CHAPTER 5

BIOLOGY IN THE OCEANOGRAPHIC ENVIRONMENT

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The earliest recorded study of the marine environment around the Prince Edward Islands was preliminary oceanographic work in the late nineteenth century done when HMS Challenger briefly visited the islands in 1873. However, it was only in 1976, that the French vessel, the *MS Marion Dufresene* undertook the first comprehensive investigation of the biology of the marine environment (Pakhomov & Froneman 1999a). Another ten years lapsed before a focussed programme began the systematic study of the marine biology of the islands and the links between physical oceanography, life in the water column, and the air breathing, land-based top predators breeding on the islands. During the late 1980s, the Marion Offshore Ecosystem Study (MOES) addressed the problem of how a tiny archipelago of two small islands could sustain the enormous populations of pinnipeds and birds that aggregate there during summer and autumn (Pakhomov & Froneman 1999a; McQuaid & Froneman 2004). The initial target of investigation was the existence of an island mass effect at the archipelago, a phenomenon of greatly enhanced primary production in a low productivity part of the ocean, and how, or whether this production fed into the top predators. The programme was unusual in laying equal emphasis on the availability of food and the importance of its physical supply to consumers. By the end of the programme an understanding of trophic relationships between autochthonous or allochthonous food sources and the top predators was developed as what became known as the “life support system” of the

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islands (Pakhomov & Froneman 1999a; Pakhomov & Chown 2003; McQuaid & Froneman 2004). Over the past decade, two further research programmes have modified and refined this concept, expanding the physical scale of study to concentrate more explicitly on the offshore environment, particularly towards the west or upstream of the islands (McQuaid & Froneman 2004). The results of these investigations have clearly demonstrated the close link between the physical environment and the distribution and species composition of the plankton assemblages within the Polar Frontal Zone in the region of the islands. More significantly, they have demonstrated the importance of both horizontal and vertical hydrodynamics as the ultimate determinants of the carrying capacity of the islands, and the intimate relationships among sea floor topography, large-scales current systems and the biology of the islands, with ramifying effects from phytoplankton primary production to nutrient exchange between land and sea. Throughout the 15 years of study of the islands' marine ecosystem, there has been a major logistic constraint on the research. Research is primarily based on the research vessel, *SA Agulhas* during re-supply cruises to the island weather station. As a result there has been limited ship's-time for research. More critically, cruises have been confined to late summer/autumn so that there is little understanding of seasonal variation in functioning of the ecosystem. This puts an important caveat on the findings: in such a high latitude region, seasonality is likely to be profoundly significant.

The physical oceanography of the region is described elsewhere (Lutjeharms & Ansorge 2008), but two broad aspects are important. The islands lie within the Polar Frontal Zone; that is north of the Antarctic Polar Front and south of the sub-Antarctic Front. The islands also lie in the path of the Antarctic Circumpolar Current, giving them a west-east or upstream-downstream axis.

5.1 Phytoplankton studies

The open waters of the Polar Frontal Zone (PFZ) of the Southern Ocean are not particularly poor in nutrients, but they are subject to almost continuous deep mixing due to wind stress. In fact, Perissinotto *et al.* (1990a) calculated that water column stability accounts for the majority of the total variance in primary production in the region of the islands. As a result, phytoplankton biomass and production is generally low and normally dominated by small-celled picophytoplankton ($< 2.0 \mu\text{m}$) (Fig. 5.1). These microalgae are able to tolerate both the poor light environment caused by a deep mixed layer, and the comparatively low macronutrient availability, (Perissinotto *et al.* 1990a; Laubscher *et al.* 1993; Balarin 2000). This allows them to dominate the overall phytoplankton community, and at times they form over 90% of total integrated biomass and production (Fig. 5.1).

Exceptions to this scenario occur in terms of both chlorophyll density and phytoplankton size structure at the two major frontal systems in the region, the sub-Antarctic Front (SAF) to the north and the Antarctic Polar Front (APF) to the south of the islands (Fig. 5.1). An exception also occurs in the shallow

shelf waters between Marion and Prince Edward Islands, which demonstrate the so-called “island mass effect” of markedly enhanced primary production close to oceanic islands (Fig. 5.2; Table 5.1) (Allanson *et al.* 1985; Boden 1988; Perissinotto *et al.* 1990a, b). In all three cases, total phytoplankton biomass and phytoplankton production are two to three times higher than in the open waters of the PFZ. Equally significant is that different size classes dominate the phytoplankton community within these areas of elevated biomass. In these areas the most important size classes are not the picophytoplankton, but the nano- (2.0–20.0 μm) and microphytoplankton (> 20.0 μm) (Fig. 5.1) (Froneman & Pakhomov 1998a; Pakhomov & Froneman 1999a).

Figure 5.1 Size fractionated chlorophyll-a concentrations at selected stations occupied in the open waters of the Polar Frontal zone upstream and downstream of the Prince Edward islands in the vicinity of the sub-Antarctic Front (SAF) during April/May 1996 (modified from Froneman & Pakhomov 1998a).

In the absence of data for most months of the year, it is not possible to assess whether there are strong seasonal patterns in total chlorophyll-a concentration and primary production in the region of the islands (see Pakhomov & Froneman (1999a) and references therein). However, studies in the PFZ in the Atlantic sector of the Southern Ocean during summer have recorded values two to three times higher than in the vicinity of the island during winter, suggesting that seasonality is likely to be marked (Laubscher *et al.* 1993; Froneman *et al.* 1995, 2001).

Using data collected during three cruises in the waters between and in the immediate vicinity of the Prince Edward Islands, Perissinotto *et al.* (1990a) showed that elevated phytoplankton biomass and productivity in the shallow shelf waters between the islands could be attributed to the vertical structure of the water column and increased availability of macronutrients. The more

pronounced vertical structure of the water column between the islands was attributed to high levels of freshwater run-off from the islands being retained over the shelf by anti-cyclonic eddies of the Taylor Cone type (Perissinotto *et al.* 1990a). In addition there was increased availability of macronutrients (mainly ammonia and urea) in these waters, derived from guano run-off from the islands, with this high nutrient water also being entrained by the anti-cyclonic eddies (Perissinotto & Duncombe Rae 1990). This combination of elevated water column stability and macronutrient availability in the inter-island region generated phytoplankton blooms dominated by chain forming diatom species of the genera *Chaetoceros* (mainly *Chaetoceros radicans*) and *Fragilariopsis*. During these blooms, the total chlorophyll-a concentration may exceed 1.5 mg chl-a m⁻³ (Allanson *et al.* 1985; Pakhomov & Froneman 1999a; Pakhomov & Chown 2003).

Table 5.1 Estimates of total phytoplankton biomass and production during the various cruises conducted in the open waters of the Polar Frontal Zone of the Southern Ocean and in the immediate waters surrounding the Prince Edward Islands. SAF = sub-Antarctic Front; ND = no data.

Source	Period	Region	Phytoplankton Biomass (mg chl-a m ⁻³)	Phytoplankton Production (mg C m ⁻² d ⁻¹)
El-Sayed <i>et al.</i> (1979)	March, 1976	Inter-island region	0.09-1.88	211
Miller <i>et al.</i> (1984)	September 1982	Inter-island region	0.01-0.5	ND
Allanson <i>et al.</i> (1985)	May, 1983	Inter-island region	0.10 –2.30	84-2100
Allanson <i>et al.</i> (1985)	November, 1983	Inter-island region	0.06-0.87	ND
Van Ballegooyen <i>et al.</i> (1989)	May 1987	Inter-island region	0.05-0.45	47-312
Perissinotto & Duncombe Rae (1990)	April, 1985	Inter-island region	0.1-2.8	70-3000
Balarin (2000)	April, 1998	Inter-island region	0.2-0.8	119-353
		Open water	< 0.2	94-442
Pakhomov <i>et al.</i> (2000b)	April, 1989	Open waters	< 0.1	ND
		Inter-island region /SAF	0.31-0.45	ND
Froneman & Balarin (1998)	April 1997	Open waters	0.29 –0.52	ND
Bernard & Froneman (2005)	April/May 2003	Open waters	0.15-0.28	ND

Figure 5.2 Spatial distribution of total chlorophyll-a concentrations at surface (A) and 50 m (B) depths in the vicinity of the Prince Edward Islands in May 1983. Units are mg chl-a m^{-3} . (Modified from Allanson *et al.* 1985).

The occurrence of Taylor Cone type eddies in the shelf waters is thought to be linked to the proximity of the SAF to the islands. 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 domination of frictional over advective forces. As a consequence, eddies are trapped between the two islands. On the other hand when the SAF lies farther south (i.e. closer to the islands), advective forces prevail and the islands act as a through-flow system (Perissinotto & Duncombe Rae 1990; Pakhomov *et al.* 2000b). Eddies are absent from the inter-island region under flow through conditions.

Although it is clear that large-scale oceanographic processes are responsible for generating periodic phytoplankton blooms in the shelf waters, recent work suggests that phytoplankton growth may also be enhanced on much smaller scales through the localised effects of kelp beds. The local kelp, *Macrocystis laevis*, forms extensive beds in shallow waters close to shore and in relatively deep water (60 m) over the Natal Bank. (Attwood *et al.* 1991; Perissinotto & McQuaid, 1992a). This species grows to nearly 30 m in length and forms a dense surface canopy that visibly subdues the effects of swells. The canopy also retains freshwater run-off from the islands. An extensive survey conducted near Marion Island demonstrated that retention of freshwater by kelp beds promotes local water column stability (Pakhomov *et al.* 2002). Thus, physical retention of freshwater in and close to kelp beds could potentially promote the growth of phytoplankton in a manner similar to that proposed for the anti-cyclonic eddies, but on very much smaller scales.

5.2 Zooplankton studies

Only a single survey has investigated the community composition and distribution of the protozooplankton ($< 200 \mu\text{m}$) in the waters surrounding the Prince Edward Islands (Froneman & Balarin 1998). This study indicated that the densities of protozooplankton ranged between 5×10^3 and $7 \times 10^3 \text{ ind. l}^{-1}$ and were numerically dominated by nanoflagellates ($< 20 \mu\text{m}$), dinoflagellates and ciliates. The values, measured during autumn, are in the range recorded in the PFZ in other sectors of the Southern Ocean during both summer and winter (Froneman & Perissinotto 1996a, b), suggesting that there is little seasonality in the densities or the broad taxonomic composition of the protozooplankton within the PFZ. Comparison of offshore and inshore waters of the islands gives no evidence of clear spatial patterns in the community structure and distribution of the protozooplankton, nor are there obvious temporal patterns on scales of days (Froneman & Balarin 1998).

When we consider the larger zooplankton ($> 200 \mu\text{m}$), it is clear that there is no endemism among the holoplankton of the PFZ (Boden & Parker 1986; Pakhomov & Froneman 1999a) and that the zone effectively acts as an ecotone. There is often extreme spatial variability in species composition of the zooplankton, which can largely be ascribed to the periodic intrusion of tongues of Subtropical surface waters from the north, and of Antarctic surface waters from the south (Pakhomov & Froneman 1999a; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003). Far field generated eddies or frontal meanders from both the Subtropical Convergence (STC) and the APF, which penetrate into the PFZ, may further contribute to the variability in the zooplankton community (Ansorge *et al.* 1999; Froneman *et al.* 1999). Because the oceanographic environment is spatially so variable, the zooplankton community within the PFZ contains animals with quite different biogeographic affinities. For example, the crustaceans include species that are sub-Antarctic, Subtropical and Antarctic in origin (Ansorge *et al.* 1999; Pakhomov *et al.* 2000a; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003).

The macrozooplankton may contribute substantially (up to 45%), to the total zooplankton biomass (Pakhomov & Froneman 1999b), but generally both numbers and biomass of the zooplankton community in the region are dominated by mesozooplankton ($200\text{--}2\,000 \mu\text{m}$) (Perissinotto & Boden 1989; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003). For example, a study by Hunt *et al.* (2001) showed that copepods comprised 52–88% of all zooplankton counted during six surveys carried out over the period 1996 to 1999. Among the mesozooplankton, the pteropod *Limacina retroversa* and small copepods ($200\text{--}500 \mu\text{m}$) of the genera *Oithona*, *Calanus* and *Metridia* are especially abundant, forming 47–71% of total numbers (Bernard & Froneman 2002). Despite this, mesozooplankton biomass is dominated by the larger ($1\,000\text{--}2\,000 \mu\text{m}$) size classes, which form an average of 66% (SD = $\pm 10.2\%$) of total biomass (Bernard & Froneman 2002). The most well represented species within these larger mesozooplankton size classes are chaetognaths (*Eukrohnia hamata* and *Sagitta gazellae*), amphipods (*Themisto gaudichaudi*) and euphausiids (*Thysanoessa* spp.).

By far the most important groups (by numbers and biomass) in the macrozooplankton are euphausiids (*Euphausia vallentini* and *Nematoscelis megalopes*), chaetognaths (*Sagitta gazellae* and *S. maximum*) and tunicates (mainly *Salpa thompsoni*) (Pakhomov & Froneman 1999b; Pakhomov *et al.* 2000a; Gurney *et al.* 2002). The contribution of these main groups demonstrates a high degree of spatial and temporal variability with no clear patterns (Pakhomov & Froneman 1999b). Average abundance and biomass of the macrozooplankton within the upper 300 m of the water column is generally low, < 20 ind. $1\ 000\ m^{-3}$ and < 300 mg dwt $1\ 000\ m^{-3}$ respectively (Pakhomov & Froneman 1999b; Pakhomov *et al.* 2000b; Gurney *et al.* 2002). There are no seasonal data on the macrozooplankton, but the presence of up to 5 million breeding pairs of top predators on the islands during summer (Williams *et al.* 1979), the majority of which are directly dependant on the surrounding oceans for their food, suggests that there is a strong seasonal pattern in macrozooplankton availability. Certainly estimates of total macrozooplankton abundance and biomass for the PFZ and indeed in the vicinity of the Prince Edward Islands during winter are nearly an order of magnitude lower than the values recorded in the PFZ in other sectors of the Southern Ocean in summer (Pakhomov *et al.* 2000b).

Patterns in the spatial distribution of zooplankton abundance and biomass in the PFZ and near the Prince Edward Islands are well documented (see reviews of Pakhomov & Froneman 1999a; McQuaid & Froneman 2004). Shifts in the zooplankton community structure within the PFZ are strongly coupled to the periodic intrusion of water masses into the region. Generally, each water mass intruding into the PFZ contains a unique zooplankton community (Fig. 5.3). In the absence of obvious oceanographic features, the open waters of the PFZ exhibit a high degree of spatial variability in zooplankton abundance and biomass with no clear patterns (Fig. 5.4) (Froneman & Balarin 1998; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003). There is however, some evidence to suggest that the lowest zooplankton abundances and biomass values in the PFZ are associated with the warmer sub-Antarctic surface waters (Hunt *et al.* 2001), while the colder Antarctic surface waters that periodically penetrate into the PFZ are usually characterised by elevated zooplankton abundance and biomass values (Hunt *et al.* 2001).

Although there are no clear patterns on such smaller scales, on larger scales, the zooplankton shows similar spatial patterns to the phytoplankton. The main frontal systems to the north and south of the islands are usually characterised by a zooplankton community with high abundances and biomass (Pakhomov & Froneman 1999a; Bernard & Froneman 2003). Just as higher chlorophyll levels at the fronts are due to the presence of large microphytoplankton cells, so elevated zooplankton biomass at the fronts is linked to an increase in the contribution of the larger macrozooplankton, particularly euphausiids, tunicates and chaetognaths to the total zooplankton abundance and biomass (Pakhomov & Froneman 1999b).

Figure 5.3 Dendrogram showing the classification of mesozooplankton abundance data collected during the first Marion Offshore Ecosystem Variability Study (MOEVS I), April 2001 (PRIMER Computer Package). SAZG – sub-Antarctic Zone Group (after Bernard & Froneman 2002).

Another spatial pattern that is emerging reflects the interaction of the ACC with the South-West Indian Ridge to the west of the islands. This interaction generates both warm and cold core features that subsequently drift in an easterly direction towards the islands (Ansorge & Lutjeharms 2003; Ansorge *et al.* 2004). A biological survey conducted within a warm core feature generated in this way indicated that such features can be characterised by stocks of both macrozooplankton (mainly euphausiids and amphipods) and micronekton that are higher than in the surrounding waters (Pakhomov *et al.* 2003). This is because the features are spawned from the frontal systems, which are characterised by elevated zooplankton biomass (Pakhomov & Froneman 1999b; Bernard & Froneman 2003). This characteristically high biomass of macrozooplankton and nekton biomass makes it likely that these features, especially their edges, represent important foraging grounds for some of the top predators found at the islands, such as the Grey-headed Albatross, *Thalassarche chrysostoma* (Nel *et al.* 2001). More recently, a similar pattern has been shown for Frigatebirds in the Mozambique Channel (Weimerskirch *et al.* 2004).

While the zooplankton and phytoplankton show similar increases at the fronts, they show contrasting patterns close to the islands. Diatom blooms often occur in the inter-island region, but in the immediate vicinity of the islands, total zooplankton biomass is generally lowest in the shallow shelf water between the two islands. This is especially true during the daytime (Perissinotto & McQuaid 1992b; Pakhomov & Froneman 1999a, b). The observed pattern was thought to reflect the predation impact of the large number of top predators feeding on zooplankton trapped by the shallow bottom topography of the shallow shelf waters and so unable to avoid predation by sinking to depth (Perissinotto & McQuaid 1992b). The zooplankton in the shelf water would subsequently be replenished during the night when the majority of the top predators were inactive. This process was termed the “*replenishing hypothesis*” (Perissinotto & McQuaid 1992b), and preliminary calculations showed that approximately 3 200 tons of zooplankton and 310 tons of myctophid fish could be advected over the island shelf every 24 hours (Perissinotto & McQuaid 1992b). This mass of zooplankton would be sufficient to sustain the zooplanktivorous top predators on the two islands (Perissinotto & McQuaid 1992b). The advection of zooplankton to the islands by the easterly flowing ACC and the periodic development of dense phytoplankton blooms between the two islands generated by the anti-cyclonic eddies trapped on the shallow shelf waters was subsequently termed the “*life support system*” of the Prince Edward Islands (Pakhomov & Froneman 1999a; Pakhomov & Chown 2003; McQuaid & Froneman 2004).

A more recent survey employing both trawling and acoustic surveys (Fig. 5.4) suggested that the low zooplankton biomass observed on the shallow island shelf could be ascribed to the interaction between the physical environment and behavioural patterns of the macrozooplankton rather than the predation impact of the top predators on the islands (Pakhomov & Froneman 1999b). Because the islands act as an obstacle to flow of the ACC, it is suggested that flow acceleration will cause the bulk of the water containing the zooplankton to flow around, rather than between the two islands (Pakhomov & Froneman 1999b). Also, many of the larger zooplankton are found below the depth at which water would be transported onto the shallow island shelf. As a result, the macrozooplankton would drift around the islands forming a belt of high concentration in close proximity to the island shelf (Fig. 5.5). The elevated macrozooplankton stocks associated with the outer edges of the island shelf would be likely to form important foraging grounds for many of the top predators found on the islands.

Finally, on a very small scale, a distinctive zooplankton community is associated with the kelp beds (Pakhomov *et al.* 2002). Combined with the suggestion that water column stability within kelp beds may enhance phytoplankton production, this suggests that not only the benthos of the kelp beds is unique, but the pelagic communities of kelp beds may also be quite different from those of the open waters of even the inshore region.

Figure 5.4 Acoustic surveys in the vicinity of the islands highlighting the spatial variability in the macrozooplankton biomass in the offshore waters and in the waters between and adjacent to the Prince Edward Islands; SAF = sub-Antarctic Front (after Pakhomov & Froneman 2000).

Figure 5.5 Spatial variability in total mesozooplankton abundance and biomass during the MOES cruise conducted in 1989. Abundance: 1: < 10; 2: 10-49; 3: 50-99; 4: 100-200; 5: > 200 individuals m^{-3} . Biomass: 1: < 1; 2: 1-5; 3: 5-10; 4: 10-20; 5: > 20 mg dwt m^{-3} (after Pakhomov *et al.* 2002).

Short-term variability in the zooplankton community structure and biomass in the shallow shelf region of the Prince Edward Islands has been investigated by Pakhomov *et al.* (2000a). Results of these studies indicate that shifts in the zooplankton community within the region were strongly coupled with pronounced water pulses that occurred within the trench located between the two islands. In accord with previous studies (Pakhomov & Froneman 1999b), the biomass of macrozooplankton in the offshore region was three to eight fold higher than that recorded within the waters of the shallow island shelf region (Pakhomov *et al.* 2000c).

Thus we see high spatial variability in the zooplankton, partly because the PFZ is functionally an ecotone, and partly because of permanent (frontal systems, island shelf region) and temporary (upstream eddies) features of the area. In addition to this spatial variability, a key feature of the larger zooplankton in particular is the extreme inter-annual variability in biomass and species composition of the major taxonomic groups (Grindley & Lane 1979; Boden & Parker 1986; Perissinotto & Boden 1989; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003, 2005). Estimates of total zooplankton abundance and biomass in the open waters of the PFZ and close to the islands demonstrate a high degree of inter-annual variability and range from < 10 to $4\,500$ ind. m^{-3} and between < 0.01 and 150 mg Dwt. m^{-3} , respectively (Table 5.2; Fig. 5.5). While there is no doubt that there is enormous real inter-annual variability, some of the differences in estimates of zooplankton abundance and biomass may be ascribed to the differences in sampling methodology (both the gear employed and depth of sampling) during the different surveys (Pakhomov & Froneman 1999a). It is also likely that the contribution of the larger macrozooplankton (> 2 cm) to total zooplankton abundance and biomass was underestimated as the majority of surveys used sampling gear (Bongo or WP-2 nets) that would have under-sampled the larger components of the zooplankton because of net avoidance.

One species deserves special consideration as a key component of the zooplankton community of the entire ecosystem, the caridean shrimp *Nauticaris marionis*. *Nauticaris marionis* is restricted to the shallow shelf waters within the inter-island region (Perissinotto & McQuaid 1990; Pakhomov *et al.* 1999; Vumazonke *et al.* 2003) with maximum abundances typically occurring at depths of 50 to 100 m (Branch *et al.* 1993). Although no quantitative surveys on the abundance and distribution of the shrimp have been undertaken around the islands, preliminary data from dredge and photographic surveys suggest that the shrimp ranks only after bryozoans in terms of total shelf benthic biomass (Perissinotto & McQuaid 1990). Further evidence of its numerical abundance in the shallow shelf waters can be derived from gut content analyses of a number of top predators that feed relatively close inshore, with foraging ranges of < 300 km. *Nauticaris marionis* forms a substantial component in the diets of a variety of penguins including the King, Macaroni and Gentoo Penguins (Adams & Klages 1987, 1989), flying seabirds (e.g. Crozet Shag) (Espitalier-Noel *et al.* 1988) and demersal fish (Pakhomov & Froneman 1999a).

The life history and population dynamics of the shrimp have recently been investigated in the waters surrounding the Prince Edward Islands (Vumazonke 2004). These studies indicate that the shrimp is a partially protandric hermaphrodite with peak reproduction in late summer/early autumn (March-May). It was previously assumed that the extensive kelp beds in the shallow shelf waters provided a refuge for the planktonic larvae of the shrimp. However, a survey conducted within the kelp beds showed that larvae of *N. marionis* were rare and as a consequence, the kelp beds could be ruled out as a primary

habitat for its larvae (Pakhomov *et al.* 2002). The mechanism by which larvae of the shrimp are retained in the vicinity of the islands, rather than being swept downstream, remains unknown (Pakhomov *et al.* 2002).

Table 5.2 Estimates of the total zooplankton abundance and biomass during the various surveys conducted to the region of the Prince Edward Islands over the period 1976 to 2004.

Source	Season	Abundances (ind. m ⁻³)	Biomass (mg dwt. m ⁻³)	Net type
Grindley & Lane (1979)	March, 1976	400-4850	8.7-28.4	WP-2
Grindley & Lane (1979)	November, 1976	1575-1854	14.6-34.9	WP-2
Boden & Parker (1986)	May, 1983	22-594	13.0-53.0	N70V
Perissinotto (1992)	April, 1985	150-229	17.4-30.0	Bongo
Perissinotto (1992)	April, 1989	130-191	32.3-56.8	Bongo
Froneman <i>et al.</i> (1998a)	April, 1996	23-184	0.76 – 8.39	Bongo
Froneman <i>et al.</i> (1998b)	April/May, 1997	5- 263	0.55-15.7	Bongo
Ansorge <i>et al.</i> (1999)	April, 1989	10-312	2.47-62.70	Bongo
Bernard & Froneman (2002)	April/May, 2001	49-1512	0.7-25.0	Bongo
Bernard & Froneman (2003)	April, 2002	78-1034	9.8-27.9	Bongo

5.3 Nekton studies

Nekton tends to be scarce around the islands, with generally low values of abundance and biomass in both offshore and inter-island waters of the Prince Edward Islands (Gon & Klages 1988). Typical values are < 1.5 ind. 1 000 m⁻³ and < 0.1 g dwt. 1 000 m⁻³ (Pakhomov *et al.* 2001; McQuaid & Froneman 2004), though these may be underestimates, as they include data from surveys that employed Bongo nets for sampling, when net avoidance was undoubtedly a problem.

Although there are no significant differences in total nekton abundance or biomass between the open waters of the PFZ and the inter-island shelf waters, there is a distinct spatial pattern in the composition of the nekton community (Pakhomov *et al.* 2001). Adult mesopelagic fish predominate in the open waters of the PFZ, but are virtually absent within the inter-island region, where only their larvae occur (Pakhomov *et al.* 2001). This pattern is believed to reflect the behavioural responses of individual fish and the consequences of their vertical migration patterns, rather than the removal of adults by top predators foraging from the islands (Pakhomov *et al.* 2001; McQuaid & Froneman 2004). Within the shelf waters, numbers and biomass of the nekton are dominated by demersal fish species. The situation is quite different in the vicinity of the SAF and the APF, where demersal fish show low numbers and biomass (> 2 ind. 1 000 m⁻³ and > 0.5 mg dwt. 1 000 m⁻³), but densities of mesopelagic fish are elevated (Pakhomov & Froneman 1999b).

5.4 Biological interactions

Studies of the biological interactions among the biota of the system have focussed on trophic relationships (Perissinotto *et al.* 1990a; Froneman *et al.* 2002; Gurney *et al.* 2002; Bernard & Froneman 2002, 2003). These studies have spanned a wide range of spatial and size scales, particularly addressing the role of grazing in controlling phytoplankton populations and of predation in regulating prey populations. An important trend is the tendency for grazing efficiency, food chain length, the efficiency of energy transfer and the dominant patterns of energy flow to be set according to which size classes of phytoplankton predominate. Thus absolute levels of primary production may ultimately determine zooplankton biomass, but which groups of zooplankton predominate depends largely on the size composition of the phytoplankton. The size structure of the phytoplankton in turn mainly depends on conditions of mixed layer depth and nutrient availability. This dependence highlights the intimate connection between oceanographic conditions and the biology of this ecosystem, but there are other ways in which physical conditions, particularly hydrodynamics, influence biological interactions. One is the concentration of macrozooplankton around the perimeter of the island plateau because of flow patterns around the obstacle formed by the islands themselves. This has implications for biological interactions over the shallow shelf waters and for where the land-based predators are likely to find profitable foraging grounds. A second example is the generation of anti-cyclonic eddies formed upstream of the islands by the interaction of the ACC and the South-west Indian Ridge. These offer high concentrations of zooplankton around their margins, which make them potentially good foraging sites for birds. A third is the existence of different zooplankton communities within and outside the kelp beds, partly due to the changes in water movement characteristics imposed by the dampening effects of kelp fronds.

Turning to the importance of phytoplankton size structure, we have already seen that picophytoplankton dominate in the open waters of the PFZ, with larger cells forming the bulk of primary producer standing stocks at the fronts and close to the islands (Fig. 5.1). As a result there are two broad scenarios in which the primary consumers of phytoplankton differ and different groups form the bulk of consumer biomass. The open waters of the PFZ are characterised by small organisms such as picophytoplankton, protozooplankton and copepods, while the fronts and the waters in the vicinity of the islands are similar in supporting additional components of large organisms such as microphytoplankton, macrozooplankton and mesopelagic fish.

The situation is not always so simple as the zooplankton appear to track phytoplankton biomass under some conditions, but not others. For example the biomass of both groups is higher at the fronts than in open waters of the PFZ, but this does not hold near the islands where the phytoplankton form occasional blooms of very high biomass, but zooplankton biomass over the shelf is relatively low. The broad correlation of producer and consumer

biomass is not unexpected, but there are competing hypotheses to account for the breakdown of this correlation at the islands: predation by the land-based predators and advection around the perimeter of the island plateau (see above).

Estimates of the protozooplankton grazing impact on phytoplankton in the waters surrounding the islands range between 1 and 8% of the daily standing stock and between 9 and 71% of potential primary production (Froneman & Balarin 1998). A distinct spatial pattern in the grazing activities of protozooplankton was evident, with the lowest rates being recorded upstream of the islands, where picophytoplankton predominate, and the highest downstream, where large phytoplankton cells are more abundant (Froneman & Balarin 1998). Thus the pattern in protozooplankton grazing pressure reflects the difference in size structure of the phytoplankton community, which in turn reflects the physical environment. The estimates of grazing impact of the protozooplankton for the region are in the range reported for other aquatic environments where small picophytoplankton cells dominate total chlorophyll-a concentration (Froneman & Perissinotto 1996a, b; Froneman *et al.* 1997).

The feeding ecology of the numerically dominant meso- and macrozooplankton within the region of the islands and in the open waters of the PFZ during austral autumn and winter has received considerable attention over the past two decades (see for example Perissinotto & Boden 1989; Perissinotto 1992; Gurney *et al.* 2002; Bernard & Froneman 2003; Froneman & Bernard 2004). Unfortunately data for the other seasons are lacking, so that it is not possible to gauge the strength of seasonality in grazing impact of the zooplankton that undoubtedly exists within the region.

In the open waters of the PFZ the grazing impact of the mesozooplankton is highly variable, but generally their effect on the phytoplankton is only moderate, accounting for < 25% of the integrated chlorophyll-a biomass or < 50% of the daily-integrated phytoplankton production (Perissinotto 1992; Bernard & Froneman 2002, 2003). The relatively weak effect of zooplankton grazing is attributable to the size composition of the phytoplankton, which is dominated by picophytoplankton cells that are too small to be grazed efficiently (Fortier *et al.* 1994). Paradoxically, during periods when phytoplankton blooms occur in the vicinity of the islands, mesozooplankton grazing impact is even lower. The daily impact of the zooplankton under these conditions accounts for < 10% (range 5-10%) of the chlorophyll-a standing stock and < 20% (range 9-17%) of the daily phytoplankton production (Perissinotto 1992). This is unexpected as these blooms are formed by diatoms, however, the predominant species are large chain forming species (e.g. *Chaetoceros* spp.), which are too large for the mesozooplankton to feed on (Perissinotto 1992). As a result, the bulk of bloom production appears to be exported to the benthic community of the inter-island shelf (Perissinotto 1992; Pakhomov & Froneman 1999a).

There have been limited studies of macrozooplankton grazing, but they appear to take an even smaller proportion of integrated chlorophyll-a biomass and

production, usually $< 5\%$ (Gurney *et al.* 2002). This is due partly to the small size of phytoplankton cells in the PFZ, and partly to the low abundances of the macrozooplankton throughout the region (see above).

In response to the unfavourable size composition of the phytoplankton, the zooplankton consume alternative carbon sources to meet their daily carbon requirements. A response of the zooplankton to the unfavourable phytoplankton size composition within the PFZ is a broadening of diet to include alternative carbon sources in order to meet their daily carbon requirements. These include protozooplankton and metazoans, and, closer to the islands, detritus derived from the extensive kelp beds that surround them (Kaehler *et al.* 2000; Gurney *et al.* 2001; Froneman & Bernard 2004; Kaehler *et al.* 2006). Although much of the focus has been on grazing interactions between zooplankton and phytoplankton, it is important to recognise that communities in the vicinity of the island do not rely exclusively on allochthonous carbon imported as oceanic phytoplankton carried to the islands by the Antarctic Circumpolar Current. Food web analyses based on the analysis of stable isotopes indicate that the contribution of kelp detritus is considerable, particularly in the case of the near shore benthic and kelp associated communities (Kaehler *et al.* 2000). Similarly, autochthonous inter-island diatom blooms influenced the isotope signature of the benthos of the island plateau (Kaehler *et al.* 2000). Given the probability of extreme seasonality in patterns of primary production within the region, it is likely that the zooplankton show high temporal variability in diet, but there are no data available to test this.

One of the key features of the zooplankton community within the PFZ is the high contribution of the carnivorous zooplankton to total zooplankton standing stock (Froneman & Pakhomov 1998b; Froneman *et al.* 1998b, 2002; Gurney *et al.* 2002). In fact, the carnivorous zooplankton can contribute up to 20% of the total zooplankton biomass (Froneman & Pakhomov 1998b; Froneman *et al.* 1998b, 2000a). The carnivorous zooplankton may play an important role in structuring the local zooplankton community and may also increase the localised efficiency of the biological pump (Froneman *et al.* 2002).

Key groups among the zooplankton predators are chaetognaths, amphipods and medusae (Froneman & Pakhomov 1998b; Froneman *et al.* 1998b, 2000b, 2002). Gut content analyses indicate that in the waters surrounding the islands, most of these are opportunistic predators, feeding on the most abundant mesozooplankton prey, which are mainly copepods (Froneman & Pakhomov 1998b; Froneman *et al.* 1998b, 2002). The daily predation impact of the carnivorous zooplankton ranges between < 1 and 45% of the mesozooplankton standing stock with values of 20% being not uncommon (Froneman & Pakhomov 1998b; Froneman *et al.* 2002). The high variability in the effects of these predators in the region is linked to the extreme variability in their abundance and biomass, which in turn reflects the extreme variability of the oceanographic environment. Predator behaviour is also important as swarming

behaviour (e.g. among amphipods) can enormously enhance the variability driven by the physical environment of the PFZ (Froneman *et al.* 2002).

Lastly, one of the key biological interactions at the islands involves the swimming shrimp, *N. marionis*. Gut content analyses and feeding experiments indicate that *N. marionis* is an opportunistic predator feeding on a variety of prey including detritus, benthic organisms and plankton (Pakhomov *et al.* 1999; Vumazonke *et al.* 2003). Preliminary evidence suggests that there are distinct differences in the composition of the diet of males and females, with the diet of females comprising a greater proportion of plankton compared to the males (Vumazonke *et al.* 2003). Localised diatom blooms are poorly grazed, with much of their biomass sedimenting out and fuelling the benthic suspension feeders. *Nauticaris marionis* in turn feeds on both benthic species and detritus (Perissinotto & McQuaid 1990). Because it forms a substantial component of the diets of seabirds feeding close to the islands, *N. marionis* appears to be a key species, indirectly routing autochthonous diatom production to the land-based predators. *Nauticaris marionis* is thus important in coupling the pelagic and benthic components and also the marine and terrestrial components of the Prince Edward Island ecosystem (Pakhomov *et al.* 1999; Vumazonke *et al.* 2003).

It is clear that there are especially intimate links between the physics and the biology of this ecosystem, with the consequences of physical effects ramifying to the very top of the food chain. This implies that long-term shifts in the oceanographic environment will have extremely powerful, if indirect, effects on the top predators.

5.5 Impact of global climate change on biology of the oceanographic environment

Although evidence of the impact of global climate change on the terrestrial ecosystem of the Prince Edward Islands is now relatively well documented (Smith & Steenkamp 1990; Smith 1992, 2002; Chown & Smith 1993; le Roux & McGeoch 2008), the impact of global climate change on the marine ecosystem of the Prince Edward Islands has only recently received attention. Global climate change in the Southern Ocean is likely to be associated with shifts in the position and intensity of the major frontal systems and changes in oceanic circulation patterns within the region of the islands. There are clear signs of change associated with warming effects. In each case these changes seem ultimately to be driven by a southward shift in the average latitude at which the sub-Antarctic Front is found (see also le Roux 2008). Perhaps the strongest evidence of long-term changes in the ecosystem associated with climate change, concerns long-term changes in the average meridional position of the SAF and changes in seabird populations. Data collected over 16 years suggested that, since the 1970s, the SAF has shown an erratic, but discernible shift to the south (Hunt *et al.* 2001). While there is enormous inter-annual (and shorter-term) variability in the position of the front, it is generally recorded 1 degree of latitude farther south at present than in the 1970s.

The most direct effect of a meridional shift in the position of the SAF concerns the species composition of the zooplankton. An examination of the zooplankton community structure in the region of the islands over the past two decades indicates that the contribution of Antarctic species to total zooplankton species richness has decreased by some 20% (Pakhomov *et al.* 2001), while at the same time, the contribution of subtropical species has increased from 6% to 26% (Pakhomov *et al.* 2001) (Fig. 5.6). This shift in species composition of the zooplankton is likely to be associated with an increase in the frequency of intrusions of warmer waters into the PFZ resulting from southward migration of the SAF (Pakhomov *et al.* 2001). In addition to changes in the zooplankton species composition, Hunt *et al.* (2001) suggested that the more frequent intrusion of sub-Antarctic surface waters into the PFZ will coincide with a decrease in the total zooplankton biomass in the vicinity of the islands as sub-Antarctic surface waters are generally characterised by low productivity (Hunt *et al.* 2001; Bernard & Froneman 2003).

Less direct than the effects of long-term changes on species composition, but perhaps more significant, are changes in hydrodynamics around the islands. Because flow speeds are relatively high at the SAF, a shift in the position of the front implies changes in the balance between advective and frictional forces where the ACC interacts with bottom topography around the islands. Essentially, we anticipate that, if the front becomes closer to the islands and advective forces become more powerful, then retention of water over the island plateau will become less frequent, while through-flow conditions become more frequent. This should result in less frequent diatom blooms over the plateau, so that sources of primary production near the islands change, while the feeding grounds of the front itself shift farther south, decreasing foraging distances for land-based predators on the islands.

Support for both predictions is strong. Considering first a change in the types of food available to consumers, a stable isotope study of the swimming prawn *N. marionis*, indicated that the $\delta^{13}\text{C}$ values of the shrimp had undergone a significant decrease over the period 1984 to 2000 (Pakhomov *et al.* 2004). The decrease in $\delta^{13}\text{C}$ signature suggests a shift in the primary carbon sources utilised by the shrimp. The most likely driving force for the shift in the diet of the shrimp is a reduction in overall marine productivity in the region of the islands, mediated by a reduction in the frequency of occurrence of diatom blooms within the inter-island region (Pakhomov *et al.* 2004). This is linked to predictions on higher-order consumer populations. The absence of phytoplankton blooms within the inter-island region is likely to coincide with a decrease in the biomass of *N. marionis*. We have no data on the population dynamics of *N. marionis*, but there is strong evidence from long-term changes in bird populations that the indirect effects of a meridional shift in the position of the SAF have ramifications to the top of the food chain. The period over which the SAF has shifted south has seen medium- to long-term increases in populations of offshore feeding birds such as Grey-headed Albatrosses and Northern Giant Petrels, that are

likely to feed at the front, and a simultaneous decrease in inshore feeders such as Rockhopper Penguins (Pakhomov & Chown 2003; see also Ryan & Bester 2008). Interestingly, species with mixed diets, like the Macaroni Penguin, have showed less of a decline over the corresponding period.

Figure 5.6 Long term changes in the contribution of Antarctic, sub-Antarctic and subtropical species to total zooplankton in the vicinity of the Prince Edward Islands. Values at the top of the bars indicate the number of species positively identified (after Pakhomov *et al.* 2001).

The observed changes in zooplankton community structure, isotopic signature of *N. marionis* and the dynamics of bird populations all suggest that global climate change has already influenced the biology of the region in quite profound ways. There is always an argument for further study of an ecosystem. However, in this case, it is clear that the entire system is in a state of perhaps dramatic flux and if we are to be able to differentiate between natural background variability in the system and long-term trends driven by extrinsic forces such as climate change, then long-term research on the biology of the marine ecosystem of the Prince Edward Islands is critical.

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