing the length of foraging excursions. A through-flow situation may also result in larger zooplankton being washed around the islands, rather than between them, concentrating the zooplankton just downstream.[45] When the SAF lies farther north, trapping of water over the plateau is more likely, which in the long term should favour near-shore feeders through more frequent development of local diatom blooms, feeding into the benthos through senescence, and thus into populations of *Nauticaris marionis.*[44]

There is a remarkable congruence of these ideas with observations on long-term shifts in the average position of the SAF and of changes in bird populations. Over the last 30–40 years, the islands have become warmer and drier[47] and have also experienced a rise in sea temperatures as the SAF has on average shifted farther south. As predicted by the scenario described above, this is correlated with long-term increases in populations of offshore feeding seabirds, such as the grey-headed albatross and the northern giant petrel, and decreases in numbers of near-shore feeders, such as rockhopper penguins. Species with mixed diets (e.g. Macaroni penguins) have maintained much more stable numbers over this period (Fig. 4).

Detailed studies of both phytoplankton and zooplankton communities revealed good correlations between biology and oceanographic features. Frontal systems were clearly identified as areas of abrupt change in both total chlorophyll and community composition of diatoms.[26,48,49] Enhanced chlorophyll levels were repeatedly recorded at fronts (the Subtropical Convergence and the Sub-antarctic Front) and were invariably associated with high abundances of diatoms and a substantial contribution of the microphytoplankton to total chlorophyll. Thus the fronts act not only as biogeographic boundaries for diatoms, but also as centres of high efficiency in the biological pump. However, these effects were recorded only where the fronts were of high intensity, for example the STC immediately south of Africa.[27,50] Where weaker (e.g. in the mid-Indian Ocean), the Subtropical Convergence (STC) had no such effects.[27] On more local scales, chlorophyll levels around the islands were well correlated with oceanographic features. Low chlorophyll levels and small cell sizes were repeatedly found in the Antarctic Polar Front Zone, particularly in cold-water intrusions with deep mixed layers. In contrast, chlorophyll levels were relatively high downstream of the islands, with evidence that this chlorophyll originated in the inter-island region. Like the phytoplankton, zooplankton densities and biomass were enhanced at the fronts as well as close to the islands and farther downstream.[45]

In the open ocean where the primary producers are small, zooplankton grazing is generally dominated by copepods and pteropods,[36,49,51] though recent work indicates that ostracods too can exert considerable grazing pressure.[52] However, a characteristic of the zooplankton around the islands is that larger carnivorous species periodically dominate total biomass. The main groups of carnivores are chaetognaths, euphausiids, decapods, amphipods, and gelatinous species, with the first two groups forming up to 90% of carnivore biomass. Collectively, these species can remove up to 40% of mesozooplankton standing stocks through predation, though generally the value is <5%.[26,53] Nevertheless, because they exhibit vertical migration and form fast sinking faecal pellets, such carnivores may increase the local efficiency of the biological pump and form an important link between the smaller mesozooplankton and the top predators.

Apart from characterizing the Prince Edward Island ecosystem specifically, the work on grazing food chains has made a theoretical contribution by demonstrating trophic cascading in this system. Essentially, the theory of trophic cascading predicts that the presence of a predator will have a powerful indirect effect on the phytoplankton by controlling densities of grazers and minimizing their effect on primary producer populations. This has led to the prediction that food chains with even and uneven numbers of steps will show strong and weak effects of grazers on phytoplankton biomass, respectively,[54] a prediction supported by our findings.[55]

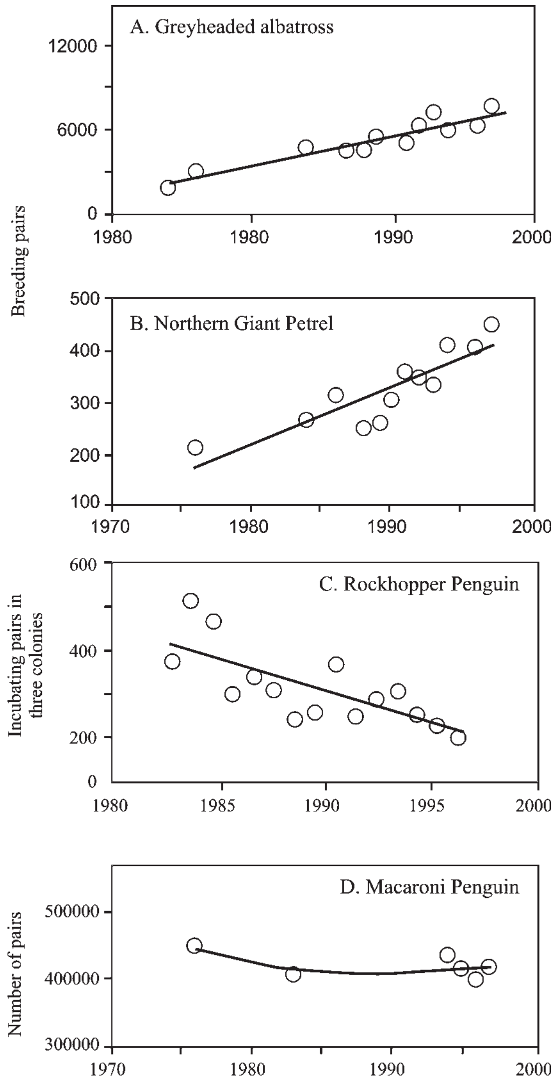

Fig. 4. Long-term trends in populations of selected seabirds at the Prince Edward Islands. **A** and **B**, offshore feeders; **C**, inshore feeder; **D**, mixed diet. Data from Pakhomov E.A., Froneman P.W., Crawford R. and Cooper J. (1999) Decadal changes in the environment around the sub-Antarctic Prince Edward Islands: climate change and its ecological consequences. *34th European Marine Biology Symposium, Azores.*

Nauticaris marionis is a key species in the Prince Edward Islands ecosystem because of its abundance and its role as food for near-shore feeding birds. The shrimp is an opportunistic feeder with a preference for detritus, benthic amphipods and gastropods, thus acting as an indirect trophic link between local primary production, much of which enters the benthic community, and thus the birds.[56,57] It can live for up to seven years under natural conditions and has a curious life cycle, being a partially protandric hermaphrodite with most juveniles developing directly into males.[58] Females form in several ways. Primary females emerge directly from a minority of juveniles by developing an ovary and losing the characteristically male appendix interna from the first pleopod during moulting. Secondary females develop by an alternative route, becoming males first and then developing an ovary to form an intermediate sexual form called a *tertium quid,* or 'third thing'. Again, there are two forms of *tertium quid.*[57] It is unclear whether sexual differentiation occurs in the plankton or just after *N. marionis* settles on the benthos. At this stage it is also unclear how populations of the squid are maintained at the islands in the face of potential downstream advection of larvae into uninhabitable deep waters by the ACC. One hypothesis that larvae find refuge in near-shore kelp beds appears to be untrue,[59] and the problem remains unsolved.

The Marion Offshore Variability Ecosystem Study

In contrast to the near-shore system around the Prince Edward Islands, the remote offshore environment remained poorly studied during the previous programmes. This was an important lacuna because of the dependence of a high proportion of the land-based predators on feeding grounds far from the islands.

During earlier programmes, physical oceanographers examined and discarded a series of hypotheses attempting to explain why the island region is an area of unusually high variability. Cyclonic and anticyclonic mesoscale eddies are frequently observed around the islands and appear to be linked to high primary productivity.[60] As the physical scale of these investigations has grown, it has become obvious that theories based on local hydrography and topographic effects are inadequate and that it is important to set the islands in a larger physical context. Persistent cloud cover in the region hampered earlier studies based on sea-surface temperature. A new approach, based on sea-surface altimetry, indicates that the islands are positioned on the northern edge of a region of high variability reflecting downstream turbulence in the wake of the South-West Indian Ridge.[60] Sea-surface anomalies generated by the flow of the ACC over the South-West Indian Ridge appear to be funnelled through the channel between the Conrad Rise and the Del Cano Rise; the Prince Edward Islands lie at the mouth of this channel.[61] Given the apparent tendency of some of the flying seabirds to feed near the margins of these features,[62] recent efforts have concentrated on examining the zooplankton and phytoplankton communities inside and at the margins of these features. Preliminary data collected during 2004 suggest that topographic steering of the ACC, where it crosses the South-West Indian Ridge in the region of the Andrew Bain Fracture Zone, can result in convergence of two major frontal systems, the Sub-antarctic Front and the Antarctic Polar Front. This convergence forms a region of enhanced biological activity, with elevated biomasses of pelagic fish and cephalopods,[63] highlighting the importance of the region upstream of the Prince Edward Islands as a potential foraging ground for the top predators.

The current programme has also involved the use of stable-isotope analysis to elucidate the island-associated marine food webs, both pelagic and benthic. This led to two important findings. First, autochthonous production is more important that previously suspected. Locally produced kelp detritus forms an important carbon source for near-shore benthic communities, whereas the offshore benthos of the inter-island plateau depends largely on the microphytoplankton of autochthonous local blooms. Only the planktonic grazers depend primarily on allochthonous, oceanic nano- and picophytoplankton[64] (Fig. 5).

Second, the bottom-associated shrimp, *Nauticaris marionis,* has exhibited a significant decline in $\delta^{13}C$ values over the last 16 years. This suggests a change in the carbon signature at the base

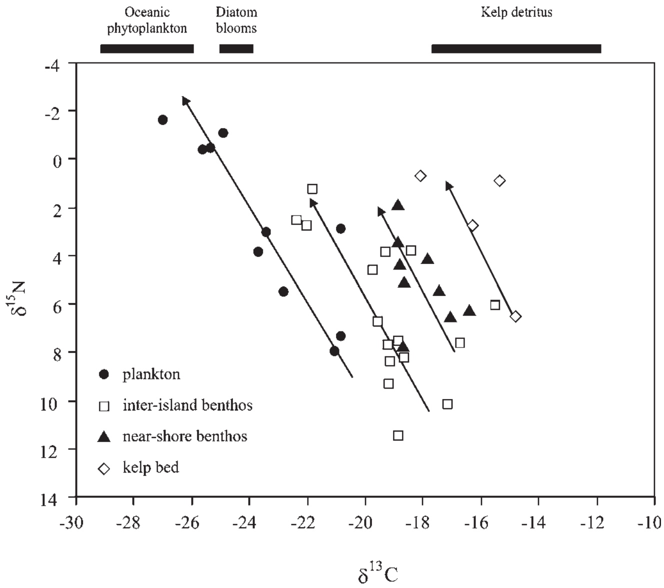

Fig. 5. Stable carbon and nitrogen isotope signatures (in units of ‰) of consumers and carbon signatures of primary producers at the Prince Edward Islands. Data provided by S. Kaehler.

of the food chain, linked to changes in the overall productivity of the inter-island system, possibly driven by long-term climate change.[65]

Overview

The success of the Southern Ocean Group has been mainly due to the effectiveness of the researchers employed, but another crucial ingredient has been the very close working relationships with the physical oceanographers at the University of Cape Town, under the leadership of Johann Lutjeharms. Throughout the last 17 years, a hallmark of the science done by the Southern Ocean Group has been an unusually close integration of physics and biology, made possible through this collaboration.

It is also worth considering the productivity of the group. Gotthilf Hempel from the Alfred Wegener Institute in Germany and editor of *Polar Biology* described the group in an unpublished letter as 'one of the most productive in planktonology' — which must be a German word, but the sentiment is clear.

Funding for the Southern Ocean Group was never lavish. At no time have there been more than two postdoctoral researchers employed by the group and its extraordinary productivity is due to the drive and energy of these individuals. Nevertheless, the effects of cuts in funding are obvious. While other oceanographic teams were eliminated entirely from SANAP during progressive reductions in funding, the Southern Ocean Group maintained itself until the point where funding for dedicated posts was ruled out of bounds across the board. This occurred at the start of the fourth programme. At that point publications declined dramatically and it was only the timely and generous intervention of Rhodes University that allowed the group to continue. With the recent transfer of SANAP to the Department of Science and Technology, there is the promise of increased funding. This will undoubtedly improve the situation, but the outstanding lesson learnt during this research reinforces the need for dedicated manpower. A revitalization of interest in and funding for Southern Ocean research holds promise for the future, but it will take time to rebuild the capacity lost during SANAP's long polar twilight. Alexander the Great would probably agree that it is easier to destroy than to create.

We must firstly acknowledge funding provided over many years by the Department of Environmental Affairs and Tourism, in what was at times a very difficult funding environment. When the crunch came, Rhodes University very generously threw the Southern Ocean Group a lifeline that saved it from shipwreck and for this we are extremely grateful. The unstinting and ungrudging assistance of the officers and crew of the *SA Agulhas* helped enormously in the conduct of this research, as did the intellectual, practical and moral support of our colleagues in the Oceanography Department of the University of Cape Town. A great many friends, colleagues and students contributed over many years to these programmes – we thank them all.

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