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**Physical Control and Biological Productivity of
the Seas Around the Prince Edward Archipelago,
Southern Ocean**

by

Renzo Perissinotto

Submitted in partial fulfillment of the requirements

for the degree of Ph.D

at

Dalhousie University

Halifax, Nova Scotia

1990

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Abstract

Interactions between currents and oceanic islands may underly biological enhancement in circuminsular waters (island mass effect). It is often assumed, although demonstrated only in a few cases, that eddy-shedding in the island wake is the dominant physical process involved in this effect. Due to dominance of the Earth's rotation over frictional and advective effects, vortex-shedding events are not likely to occur around Southern Ocean islands. Nevertheless, enhanced biological productivity around these islands is well documented, and is thought to support the large local populations of seabirds and pinnipeds. Thus, this study addresses the question: "How is the island mass effect generated in a Southern Ocean archipelago, and how does it contribute to the energy source that supports the biomass build-up of the land-based predators?"

Analysis of data and samples, obtained during eight cruises to the Prince Edward Archipelago (47°S, 38°E), showed the occurrence of anticyclonic anomalies in the island seas and the doming of isotherms and isopycnals over the plateau. These observations and the results of dimensional analysis indicate that appropriate conditions exist for the formation of closed streamline, stratified Taylor columns.

Variations in mixed layer depth, vertical stability and reduced nitrogen accounted for up to 80% of the variability associated with phytoplankton photosynthetic capacity (P_m^B). It is suggested that high rainfall ($\approx 250 \text{ mm month}^{-1}$) and guano excretion ($\approx 1.2 \times 10^6 \text{ mol N d}^{-1}$) on the archipelago result in nitrogen-rich freshwater run-off. Phytoplankton blooms ($1.5\text{--}2.5 \text{ mg Chl-}a \text{ m}^{-3}$) may develop in the island seas when this freshwater run-off is retained by anticyclonic eddies for a sufficient period of time (several days).

Estimates of *in situ* zooplankton grazing rates showed that only 10–20% of daily primary production is consumed by pelagic herbivores. A great portion of the phytoplankton standing stock appears to be transferred to the benthic subsystem, thus explaining the high biomass of suspensoid feeders observed ($\approx 50\%$ of total epibenthic biomass). This resource is largely exploited by the benthic shrimp *Nauticaris marionis* which, in turn, represents the staple food item of bottom-feeding seabirds.

On the other hand, much of the food requirements of the community of surface-feeding predators may be met by nighttime, surface migration of allochthonous zooplankton. This process could account for a carbon supply equivalent to the local maximum phytoplankton production.

List of Abbreviations and Symbols

Symbol	Description
Γ	Adiabatic lapse rate
ACC	Antarctic Circumpolar Current
APF	Antarctic Polar Front
APFZ	Antarctic Polar Front Zone
N	Brunt-Väisälä frequency
B	Burger number
f	Coriolis parameter
Z_{crit}	Critical depth
H_d	Decay height
x	Distance from boundary layer
C_D	Drag coefficient
DW	Dry weight (biomass)
E_k	Ekman number
Z_{eu}	Euphotic depth
F_I	Feeding impact
b'	Fractional pigment loss
FGGE	First GARP Global Experiment
u_*	Friction velocity
d_z	Frictional bottom layer
F_r	Froude number
μ	Growth rate
G	Gut pigment content
K	Gut evacuation rate
A_x	Horizontal eddy viscosity
L	Horizontal length scale
U	Horizontal velocity scale

Symbol	Description
I	Ingestion rate
P_{max}	Maximum photosynthetic rate
Z_{mix}	Mixed layer depth
P_m^B	Photosynthetic capacity
ΣP	Potential primary production
R_e	Reynolds number
R_o	Rossby number
β	Salinity expansion coefficient
E	Stability parameter
SAF	Subantarctic Front
$Z_{0.1}$	10% light depth
α	Thermal expansion coefficient
h_0	Topographic height
H	Vertical length scale
S	Vertical section (area)
κ	Von Kàrmàn constant
A	Zooplankton abundance

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GENERAL INTRODUCTION

Perturbations produced by islands in the general oceanic circulation depend upon various factors such as the direction and speed of prevailing currents, size and topography of the island, shape and depth of surrounding shelf and latitude. Often such perturbations result in physical events that cause an increase in the biological productivity (by up to several orders of magnitude) of the circuminsular waters, compared to the open ocean environment. This phenomenon is known as the "island mass effect" (Doty and Oguri, 1956; Dandonneau and Charpy, 1985). Because of directional flow, downstream physical events (*e.g.*, advection of shed eddies) may extend the biological enhancement to distances of up to 10-15 times the diameter of the islands (Chopra, 1973; Heywood *et al.*, 1990). Thus, although islands represent a negligible part of the total oceanic area, their effects on the water productivity have importance far out of proportion to their physical size.

Enhancement in the marine productivity around islands in the Southern Ocean is of particular relevance because these areas support very large populations of land-based predators. Nowhere is the proportion of sea to land greater than in the Southern Ocean, where a vast oceanic region lies between 35 and 70° S. This results in breeding localities being restricted to a fairly narrow latitudinal band where 23 small island groups are concentrated (mostly in the Atlantic and Indian sectors). Therefore, land-based predators have their greatest impact on food resources around these small, localized oceanic areas (Croxall, 1984; Siegfried, 1985). It is not known how these food requirements can be met in the islands marine ecosystems and which mechanisms are responsible for the origin of the energy that generates the island mass effect.

Of the whole chain of Antarctic and sub-Antarctic islands, the Prince Edward Archipelago represents an ideal case study since it has been subject to the most intensive investigation during the past decade. A unique set of physical, chemical and

biological data has been accumulated from eight cruises to the area between 1976 and 1989 (Arnaud and Hureau, 1979; Duncombe Rae, 1989a). The Prince Edward Archipelago (47° S, 38° E) includes two islands, Marion and Prince Edward, and is located in the Antarctic Polar Front Zone (APFZ), between the Sub- Antarctic (SAF) and the Antarctic Polar Fronts (APF) (Lutjeharms, 1985; Fig 0.1). Like most islands in the Antarctic and sub-Antarctic regions, the archipelago represents the focus of a large breeding community of seabirds and mammals, numbering in excess of two million pairs (Williams *et al.*, 1979; Condry, 1981). As this community is almost exclusively dependent on marine resources for its food, a highly productive ecosystem must be available in the surrounding ocean.

Recent investigations have found that phytoplankton production in the islands' shelf is greatly enhanced compared to the surrounding open ocean (El Sayed *et al.*, 1979; Allanson *et al.*, 1985; Boden, 1988). When measured quasisynoptically, potential primary production levels at the Prince Edward Archipelago are an order of magnitude higher than at either the Subtropical or Antarctic Polar Fronts (Boden, 1988). The most obvious feature of this island mass effect is the regular, seasonal occurrence of relatively dense phytoplankton (diatoms) blooms in the island seas. The generation and retention of such blooms seems to result from a dynamic interaction between the oceanic circulation and the local topography. However, the interpretations so far proposed on the nature of this interaction are based on the assumption that the physical processes involved are either coastal upwelling events (Grindley and David, 1985) or eddy shedding of the Von Kàrmàn type (Allanson *et al.*, 1985). In both cases phytoplankton production would be enhanced by a pulse of nutrients input into the surface mixed layer due to upwelling of deep waters. A wind-driven divergence of flow in the upper layer induces upward flow of deep water because of continuity (conservation of mass). On the other hand, vortex shedding in island wakes would also produce upwelling in the initial phase of eddy formation as a result of baroclinic adjustment. Neither the wind-induced coastal upwelling nor the island vortex shedding hypotheses has yet been tested or theoretically examined

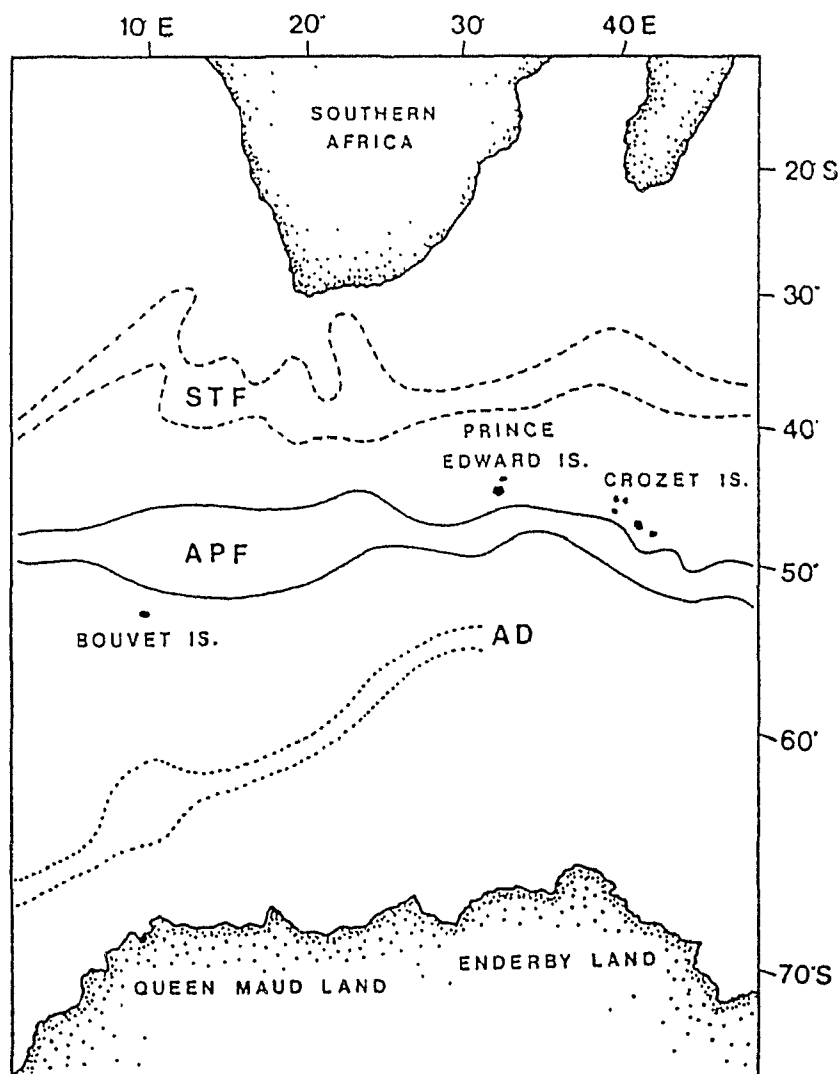


FIGURE 0.1. Position of the Prince Edward Islands and of the main frontal systems south of Africa (redrawn after Lutjeharms, 1985 and Hofmann, 1985). STF: Subtropical Front; APF: Antarctic Polar Front; AD: Antarctic Divergence.

in detail. Also, it is not clear how the increased primary production is transferred through the food web to the land-based predators. A major problem in identifying this link is represented by the zooplankton standing stock which is relatively low and does not parallel the enhancement in phytoplankton productivity (Boden, 1988).

The objective of this work is, therefore, to address the general question "How is the island mass effect generated and how does it contribute to the energy source that supports the biomass build-up of the land-based predators?" This is defined more clearly in the following five specific components, each of which is dealt with in a separate chapter.

- 1) What kind of relevant flow perturbations does the interaction between the Antarctic Circumpolar Current (ACC) and the Prince Edward plateau produce, and what is their role in the dynamics of the island mass effect?
- 2) What are the primary physico-chemical factors controlling marine phytoplankton production and biomass in the island seas?
- 3) What are the factors responsible for the spatio-temporal variations in zooplankton biomass, and what are the consequences of these variations for the higher trophic levels?
- 4) How much of the biomass of the phytoplankton blooms is consumed in the pelagic subsystem and how much is available for transfer to the benthic subsystem?
- 5) How is the portion of phytoplankton biomass that is transferred to the benthic subsystem eventually utilized by the land-based predators?

CHAPTER 1

OCCURRENCE OF ANTICYCLONIC EDDIES ON THE PRINCE EDWARD PLATEAU: EFFECTS ON PHYTOPLANKTON BIOMASS AND PRODUCTION

1.1 Introduction

The Prince Edward Islands archipelago (47°S, 38°E) is an isolated feature situated in the Antarctic Circumpolar Current (ACC). It consists of two islands, Prince Edward and Marion, separated by a shoal platform with a mean depth of about 180 *m* which falls off rapidly to 3000 *m* (Fig 1.1).

Extensive investigations carried out on the oceanic frontal systems south of Africa since 1979 by Lutjeharms (1985) show that the group lies in the Antarctic Polar Front Zone (APFZ), between the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF).

The large scale circulation pattern of the ACC in this part of the Southern Ocean is strongly influenced by the local bottom topography. The generally eastward flow is markedly deflected south-west of the archipelago and turns abruptly north-eastward along the Prince Edward Fracture Zone (Gordon *et al.*, 1978; Patterson, 1985; Piola *et al.*, 1987), joining and intensifying the Agulhas Return Current near 40°S (Colton and Chase, 1983; Gordon *et al.*, 1978).

Reliable measurements of the mean surface speed of the ACC in the vicinity of the plateau are not available, but a preliminary current meter survey in the area (Parker, 1984) seems to indicate that it can exceed 50 *cm s*⁻¹. Estimates of the mean near-surface speed in adjacent areas obtained from the analysis of the FGGE (First Global Experiment of the Global Atmospheric Research Program, GARP) satellite-tracked drifters (Hofmann, 1985; Piola *et al.*, 1987; Lutjeharms *et al.*, 1988) show a wide range from 19.0 to 34.9 *cm s*⁻¹.

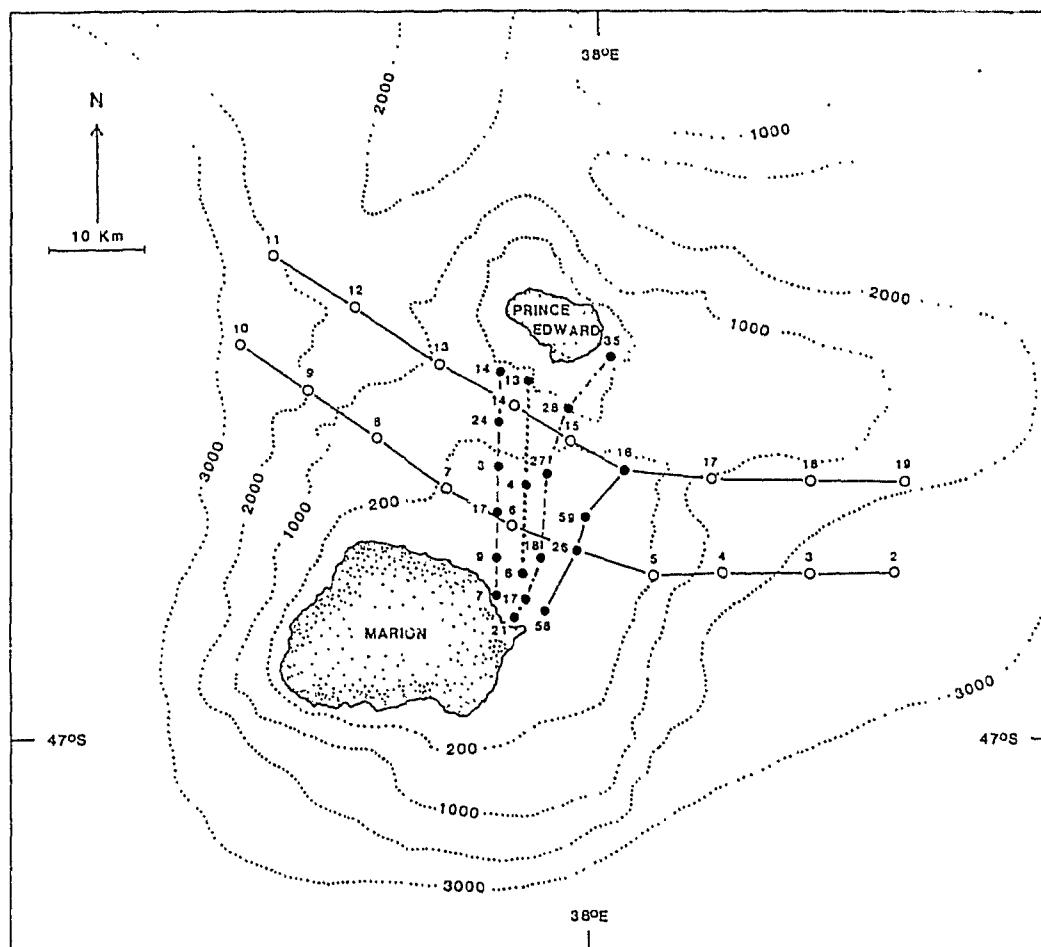


FIGURE 1.1. The Prince Edward Archipelago (depth contours are in metres).
 Open circles: CTD transects of Figure 1.4, April 1987. Closed circles:
 Prince Edward-Marion transects of Figure 1.6, - . -: March 1976; . . . :
 May 1983; - - -: March 1984; —: April 1987.

Recent work has demonstrated the regular occurrence of phytoplankton blooms in the area (El Sayed *et al.*, 1979; Allanson *et al.*, 1985; Boden, 1988). Highest values of both chlorophyll-*a* concentration and primary production potential during these bloom periods occur above the plateau around the two islands. It has been suggested that the archipelago generates an island mass effect (Doty and Oguri, 1956), related to possible interactions of the free-stream ACC with the local topography and to nutrient inputs via run-off from the islands themselves (Allanson *et al.*, 1985; Boden, 1988).

There is evidence that a diffuse eddy is consistently found over the saddle between the islands (Allanson *et al.*, 1985; Parker, 1984). Allanson *et al.* have suggested that vortex-shedding dynamics resembling a von Kàrmàn street may occur in the plateau wake. Eddies that are trapped in the inter-island region protract the residence time of water masses that otherwise would be quickly advected past the plateau. As a result, the island run-off nutrients and plankton appear to be retained for a time sufficient for a response to develop to the direct factors of growth (Sverdrup, 1953; Smetacek and Passow, 1990), thus leading to the formation and maintenance of phytoplankton blooms.

In this chapter I present some considerations on possible mechanisms of flow interaction with isolated topography that can generate and retain eddies, and discuss the implication of the predicted and observed features to phytoplankton biomass and production.

1.2 Dimensional analysis

The relative importance of the rotational, inertial and frictional terms of the equation of motion can be assessed by considering the Rossby (R_o) and Ekman (E_k) numbers that compare the inertial and frictional terms, respectively, with the rotational term. Since the Prince Edward Plateau is a dynamically deep-water system (*i.e.*, $d_z^2 \ll H^2$, where d_z is the frictional bottom layer and H the water

depth), the dimensionless relations $R_o = U/Lf$ and $E_k = A_x/fL^2$ are appropriate (Tomczak, 1988). Here U is the horizontal velocity scale, L the horizontal length scale, f the Coriolis parameter ($1.059 \times 10^{-4} \text{ s}^{-1}$) and A_x the horizontal eddy viscosity.

Considering the entire plateau as an obstacle in the path of the ACC, then the length scale is the width of the island plateau, $\approx 50 \text{ Km}$. The free-stream current velocity, U , is given a value of 0.35 m s^{-1} , which corresponds to the mean near-surface speed estimated by Hofmann (1985) at the Polar Frontal Zone in the sector between 31° and 60°E . This value is likely to be more representative of the true free-stream current in the area of the Prince Edward Islands than estimates based on other FGGE buoys.

Choice of A_x is difficult, as it is not easy to determine and covers a wide range of values ($0.5 < A_x < 10^5 \text{ m}^2 \text{ s}^{-1}$, Pond and Pickard, 1978; Pattiaratchi *et al.*, 1987). An order of magnitude estimate can be obtained from the logarithmic profile expected in turbulent shear-flow with constant stress, away from the viscous sublayer. For this flow:

$$dU/dx = u_*/\kappa x, \text{ or } u_*^2 = (dU/dx) u_* \kappa x,$$

which, integrated, gives (Tennekes and Lumley, 1972):

$$U = (u_*/\kappa) \ln(x/x_0).$$

In these relations, κ is the von Kàrmàn constant (≈ 0.4), u_* the friction velocity, x_0 the roughness parameter, a constant of integration, and x the distance from the boundary normal to the flow. Since the stress:

$$u_*^2 = A_x(dU/dx),$$

we obtain:

$$A_x = u_* \kappa x.$$

u_* is given by $UC_D^{1/2}$, with C_D a drag coefficient. Assuming $C_D \approx 2.5 \times 10^{-3}$ (Pattiaratchi *et al.*, 1987), $u_* = 5 \times 10^{-2}U$ and given a distance from the lateral

boundary layer (x) $\approx 1 - 10 \text{ Km}$, $A_x \approx 7 - 70 \text{ m}^2 \text{ s}^{-1}$.

For these values, $R_o \approx 6.6 \times 10^{-2}$ and E_k ranges between $\approx 2.6 \times 10^{-5}$ and 2.6×10^{-4} . This implies that the flow regime around the Prince Edward Islands is dominated by the Earth's rotational effects rather than frictional and advective effects.

The structure of the wake behind obstacles immersed in a uniform flow has been extensively studied in laboratory experiments (see for instance Batchelor, 1967; Zdravkovich, 1987). The form of the wake is dependent on the Reynolds number (R_e), the ratio of the inertial to viscous forces ($R_e = R_o/E_k = U L/A_x$; Tomczak, 1988).

For a circular cylinder, a flat plate and a salient edge, the transitions from fully attached flow to formation of standing eddies to periodic oscillations of the wake to eddy shedding occur at R_e around 2, 40 and 70 respectively. At very high R_e ($> 70 - 150$) vortex motion begins to cascade its energy toward smaller scale, and the flow becomes turbulent (Batchelor, 1967; Pattiaratchi *et al.*, 1987; Jackson, 1987). The flow around islands seems to be consistent with the two dimensional wake flow observed in the laboratory except at very shallow depths, where the stabilizing effect of bottom friction becomes a very important factor (Ingram and Chu, 1987; Tomczak, 1988).

From the above estimations of R_o and E_k , a Reynolds number of $R_e \approx 250 - 2500$ can be expected for a wake generated by the archipelago. This indicates that the structure of the wake is dominated by turbulent dissipation. Thus the mesoscale eddies found in the area are probably not the result of a vortex-shedding process from the islands.

Another possible mechanism for the generation and retention of eddies by the plateau could be the local formation of stratified Taylor columns. A Taylor column consists of a closed streamline anticyclonic vortex that is trapped above a bump under certain conditions of current speed, stratification and topography (Hogg, 1973; Huppert, 1975; Huppert and Bryan, 1976). To test the possibility of such

an eddy occurring above the inter-island plateau, we consider the parameters for a stratified flow with constant Brunt-Väisälä frequency (N) passing a bump (Huppert, 1975).

The scaled bump height, $h_0 = h/H$, is the bump height, $h \approx 2.8 \text{ Km}$, the height of the inter-island plateau, scaled by the water depth, $H \approx 3 \text{ Km}$. The Burger number, $B = N H / f L$, gives a measure of the importance of stratification. N at the Prince Edward Islands during 1987 was $\approx 4.6 \times 10^{-3} \text{ s}^{-1}$. The length scale is here taken to be the width of the inter-island plateau, $L \approx 20 \text{ Km}$, excluding the islands. For these values $B \approx 5.9$, $R_o \approx 0.15$, and $h_0 \approx 0.93$.

At a Burger number of 5.9, the value of the critical height, h_0/R_o , the height of the bump above which Taylor columns can be expected to form, is ≈ 0.4 (from the diagram of Huppert, 1975). Since the critical height estimated for the Prince Edward Plateau is larger than this, $h_0/R_o \approx 6.2$, local conditions may lead to the formation of stratified Taylor columns on the top of the feature. No closed streamline occurs when the bump height is too low (lower h_0) or the oncoming flow is too strong (higher R_o), so that the maximum current speed for Taylor column formation is calculated from (Huppert, 1975):

$$h_0/R_o \geq 0.4, \text{ or } R_o = U/fL \leq h_0/0.4, \text{ or } U \leq 5.4 \text{ m s}^{-1}.$$

This would indicate that a Taylor column can occur under almost all flow conditions likely to occur in the region.

In a stratified system, the stratification tends to confine the column effect to the bottom. The height at which no effect is detected above the feature, the decay height (Huppert, 1975), is $H_d = f L / N \approx 500 \text{ m}$. This suggests that if Taylor columns were found at the Prince Edward Islands, their effects would be evident at the surface.

The process of vorticity redistribution that leads to the formation of Taylor columns (anticyclonic vorticity regions over a feature) is also involved in the shedding of cyclonic vorticity regions from the feature (Huppert and Bryan, 1976). These cyclonic eddies may be dispersed downstream of the obstacle or may be retained in

the vicinity of the feature, leading to a double vortex structure.

With $B > 2$, the criterion for separation of these two shedding dynamics is an inverse Froude number $F_r = N(H-h)/U$ (Huppert and Bryan, 1976). If $F_r > O(1)$, a Taylor column will form above the feature and if $F_r > O(10)$ the shed cyclonic eddy will remain in the vicinity of the feature and the retained anticyclonic eddy. At the Prince Edward Islands, for the above values, $F_r \approx 2.6$ to 4.9, dependent on U , indicating that an anticyclonic Taylor column may form and that the associated cyclonic eddy will be shed downstream and not retained.

An analytical model for the interaction of the Antarctic Circumpolar Current with topography (McCartney, 1976) and a numerical model of Taylor column formation (Huppert and Bryan, 1976) show the initial formation of a closed anticyclonic Taylor column over the bump and a cyclonic eddy on the poleward side of a meandering wake (Fig 1.2). The successive evolution of the associated isopycnals show, in the case of fast flow conditions, the cyclonic eddy rotating around the plateau, gradually elongating and eventually drifting downstream (Fig 1.3; Huppert and Bryan, 1976). Under slow flow conditions the cyclonic vorticity remains near the plateau, tightly wrapped around the anticyclonic anomaly.

In the presence of an unsteady mean flow, both cyclonic and anticyclonic (Taylor column) eddies can be shed from the topography (Verron, 1986). This occurs when the oscillation period of the oncoming flow, T_f , is of the order of the advective time scale so that $\omega L/U = O(1)$, where ω is the frequency of the time-dependent velocity (Verron, 1986). Under these conditions, enhanced vorticity dissipation over the bump and periodic dominance of advective effects result in the trapped eddies, including Taylor columns, being swept away in the lee of the obstacle. However, no parametric studies of this kind have been carried out using more realistic, stratified fluids. So that it is not known if, and to what extent, this response applies to real oceanographic situations.

1.3 Observations

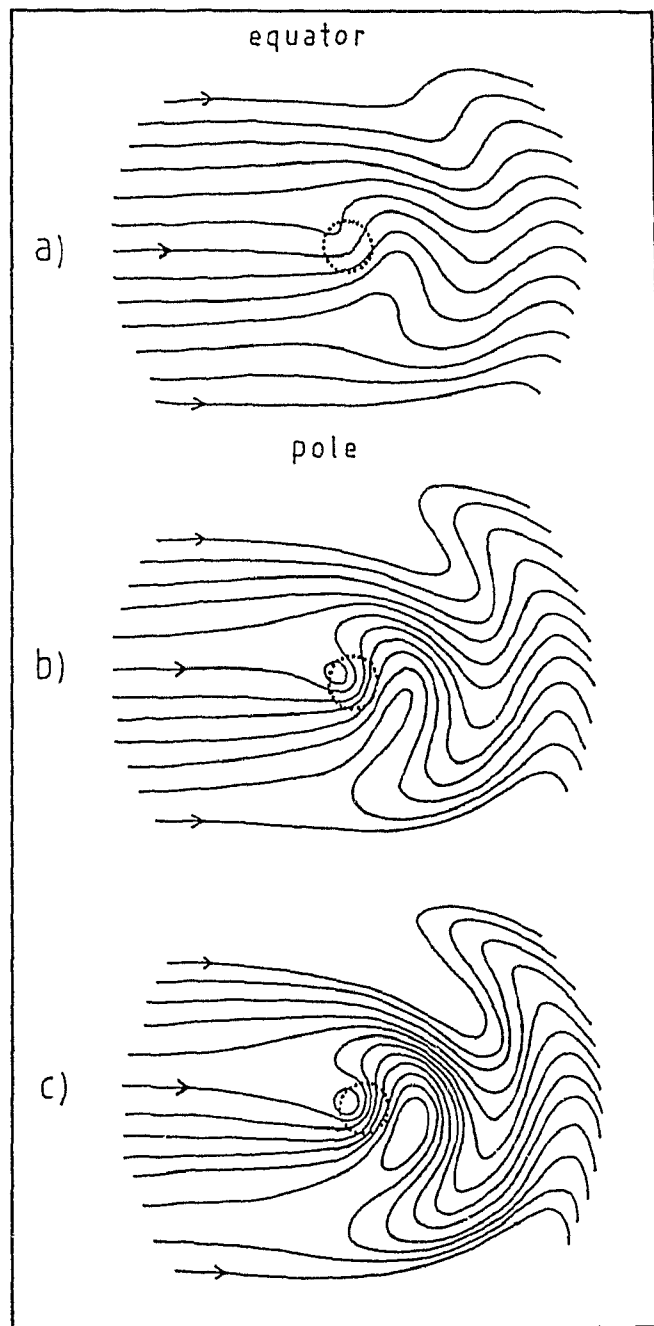


FIGURE 1.2. Streamline contours for the interaction of the Antarctic Circumpolar Current with an isolated bump. Solutions given are for $B = O(1)$ and $h_0/R_o = 2$ (a), 4(b) and 6(c). (Adapted from McCartney, 1976.)

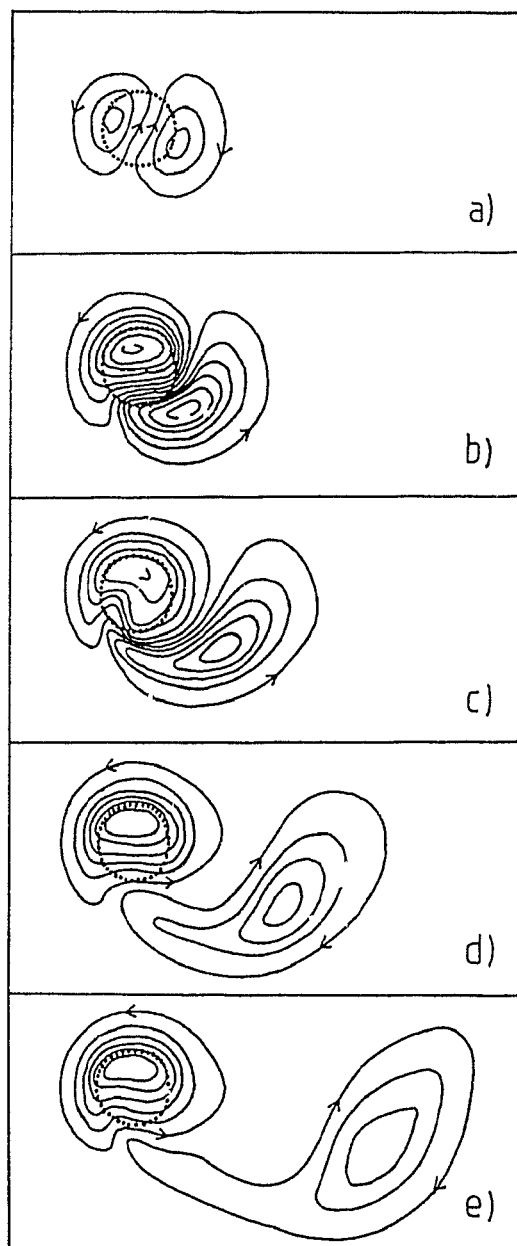


FIGURE 1.3. Time-dependent solution for the isopycnal contours of topographically generated eddies with $\beta = 2$ and $F_r = 0.39$. a) 2.3 d , b) 6.9 d , c) 13.9 d , d) 23.1 d and e) 34.7 d . (Adapted from Huppert and Bryan, 1976.)

Data were collected on six cruises to the Prince Edward Islands: *Marion Dufresne*, March 1976 (Arnaud and Hureau, 1979); *SA Agulhas*, April 1982; *RS Africana*, September 1982; *SA Agulhas*, May 1983; *SA Agulhas*, March 1984; and *SA Agulhas*, April 1987 (Duncombe Rae, 1989a). At each station, conductivity, temperature and depth (CTD) casts were made using a Neil Brown MK III probe. Chlorophyll-*a* levels were obtained by the spectrophotometric method of SCOR/UNESCO (1966). Carbon-14 uptake, determined with on-board incubation techniques (Allanson *et al.*, 1981), was used to estimate integrated primary production, $\Sigma P = P_{max} \times Z_{0.1}$ (with P_{max} = maximum photosynthetic rate and $Z_{0.1}$ = 10% light depth).

Both CTD transects crossing the saddle during April 1987 show uplifting of the isotherms and isopycnals (Fig 1.4) over the inter-island plateau, and a downward deflection in the deeper regions (below the 300–400 *m* isobath). The vertical extension of the perturbations appears to increase rapidly from the substratum of the saddle ($T \approx 5^{\circ}C$) to the $6.5^{\circ}C$ isotherm, with a maximum displacement of about 150 *m* (Fig 1.4). The extent of this raised cold water is of the order of the width of the plateau.

Surface sigma-*t* contours for the Prince Edward plateau were plotted for all six cruises from the CTD data (Fig 1.5). The isopycnals tend to be arranged circumferentially around local density minima over the inter-island region of the plateau on at least three, and possibly five, occasions. On one occasion (April 1987) a density maximum is evident to the north of the plateau (Fig 1.5 f).

During four of the above cruises, vertical temperature profiles (Fig 1.6) over the saddle show a consistent depression of the isotherms in excess of 50 *m* near the centre of the inter-island region.

Surface contours of chlorophyll-*a* (Fig 1.7) show that in all cases the highest concentrations of phytoplankton are located in the inter-island region. In particular, dense phytoplankton blooms, with chlorophyll-*a* concentrations greater than 1.2 mg m^{-3} , are often found in a wide area between the two islands (Fig 1.7 b,c,f;

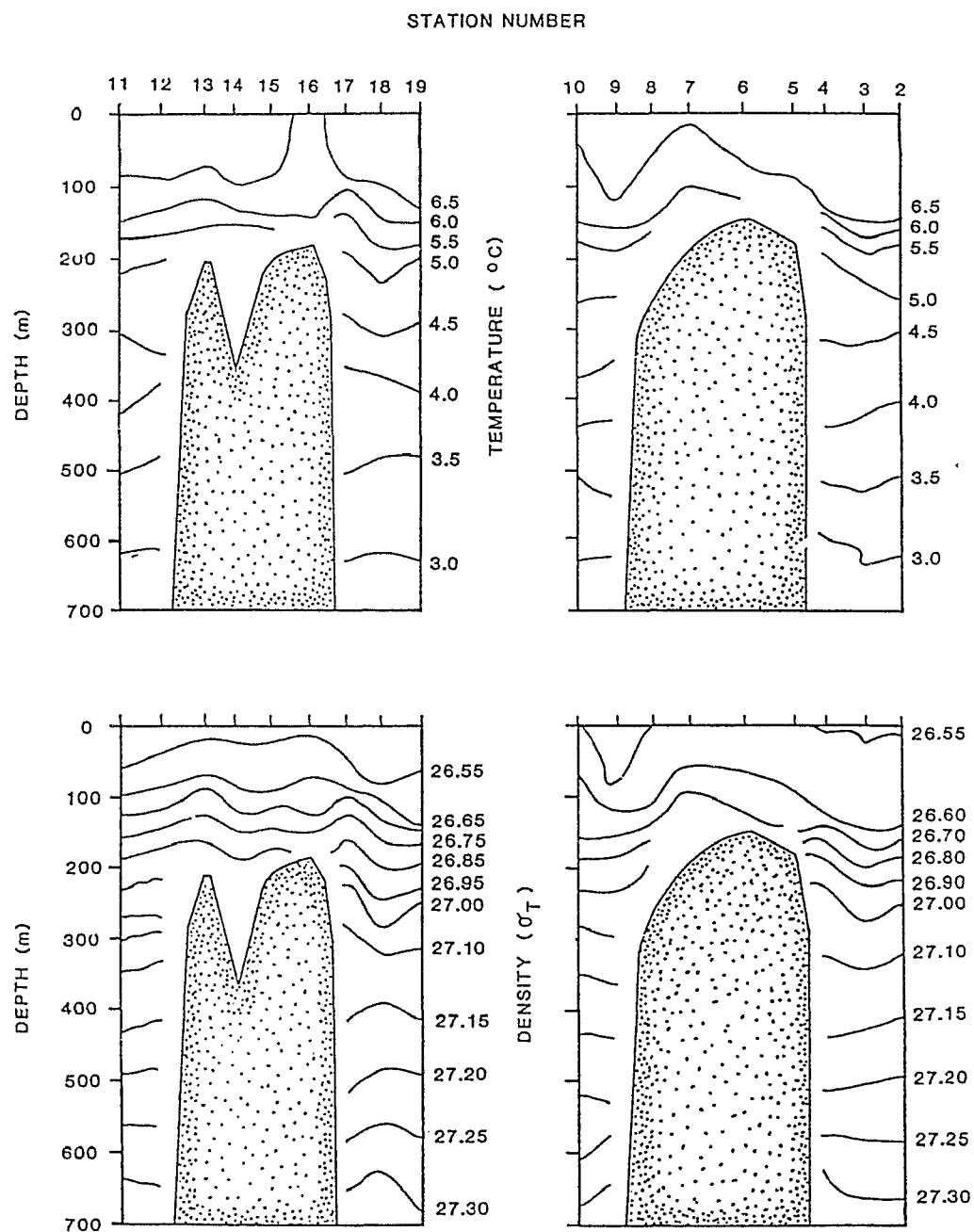


FIGURE 1.4. Temperature and density structure along the two CTD transects occupied during the MOES-1 cruise (April 1987, Fig 1.1).

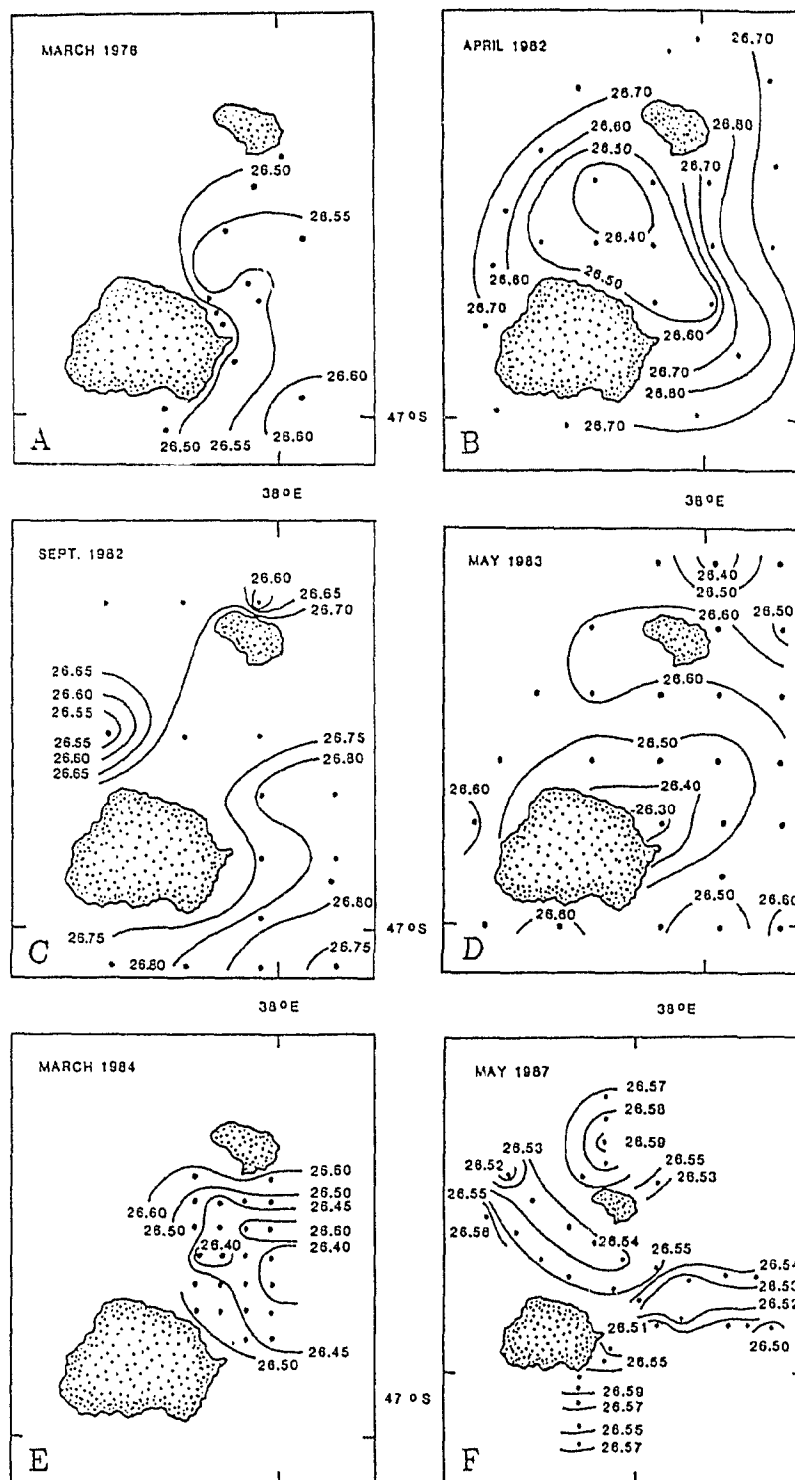


FIGURE 1.5. Surface sigma-t contours determined on the six cruises in the Prince Edward Islands region. (A,B,C,D: after Parker, 1984).

Allanson *et al.*, 1985; Boden, 1988).

Phytoplankton primary production rate in the area was estimated on three occasions (Parker, 1984; Boden, 1988). A sharp increase in primary production potential is always observed on the downstream side of the plateau (Fig 1.8), with the highest levels ($120\text{--}200\text{ mg C m}^{-2}\text{ h}^{-1}$) occurring both in the inter-island region and in the lee of the islands.

1.4 Discussion

The evidence for the occurrence of Taylor columns in the oceanic environment is scant. With only a few exceptions, these features have been identified indirectly, based on thermohaline structure (Roden, 1987).

Among the physical features used to identify Taylor columns at oceanic seamounts are narrow, bottom-intensified, vertical perturbations of the density field. The width of these upward excursions of the isolines, visible in the temperature, salinity and density fields, is of the order of the width of the seamount (Roden, 1987). In our observations, bottom-confined doming of the isopycnals is evident over the saddle. Another feature, seen in conjunction with this doming, is downward deflection of the isolines in the deeper regions, below the 300–400 m isobath. Although deflections of this kind have been observed in other situations of flow interaction with isolated topography (Genin and Boehlert, 1985; Roden and Taft, 1985), they are not predicted by Taylor column theory and may represent the result of different physical processes on sloping surfaces.

At the Prince Edward Islands, the density minima over the saddle (Fig 1.5), evident as a depression of the centre of the dome in Figure 1.4 and in the saddle sections in Figure 1.6, suggest anticyclonic eddies. Only in one of the data sets is there some evidence of cyclonic eddy formation, in the form of a density maximum to the north of Prince Edward. This may be associated with Taylor column formation, although the dimensional analysis shows that once the column is formed the cyclonic eddy should be advected downstream, rather than retained near the islands.

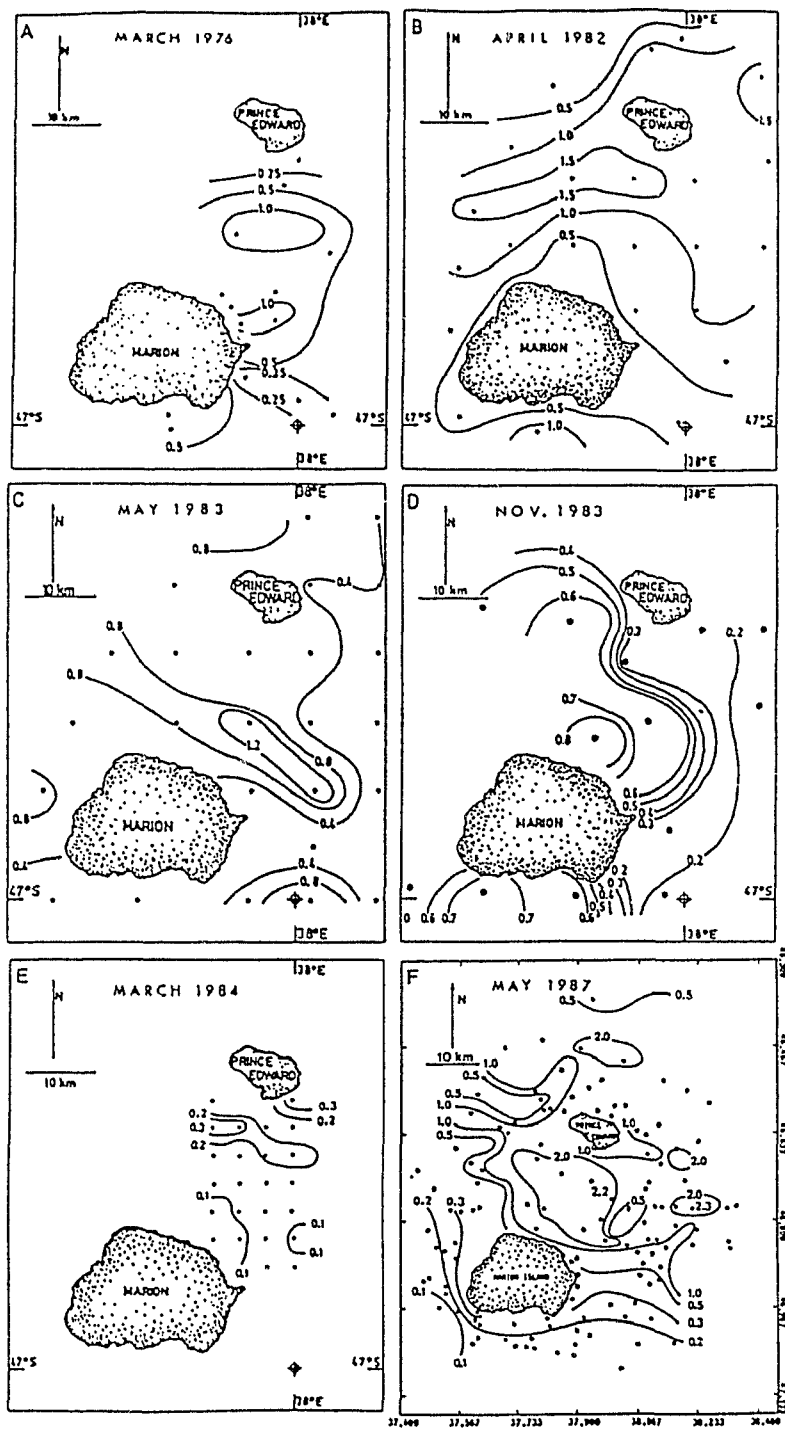


FIGURE 1.7. Surface chlorophyll-*a* ($\text{mg Chl-}a \text{ m}^{-3}$) contours determined on the six cruises to the Prince Edward Islands. (A,B,C,D,E: after Parker, 1984).

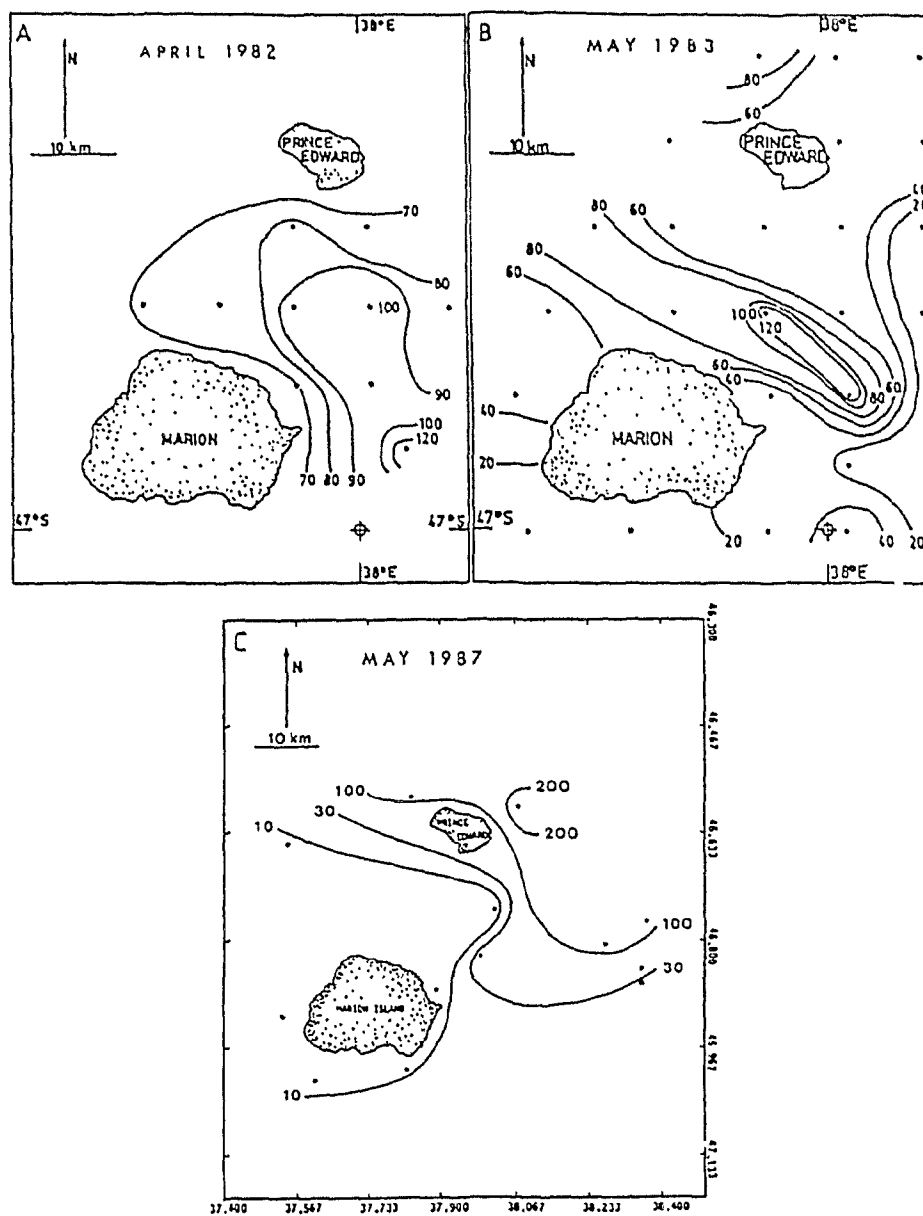


FIGURE 1.8. Potential primary production contours ($mg\ C\ m^{-2}\ h^{-1}$) determined on three cruises to the Prince Edward Islands. (A,B: after Parker, 1984).

At present, however, I cannot provide conclusive evidence of Taylor column phenomena at the Prince Edward plateau, as our observations lack sufficient spatial resolution. More conclusive results probably could be obtained only by direct high resolution current measurements with mooring arrays (Owens and Hogg, 1980) or by satellite altimeter and infra-red imagery that allow the assessment of the meso- and layer scale variability (Roden, 1987). Unfortunately, no satellite imagery is available for the area around the Prince Edward Archipelago. Persistent attempts to ascertain the circulation pattern in the area by this technique have been foiled by almost continual cloud coverage.

Other processes could be responsible for the generation of eddies, or similar hydrographic surface features, in the area. Occurrence of island-induced upwelling, for instance, has been inferred on the basis of indicator zooplankton species by Grindley and Lane (1979). However, successive investigations have shown that thermocline slopes, nutrient and chlorophyll profiles do not provide evidence for upwelling of deep water in the vicinity of the Prince Edward Islands (Allanson *et al.*, 1985). The presence of the two islands, which attain altitudes in excess of 1200 *m* in the case of Marion and 600 *m* in the case of Prince Edward, would alter the wind stress curl exerted by the strong, constant, north-westerly winds. The change in the wind stress curl would be greatest before and behind the islands and in the saddle area. However, any upwelling probably would occur in the open ocean sense, rather than as a coastal divergence since the length scale of the islands is too short ($\approx$ two times the Rossby radius of deformation). Also, it seems likely that, in the event of a coastal divergence, mass conservation can be achieved by advection of water from around the sides of the islands, rather than by upward flow of deep water. Close to the islands, the wind effects appear to be confined to the upper mixed layer ($\approx$ 50 – 100 *m* depth).

A more likely process to occur in the Prince Edward Island seas, is related to the generation of eddies in the far-field, rather than in the vicinity of the islands by local topography. The Sub-Antarctic and Antarctic Polar fronts, in particular, seem

to be the genesis of spin-out eddies (Lutjeharms and Baker, 1980) that could be advected into the area by the Antarctic Circumpolar Current and become trapped in the archipelago.

The repeated occurrence of stationary eddies at the Prince Edward Islands appears to have important biological implications for the plankton distribution and production near the islands (Lucas and Probyn, in press; Boden, 1988; Perissinotto *et al.*, in press). On all cruises the highest chlorophyll-*a* concentrations and all the phytoplankton blooms were found in the anticyclonic region around the two islands.

The mechanisms responsible for the increase in phytoplankton biomass within eddies, as compared to the surrounding waters, are well known in a variety of oceanic environments. These usually involve frictional vertical decay of the thermohaline anomaly, bringing fresh nutrients into the surface mixed layer (Angel and Fasham, 1983; Franks *et al.*, 1986). However, in the Southern Ocean, including the Prince Edward Islands, the major nutrients are always present in excess of phytoplankton demand and, due to the continuous upwelling at the Antarctic Divergence, their concentrations are the highest found anywhere in the surface waters (Holm-Hansen, 1985). Typical value ranges observed around the Prince Edward Islands are 13–26 $\mu\text{mol l}^{-1}$ for nitrate, 0.5–2.0 $\mu\text{mol l}^{-1}$ for phosphate and 0.5–10 $\mu\text{mol l}^{-1}$ for silicate (Allanson *et al.*, 1985; Boden, 1988; Duncombe Rae, 1989b).

It seems therefore that the enhancement in phytoplankton biomass within these eddies originates from different dynamics. A mechanism of purely mechanical action of advection/retention of upstream-generated phytoplankton at convergences in the eddy field is possible on theoretical grounds. This hypothesis was supported for an anti-cyclonic eddy off King George Island in the South Shetland archipelago by the model studies of Heywood and Priddle (1987). However, at the Prince Edward Islands the hypothesis can be discarded as a mechanism for biomass enhancement, since measurements of primary production rate (Fig 1.8) show that the increase of chlorophyll-*a* concentrations above the plateau was consistently matched by locally enhanced growth rates.

An estimate of the maximum phytoplankton growth rate in the area during May 1987 can be obtained following the procedure suggested by Parsons *et al.*, (1984). To an initial bloom biomass of $C_0 \approx 2.3 \text{ mg Chl } m^{-3}$ equivalent to $\approx 58 \text{ mg C } m^{-3}$ (using a Chl:C ratio of 1:25), the measured diel increase of phytoplankton, D_c , is added after a day's growth (12 hours), assuming the maximum rate of primary production to be approximately $250 \text{ mg C } m^{-2} h^{-1}$ with an euphotic depth of 50 m ($D_c \approx 60 \text{ mg C } m^{-3}$). This yields a total biomass:

$$C_t = C_0 + D_c \approx 118 \text{ mg C } m^{-3},$$

representing a growth rate:

$$\mu = 1/t \ln(C_t/C_0) \approx 0.71 \text{ [e-foldings } d^{-1}] \approx 1.0 \text{ [doublings } d^{-1}].$$

Enhanced growth rates within an eddy would result in a front of phytoplankton moving inwards towards the centre of the eddy with minimum velocity $v = 2\sqrt{(\mu K)}$ (Angel and Fasham, 1983) where K is a constant horizontal eddy diffusivity, of the order $\approx 10^4 \text{ cm}^2 \text{ s}^{-1}$. In the area under consideration, the velocity of the front would be about 0.7 cm s^{-1} . This means that the time scale required for a local focus to extend to an area of the size of the bloom observed in March 1987 ($\approx 10 \text{ km}^2$) would be of the order of about 15 days. Unfortunately this data set is not suitable for an estimation of the residence time of the anticyclonic eddies in the area. However, high resolution Lagrangian and Eulerian current observations in the North Atlantic have shown that entrainment periods up to several weeks (Richardson, 1980) and even several months (Owens and Hogg, 1980) can be expected for Taylor columns.

The factors which result in the generation of phytoplankton blooms by interaction with eddy fields are still uncertain for the Southern Ocean (see for instance reviews by Priddle, *et al.*, 1986; Sakshaug and Holm-Hansen, 1984; El Sayed, 1984). There is, however, some evidence that the stability and the depth of the mixed layer play important roles in regulating the primary productivity in Antarctic waters (Sakshaug and Holm-Hansen, 1984; Holm-Hansen, 1985). I suggest that the fresh water runoff from the islands, retained by the eddy field, may represent a signifi-

cant input of buoyancy into the surface layer, thereby increasing the stability of the water column over the plateau as compared to the surrounding ocean. The Prince Edward Archipelago receives a high annual rainfall, a mean precipitation of about $210 \text{ mm month}^{-1}$, with two peaks of about $250 \text{ mm month}^{-1}$, one in December-January and the other in April-May (South African Weather Bureau, pers. comm.). Run-off of this magnitude has been shown by Duncombe Rae (1989b) to decrease significantly the density of the surface mixed layer, with consequent local increase in water-column stability.

An estimate of the freshwater residence time in the inter-island region can be obtained by calculating the volume of run-off required to cause the observed dilution in the mixed layer. Given the area of diluted waters $A_D \approx 4 \times 10^8 \text{ m}^2$, with mixing depth $Z_D \approx 50 \text{ m}$ and the average salinity of the diluted mixed layer, $S_D \approx 33.812 \times 10^{-3}$, and of undiluted oceanic waters, $S_S \approx 33.841 \times 10^{-3}$ (from data obtained during April 1987, Duncombe Rae, 1989a), the required volume of freshwater run-off, V_R , is:

$$V_R = A_D \times Z_D [1 - (S_D/S_S)] \approx 17 \times 10^6 \text{ m}^3$$

With a rainfall rate of $\approx 7 \text{ mm d}^{-1}$ and a catchment area of $\approx 200 \times 10^6 \text{ m}^2$ (i.e., half of the total area covered by the two islands), the volume of freshwater run-off from the islands would be of about $1.4 \times 10^6 \text{ m}^3 \text{ d}^{-1}$. Then, to account for the observed dilution levels in the mixed layer of the island seas, a minimal residence time of ≈ 12 days is required.

The islands' run-off is also heavily loaded with nutrients. The high guano production observed at the islands has been estimated to be of the order of $\approx 3 \times 10^4$ tons of fresh guano per year (Burger *et al.*, 1978). Virtually all of this is voided on the coastal plain of the islands, particularly on the eastern coast of Marion Island (Burger *et al.*, 1978). As a result of the high rainfall, the guano does not accumulate on the islands themselves, but is dissolved and carried into the marine environment via run-off spreading out from the islands. Thus, a large amount of reduced nitrogen (as urea and ammonia) is made available to the marine primary

producers. In the near-shore area, off the penguin colonies, ammonia and urea concentrations as high as 16.69 and 2.89 mmol m^{-3} , respectively, are commonly measured (Perissinotto, unpubl. data). Recent studies on nitrogen uptake by size fractionated phytoplankton in the Southern Ocean have shown that in spite of the domination of the nitrogenous nutrient pool by nitrate and nitrite, ammonia and urea are the preferred nutrients used by phytoplankton of all size classes (Probyn and Painting, 1985; Lucas and Probyn, in press). Analysis of the meso-scale distribution of reduced nitrogen sources in the Prince Edward Archipelago shows strong correlation with phytoplankton biomass and production and significantly accounts for their variability (Table 1.1). It is likely, therefore, that guano run-off from the islands, entrained by the anticyclonic eddy, may represent one of the most important factors involved in the formation of the blooms in the Prince Edward Islands region.

Table 1.1. Simple correlation analysis of phytoplankton biomass and production *versus* ammonia and urea levels. All data were $\log_{10}$ -transformed before the analysis. Significance levels: * = 95%, ** = 99%, n.s. = not significant.

Dependent variable	Ammonia		Urea	
	<i>p</i>	R^2	<i>p</i>	R^2
April/May 1983				
Surface chlorophyll- <i>a</i>	*	26.3	<i>n.s.</i>	3.1
Integrated chlorophyll- <i>a</i>	<i>n.s.</i>	5.6	<i>n.s.</i>	8.9
Primary production	<i>n.s.</i>	11.6	**	59.1
Photosynthetic capacity	<i>n.s.</i>	9.3	**	65.7
Assimilation number	*	17.2	*	41.6
April/May 1987				
Surface chlorophyll- <i>a</i>	**	33.9	—	—
Integrated chlorophyll- <i>a</i>	**	36.3	—	—
Primary production	*	29.5	—	—
Photosynthetic capacity	<i>n.s.</i>	9.7	—	—
Assimilation number	*	21.2	—	—

CHAPTER 2

VERTICAL STABILITY AS A CONTROLLING FACTOR OF THE MARINE PHYTOPLANKTON PRODUCTION AT THE PRINCE EDWARD ARCHIPELAGO

2.1 Introduction

The continuous upwelling at the Antarctic Divergence results in the Southern Ocean having the highest known nutrient levels for pelagic ecosystems (Sakshaug and Holm-Hansen, 1984; Priddle *et al.*, 1986). In spite of the high growth potential which characterizes the local primary producers (Holm-Hansen, 1985) the phytoplankton production and biomass range far below the levels expected from the nutrient concentrations. The paradox of oligotrophic, or plankton-poor, nutrient-rich waters requires an examination of the processes limiting phytoplankton production to levels of only a few percent of growth potential.

Considerable attention has recently been given to the distribution of water temperature, incident radiation and nutrients in the Southern Ocean (Holm-Hansen *et al.*, 1977; Jacques, 1983; LeJehan and Treguer, 1983; Tilzer *et al.*, 1985; Tilzer and Dubinsky, 1987). However, the distribution of these features over large areas is too uniform for them to explain the spatial distribution of phytoplankton production and biomass at all scales (Fogg, 1977; Holm-Hansen *et al.*, 1977; Sakshaug and Holm-Hansen, 1984). In particular, it has been suggested that the small- and meso-scale dynamics of phytoplankton productivity in the Southern Ocean may be regulated by the physical structure of the water-column and by the grazing pressure of herbivorous zooplankton (Hasle, 1969; El Sayed, 1984; Priddle *et al.*, 1986).

Using data collected on three different occasions in the vicinity of the Prince Edward Islands (47° S, 38° E), I examine the relationship between phytoplankton production and biomass and upper ocean stability and mixing depth.

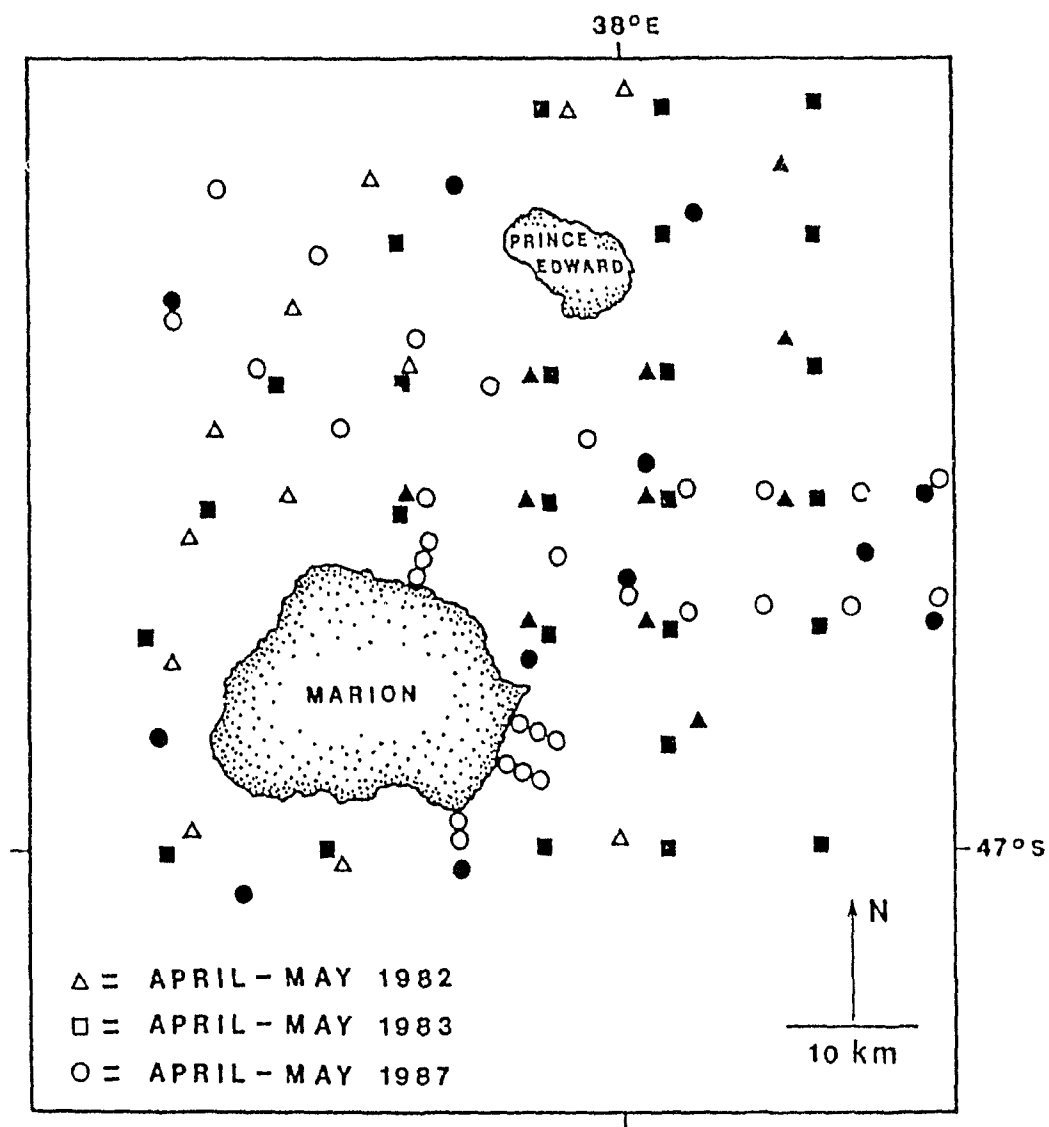


FIGURE 2.1. Station positions for the three cruises to the Prince Edward Islands. Open symbols indicate stations where only CTD casts and chlorophyll-*a* determinations were made. Closed symbols represent stations where primary productivity estimates were made in addition to the CTD casts and chlorophyll-*a* determinations.

2.2 Materials and methods

Eighty-three stations were occupied in the area by *SA Agulhas*: 15 stations in April/May 1982, 26 in April/May 1983 and 42 in April/May 1987 (Fig 2.1). At each station casts were made using a Neil Brown Mk. III conductivity, temperature, depth probe (CTD) and discrete measurements of chlorophyll-*a* concentration were obtained by the spectrophotometric method (SCOR/UNESCO, 1966). At 42 stations integrated primary production rates, $\Sigma P = P_{max} \times Z_{0.1}$, where P_{max} is the maximum potential photosynthetic rate, and $Z_{0.1}$ is the 10% light depth, were estimated by onboard incubation (Gargas *et al.*, 1976; Allanson *et al.*, 1981). Sixteen incubation flasks of 100 ml volume were inoculated with a solution of 4 μCi $\text{NaH}^{14}\text{CO}_3$. This series was incubated for 4 hours under a light regime set up by an array of neutral density filters with transmission values of 50, 25, 15, 10 and 5% of the incident light. Two bottles were exposed to 100% of the incident light flux from the bank of Phillips Daylight fluorescent tubes and a tin foil backing was used to increase the light to 150% for another two bottles. The last two bottles were wrapped in tin foil to determine the amount of ^{14}C taken up by passive diffusion and which had absorbed onto the surfaces of the phytoplankton. Phytoplankton photosynthetic capacity, P_m^B , was calculated by normalizing the maximum potential photosynthetic rate to chlorophyll-*a* concentration (Platt *et al.*, 1980). The depth of the surface mixed layer was assumed to be where a pycnocline of 0.03 kg m^{-3} occurred within 10 m (Priddle *et al.*, 1986). Vertical stability was estimated for the upper 100 m of the water column using the stability parameter:

$$E = \alpha(dT/dz + \Gamma) - \beta ds/dz \quad [\text{m}^{-1}],$$

where α is the thermal expansion coefficient, dT/dz the vertical temperature gradient, Γ the adiabatic lapse rate, β the expansion coefficient for salinity and ds/dz the vertical salinity gradient.

2.3 Results and discussion

Correlation and regression analyses (Table 2.1, Fig 2.2) showed that several phytoplankton characteristics were significantly related ($p < 0.05$) to the physical structure of the water column. Surface chlorophyll-*a* concentration was correlated with vertical stability during 1982 and 1983 but not during 1987. Negative correlation of chlorophyll-*a* with mixed layer depth was also significant on two of the three occasions (1982 and 1987). This pattern was also found for chlorophyll-*a* integrated over the water-column where this was available. The amount of variance explained (R^2) by these relationships ranged from 16 to 38% of the total (Table 2.1).

The spatial distribution of phytoplankton biomass is often dominated by local hydrodynamic effects and can account for the lack of consistency in these regressions and the relatively low percentage of variance explained. Small- and mesoscale variations in chlorophyll-*a* concentrations would be the result of physical processes causing accumulation and dissipation of phytoplankters rather than of *in situ* growth, an hypothesis which is supported by similar results reported for other areas of the Southern Ocean (Weber and El Sayed, 1985; Priddle *et al.*, 1986).

According to the hypothesis developed by Sverdrup (1953), the critical depth, Z_{crit} , at which water-column photosynthesis equals the integrated respiration, must be greater than the mixed layer depth for phytoplankton blooms to develop. As the critical depth in the Southern Ocean is generally deeper than the usual summer mixed layer ($Z_{crit} > 100\text{ m}$), it is now widely accepted that Sverdrup's hypotheses cannot explain the low phytoplankton production of these waters (Jacques, 1983; Priddle *et al.*, 1986; El Sayed, 1988). However, turbulence within the euphotic zone must play an important role in regulating the photosynthetic activity of phytoplankton. When the mixed layer depth exceeds the euphotic depth ($Z_{mix} > Z_{eu}$) phytoplankton remain in the aphotic zone during part of the day. Thus, the carbon balance would be shifted towards increasing respiratory losses following the relation:

$$K = Z_{eu}/Z_{mix}(P - R),$$

where K is the daily net growth rate, P the diurnal photosynthetic carbon accumulation and R the nocturnal respiratory carbon losses (Tilzer and Dubinsky, 1987). If

Table 2.1. Simple correlation analysis of phytoplankton biomass and production *versus* vertical stability and mixed layer depth. Phytoplankton data were $\log_{10}$ -transformed before the analysis. (All correlations between dependent variables and stability are positive, whereas correlations with the depth of the mixed layer are negative). Significance levels: * = 95%, ** = 99%, n.s. = not significant.

Dependent variable	Stability		Mixed layer depth	
	<i>p</i>	R^2	<i>p</i>	R^2
April/May 1982				
Surface chlorophyll- <i>a</i>	*	38.3	*	26.7
April/May 1983				
Surface chlorophyll- <i>a</i>	*	17.7	<i>n.s.</i>	8.3
Integrated chlorophyll- <i>a</i>	<i>n.s.</i>	12.9	<i>n.s.</i>	6.7
Primary production	**	64.3	*	31.5
Photosynthetic capacity	**	43.8	**	47.6
April/May 1987				
Surface chlorophyll- <i>a</i>	<i>n.s.</i>	11.2	*	15.9
Integrated chlorophyll- <i>a</i>	<i>n.s.</i>	6.8	*	13.6
Primary production	*	35.7	<i>n.s.</i>	5.15
Photosynthetic capacity	**	78.9	**	48.8

$Z_{mix} < Z_{eu}$, the daily production will increase and, for constant Z_{eu} , the shallower the mixed layer the higher the production. It has been reported (Holm-Hansen and Foster, 1981) that phytoplankton blooms in the Southern Ocean (with Chl-*a* concentrations $> 1.5 \text{ mg m}^{-3}$) occur predominantly in conjunction with a shallow mixed layer and Sakshaug and Holm-Hansen (1984) suggest that a pycnocline depth of 50 m may be the maximum depth allowing blooms to occur.

Although phytoplankton biomass in the Southern Ocean generally reflects the variation in primary production (Burkholder and Mandelli, 1965; Holm-Hansen *et al.*, 1977), the results of the investigations at the Prince Edward Islands indicate that most of the biomass variance is not accounted for by the degree of vertical stability. On all three occasions bloom concentrations of chlorophyll-*a* were observed over a wide range of mixed layer depths, from 20 m to 130 m. I suggest, therefore, that biomass (as chl-*a*) may not be a suitable variable to be used in small- and meso-scale analysis of the relationships between local phytoplankton variations and the vertical structure of the upper ocean.

More consistent results can be expected on considering the distribution of primary production or appropriate algal physiological indicators, such as maximum photosynthetic rate or *in vivo* fluorescence, which are good indicators of the rate of vertical mixing in the water-column (Lewis *et al.*, 1984). Data presented here (Table 2.1) show that integrated primary production was significantly related to stability in April/May 1983 and April/May 1987, when production data were available. The correlation between productivity and mixed layer depth was significant only for the 1983 data set. Strong and consistent relationships were found between the photosynthetic capacity, and the stability and mixed layer depth (Fig 2.2).

These relationships would suggest that the dominant source of variation responsible for the observed difference in local phytoplankton photosynthesis is the physical structure of the water-column. During 1987 stability explained about 80% of the total variance of phytoplankton photosynthetic capacity.

At the Prince Edward Islands recurrent phytoplankton blooms associated with

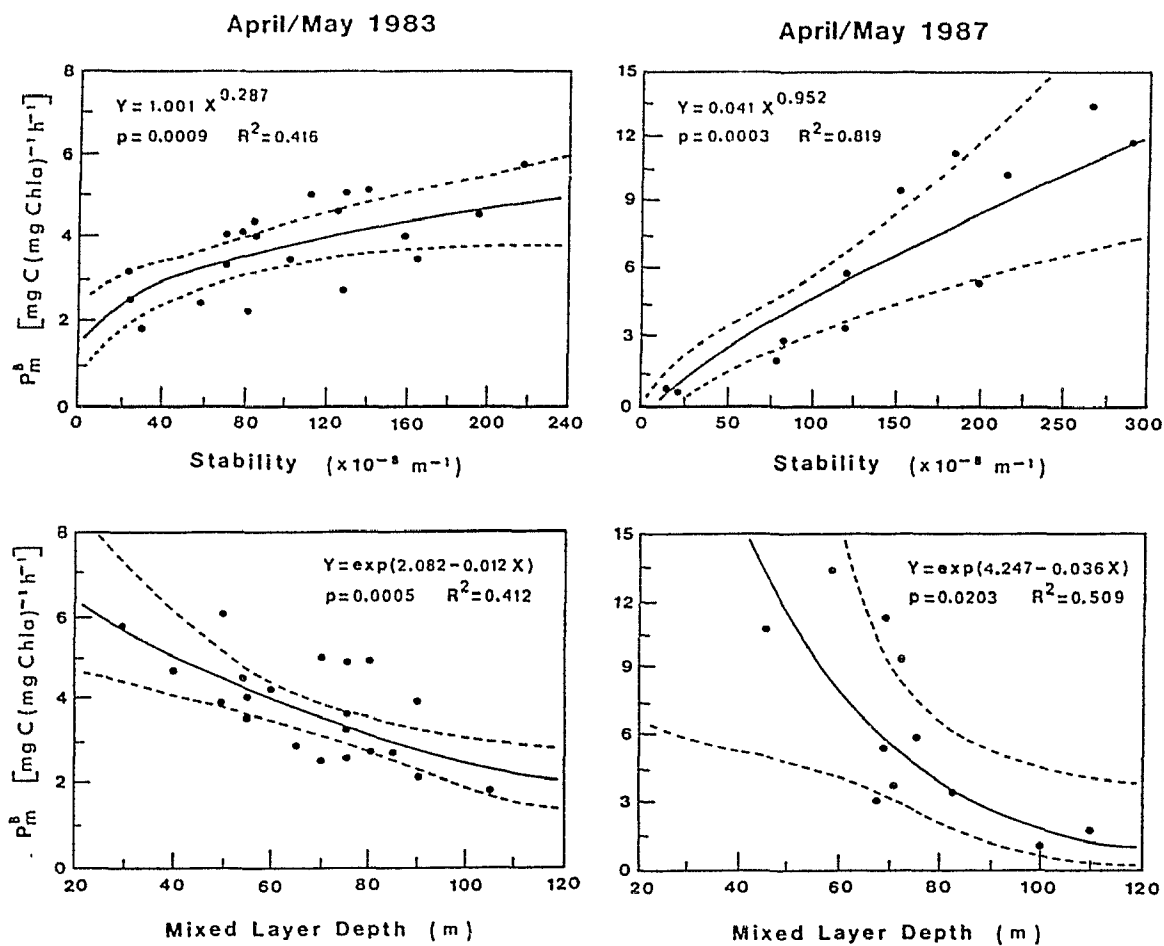


FIGURE 2.2. Regression of phytoplankton photosynthetic capacity (P_m^B) versus vertical stability and mixed layer depth. Dashed lines represent $\pm 95\%$ confidence limits.

high photosynthetic rates are found mostly over the shallow saddle between the two islands (Allanson *et al.*, 1985; Boden, 1988). This region has also been shown to be characterized by the presence of an anticyclonic eddy field (Allanson *et al.*, 1985; Chapter 1; Perissinotto and Duncombe Rae, 1990). Freshwater run-off of the high rainfall on the islands (an average of 210 *mm* per month; South African Weather Bureau, pers. comm.) retained between them by the eddy, is shown by Duncombe Rae (1989b) to decrease significantly the density of the mixed layer, thereby increasing its stability over the saddle compared to the surrounding ocean.

Similar dynamics may prevail around most of the subantarctic islands where run-off may contribute substantially to elevated phytoplankton production.

Ice-melt around the Antarctic continent also affects the vertical stability of the water-column by increasing the buoyancy of the surface layer. Although in this case the source of freshwater input is different compared to that at the Prince Edward Islands, a similar effect, with enhancement in phytoplankton production, seems to occur (Smith and Nelson, 1985; Nelson *et al.*, 1987).

CHAPTER 3

THE STRUCTURE AND DIURNAL VARIATIONS OF THE ZOOPLANKTON OF THE PRINCE EDWARD ISLANDS: IMPLICATIONS FOR THE BIOMASS BUILD-UP OF HIGHER TROPHIC LEVELS

3.1 Introduction

Recent investigations on the plankton of the Prince Edward archipelago (47° S, 38° E) have shown that there is no local endemic holoplankton (Boden and Parker, 1986), indicating that the islands' sea is not a taxonomic reproductive refuge. Nevertheless, the zooplankton biomass is high and comparable with that of the notably rich Antarctic Polar Front (Table 3.1, Boden, 1988). On the other hand, phytoplankton production rates at the Prince Edward Islands are an order of magnitude greater than at the Polar Front (Table 3.1). Also, the biomass ratio between zooplankton and phytoplankton at the Polar Front and at the islands is 31 and 17, respectively. The question posed is, "Why does not the increased growth and productivity of phytoplankton at the islands find an equal response in the zooplankton standing stock?" The answer to this has important implications for the identification of the origin energy that supports the biomass build-up of the trophic levels higher than zooplankton.

Some aspects of this complex problem were investigated during the April/May 1985 and 1986 cruises of *SA Agulhas* to the Prince Edward Islands. The major objectives of the study carried out on these occasions can be summarized as follows: a) analysis of the composition and of the small-scale spatio-temporal distribution of the microzooplankton community (20–200 μm) to which little attention has been given during previous investigations in the area and in the Southern Ocean in general;

Table 3.1. The standing stock of phytoplankton, the level of primary production and zooplankton biomass at the Prince Edward Islands compared with the surrounding ocean and the nearby frontal systems (after Boden, 1988).

Sampling Locality	Chlorophyll- <i>a</i>	Potential Primary	Zooplankton
	<i>mg Chl-a m⁻³</i>	Production <i>mg C m⁻² h⁻¹</i>	Biomass <i>mg DW m⁻³</i>
Prince Edward Islands	2.3	175	40
Open ocean, Subantarctic	0.2	10	5
Subtropical Front	1.7	88	15
Antarctic Polar Front	1.5	31	47

b) determination of the vertical migration patterns of the different groups of the mesozooplankton communities (200–20000 μm) related to the variations in bottom topography characteristic of the Prince Edward plateau.

3.2 Materials and methods

Time-course sampling of zooplankton was carried out during the 1985 cruise at two stations of 30 (stn. A) and 36 hours (stn. B), located over the Natal Bank and midway between Prince Edward and Marion Islands respectively (Fig 3.1). Two other stations, each of 24 hours, were occupied in 1986. The first was positioned on the shallow area between the eastern coast of Marion Island and the Natal Bank (stn. C), while the second station was located north of Marion Island (stn. D, Fig 3.1). Stations A and C are representative of the islands' shelf as they lie within the 200 m isobath, while stations B and D are situated offshore where the slope falls off very rapidly (Fig 3.1). The water column was sampled at regular intervals of 3–4 hours by two different methods. Microzooplankton were collected at stations C and D using a large-scale filtration apparatus with three units of 130, 80 and 22 μm nominal mesh size (Berman and Kimor, 1983). Water was pumped through the filtration system at a flow rate of about 15 l min^{-1} by means of a submersible pump. For each sample, a total volume of 80–100 l was pumped and filtered. Depth-integrated samples were obtained from two standard layers, *i.e.*, one from 50 m to 25 m and the other from 25 m to the surface.

Quantitative samples of mesozooplankton were taken at all stations with a 200 μm mesh WP-2 UNESCO closing net by fractionated vertical hauls from the bottom (or from 200 m at offshore stations) to 50 m , from 50 m to 25 m and from 25 m to the surface. On a few occasions horizontal hauls with a 500 μm mesh Bongo net were also made.

Zooplankton biomass estimates were obtained by determining the displacement volume of each sample, using the vacuum extraction technique to remove the

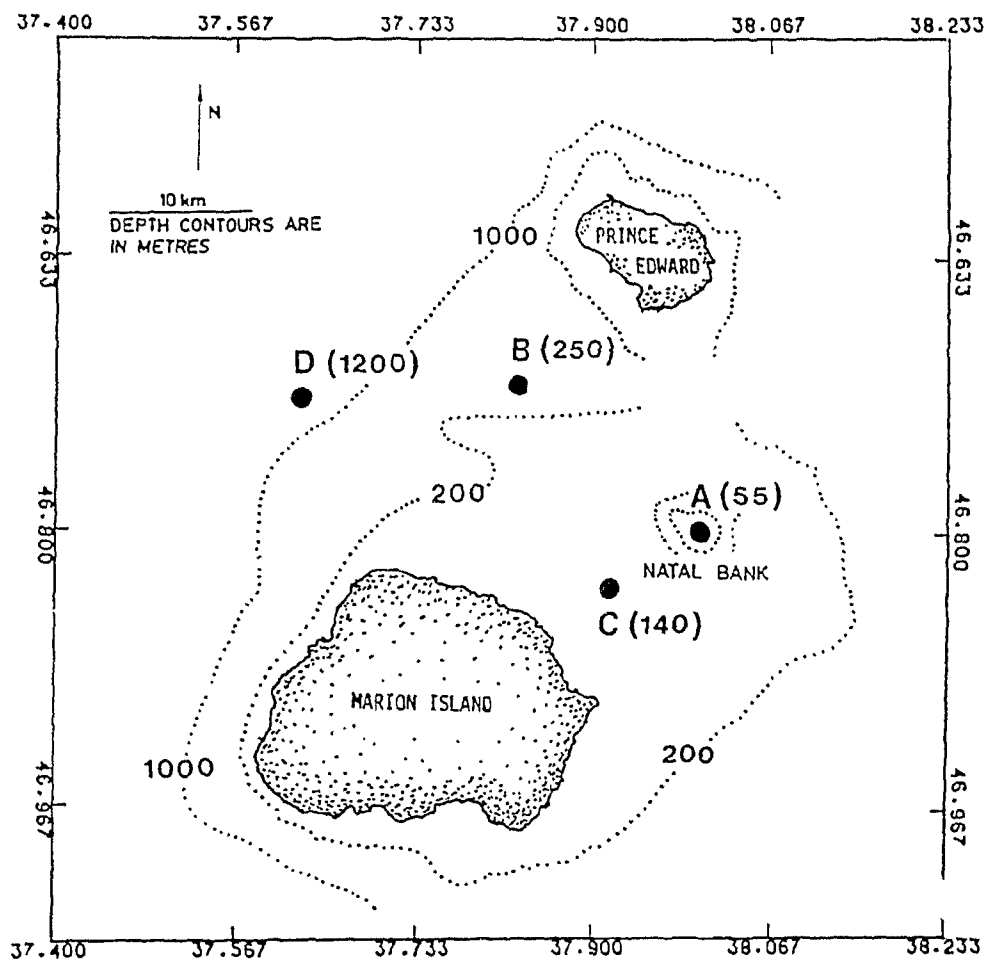


FIGURE 3.1. Position of the sampling stations at the Prince Edward Islands. Stations A, B: April/May 1985; stations C, D: April/May 1986.

solution and the interstitial liquid (Beers, 1976). The major zooplankton taxa encountered during April/May 1986 were counted in subsamples of 0.1 to 0.2 of the original samples obtained with the Wiborg's modified whirling apparatus (Kott, 1953). Microzooplankton abundance was obtained by counting entire samples.

All numerical plankton counts were normalized by the transformation $\log(x+1)$ which also accommodates zero values (Cassie, 1968). Differences in abundance between offshore versus shelf stations and between day versus night samples were tested by the analysis of variance subprogram ONEWAY of the SPSS statistical package (Nie et al., 1975). Within the subprogram, all possible *a priori* comparisons between groups were tested by the t-statistics in a pooled variance model.

3.3 Results

a) Microzooplankton. During April/May 1986, the most abundant components of the microzooplankton community of the Prince Edward Archipelago were copepod nauplii (Table 3.2). The maximum concentration reached values as high as $15 \times 10^3 \text{ ind } m^{-3}$ at both stations. The shelf station presented significantly lower nauplii concentrations compared to the offshore one ($p < 0.01$, Tables 3.2 and 3.3). The second most abundant group was represented by the cyclopoid copepods *Oithona* spp. (Table 3.2) which had the highest concentrations in the size fraction 130–200 μm . This taxon did not show any significant differences between stations or between day and night ($p > 0.1$, Table 3.3). Other numerically important taxa were the following (Table 3.2): foraminifera (size: 22–80 μm), *Microcalanus pygmaeus* (size: 130–200 μm), *Microsetella* sp. (size: 130–200 μm), the pteropod *Limacina* sp. (size: 130–200 μm), the appendicularian *Oikopleura* sp. (size: 80–130 μm) and tintinnids (size: 22–80 μm). Three of these taxa, *i.e.*, foraminifera, *Oikopleura* sp. and *Microcalanus pygmaeus* showed significant differences in abundance between stations (Tables 3.2 and 3.3). Foraminifera and *Oikopleura* sp. were both more abundant in off-shore waters. The rotifer *Synchaeta* sp. and meroplanktonic larvae

of polychaetes, bivalves and gastropods were found in very low concentrations and only in a few samples, mostly from the shelf station.

b) Mesozooplankton. This size-class was largely dominated by copepods (Fig 3.2) which constituted about 95% in numbers of the total catch. The chaetognaths, which dominated the plankton community during 1982 (Boden and Parker, 1986), were present in very low concentrations and contributed only about 2% to the total. Ostracods and euphausiids were even less abundant in terms of numbers, each constituting less than 1% of the total catch (Fig 3.2). However, euphausiids were important, if not dominant, in terms of biomass contribution.

A list of the most important taxa found during the investigation is given in Table 3.3. It is evident that the copepods *Calanus simillimus*, *Eucalanus longipes*, *Rhincalanus gigas*, *Microcalanus pygmaeus* and calyptopis/adults of euphausiids (mostly *Euphausia vallentini* and *Thysanoessa vicina*) were present in significantly higher concentrations at station D than at station C (Table 3.3). Estimates of zooplankton displacement volume ($ml\ m^{-3}$) show that a sharp decrease in total biomass occurred during the daylight period at the shelf stations relative to the offshore stations (Table 3.3, Fig 3.3). This decrease amounts to an average of $0.105\ ml\ m^{-3}$ at stations A and C as compared to an average of only $0.068\ ml\ m^{-3}$ at station B and D. However, considering the two sampling occasions separately, during 1984 the daytime biomass decrease was evident only at the shelf station, while in 1985 it occurred at both the off-shore and the shelf stations. Also, in 1986 the daytime decrease was very significant and of $\approx 0.14\ ml\ m^{-3}$, but in 1985 it was only of $\approx 0.07\ ml\ m^{-3}$. Differences between day and night biomass data at the shelf stations were highly significant in both years ($p < 0.05$, t-test).

Conclusive evidence of diurnal vertical migrations in the area was found only for the copepod *Metridia gerlachei* and the euphausiids (both calyptopis and furcilia as well as adults) as the day/night differences in the counts of these taxa were significant at both offshore and shelf stations ($p < 0.05$, Table 3.3). However, the copepods *Eucalanus longipes*, *Rhincalanus gigas* and *Microsetella* sp. also showed

Table 3.2. Mean concentrations ($\text{ind } m^{-3}$) and confidence intervals at 95% level of the most abundant microzooplankton taxa [$X = \bar{x} \pm SE \times t(0.05)$].

Station	St. C	St. C	St. D	St. D
Layer	50 m–25 m	25 m–surf.	50 m–25 m	25 m–surf.
Copepod nauplii	7903 ± 2216	8226 ± 3464	12543 ± 1933	11012 ± 2001
<i>Oithona</i> spp.	1883 ± 796	2299 ± 996	1895 ± 706	1755 ± 595
<i>Microcalanus pygmaeus</i>	802 ± 352	695 ± 400	538 ± 189	381 ± 137
Foraminifera	552 ± 221	497 ± 359	2204 ± 807	1897 ± 744
<i>Limacina</i> sp.	293 ± 304	102 ± 36	186 ± 167	131 ± 53
<i>Microsetella</i> sp.	126 ± 86	48 ± 38	73 ± 31	46 ± 19
<i>Oikopleura</i> sp.	23 ± 29	18 ± 14	129 ± 121	64 ± 27

Table 3.3. Zooplankton ANOVA matrix (t-statistics of pooled variance). Comparisons between stations and day-night data. Level of significance: 90% (*), 95% (**), 99% (***).

Station	A vs B	C vs D	AC vs BD	A vs B	C vs D	AC vs BD
Time	Day	Day	Day	Night	Night	Night
Biomass (D.V.)	2.18*	2.69 **	3.10 ***	2.28*	1.66	1.08
Station	C vs D	C vs D	C vs D	C vs D	C	D
Layer	25-0 m	50-25 m	200-50 m	200-0 m	140-0 m	200-0 m
					Day vs Night	Day vs Night
Foraminifera	4.28 ***	4.06 ***	0.95	5.40 ***	0.53	0.94
Radiolaria	1.39	0.20	0.78	0.47	0.86	1.61
Ostracods	0.96	0.93	0.54	0.29	0.41	0.03
Copepod nauplii	2.44 **	3.01 ***	n.s.	3.14 ***	1.11	1.01
<i>Calanus simillimus</i>	0.9	2.79 ***	3.26 ***	2.94 ***	0.01	0.17
<i>Eucalanus longipes</i>	0.54	0.70	2.80 **	1.19 *	0.11	1.25 *
<i>Rhincalanus gigas</i>	0.72	1.01	0.12	1.23 *	0.17	1.90 *
<i>Microcalanus pygmaeus</i>	1.15	0.92	2.01 **	2.35 **	0.36	0.48
<i>Clausocalanus</i> spp.	0.80	1.73 *	1.17	0.14	0.12	0.04
<i>Metridia gerlachei</i>	0.77	0.23	0.56	0.26	5.19 ***	2.57 **
<i>Oithona</i> spp.	0.65	0.77	0.97	0.98	0.49	0.29
<i>Microsetella</i> sp.	0.89	0.27	n.s.	0.36	1.83 *	1.43
Euphausiids (furc.)	0.53	0.60	0.27	0.11	3.54 ***	2.47 **
Euph.(calypt.-adults)	1.15	1.07	0.91	1.84 *	1.73 *	1.82 *
Chaetognaths	0.61	1.96 *	1.50	1.65 *	1.16	0.45
<i>Oikopleura</i> sp.	4.19 ***	7.23 ***	1.24	7.30 ***	0.54	0.53

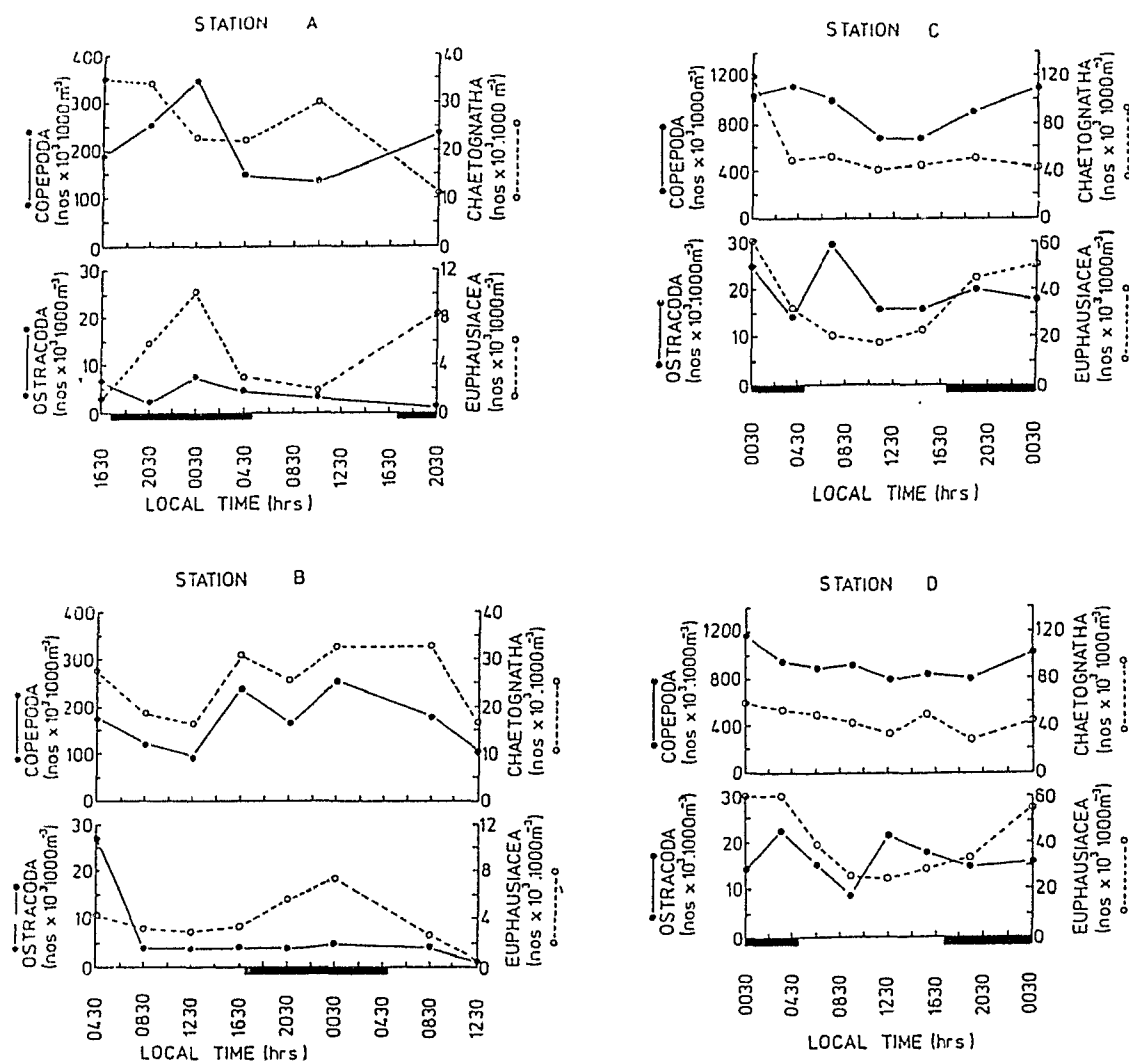


FIGURE 3.2. Abundance estimates of the four dominant components of the zooplankton community.

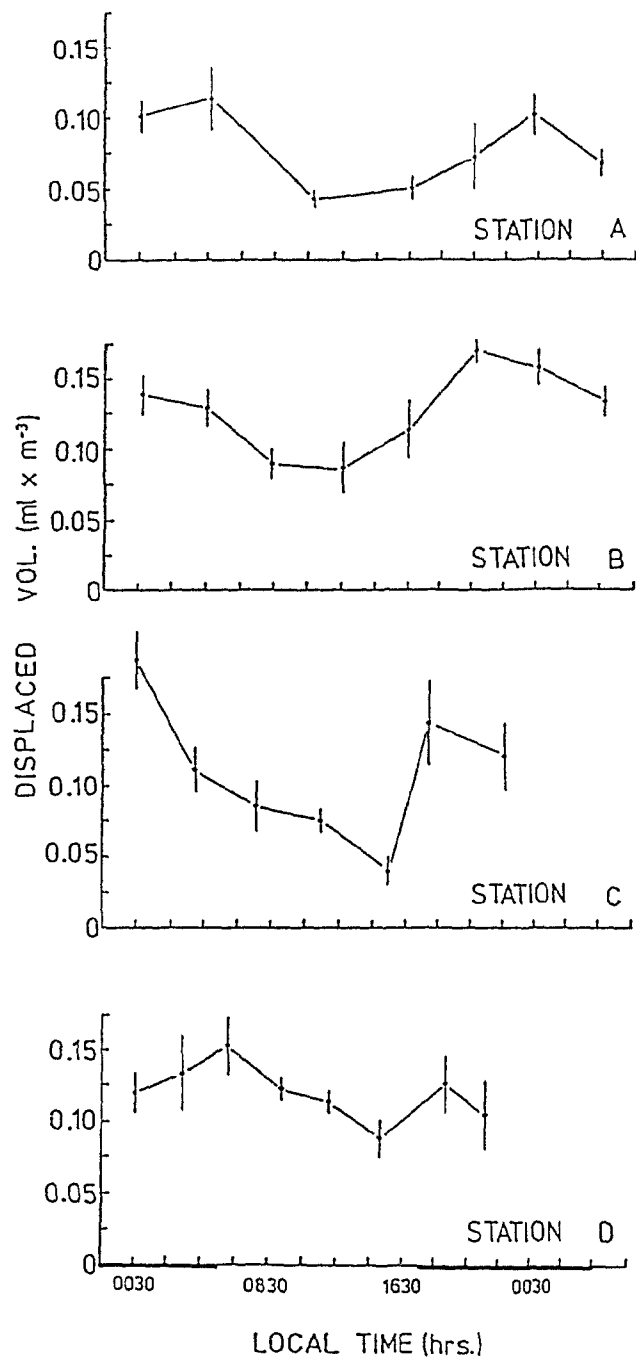


FIGURE 3.3. The standing stock of zooplankton as indicated by the displacement volume. Period of darkness is indicated by thickening of the horizontal axis.

statistical differences at one station (Table 3.3), indicating that these species probably can undergo a diel cycle as well.

3.4 Discussion

Within the microzooplankton, the holoplanktonic groups were well represented during April/May 1986. In particular, the very high concentrations of copepod nauplii indicate that the copepod population in the area had a high growth rate during the period of investigation. On the other hand, the paucity of meroplanktonic larvae of benthic invertebrates appears to be in contrast to the large benthic biomass of the islands' shelf (Boden and Parker, 1986). However, it seems that this is a general phenomenon occurring in the Southern Ocean and is possibly related to strategies of cold adaptation (Clarke, 1985). Part of this suite of strategies would involve the tendency to produce small numbers of large eggs, rather than massive release of very immature planktonic stages.

The mesozooplankton were numerically dominated by copepods but euphausiids often represented the bulk of the total biomass, especially in samples collected at night. Furthermore, since the few horizontal hauls made by towing a Bongo net at a speed of about 3 knots yielded a 2–3 fold increase over the WP-2 net haul concentration of euphausiids, it is believed that the size of their population was largely underestimated throughout the investigation. Euphausiids are very fast swimmers and their net avoidance probably results in much lower and less accurate estimates of concentration obtained by experimental fishing than by acoustic surveys (Hempel, 1985). Nets were not darkened during this survey and, therefore, daylight zooplankton escape responses might have significantly affected the absolute abundance estimates. However, this is a systematic underestimation and unlikely to account for the biomass differences between shelf and off-shore stations since vertical tows were always started from depths (140 and 200 *m*, respectively) far beyond the depth of light extinction ($\approx 50\text{--}80$ *m*; Boden, unpubl. data).

The most striking feature of the spatio-temporal variations in zooplankton biomass during April/May 1986 is the sharp decrease observed during the daylight period at the shelf station as compared to the pattern found at the offshore station (Table 3.3, Fig 3.3). In 1985, however, this decrease on the shelf was paralleled by a similar drop in biomass levels in oceanic waters. While this difference in the off-shore diurnal variations between the two years suggests the lack of a consistent pattern in these waters, the decrease observed in the shelf area on both occasions seems to represent a more general feature. Indeed, a daytime shelf depletion is also reflected in the numerical abundance data of the mesozooplankton groups and, to a lesser extent, of the microzooplankton as well (Tables 3.2 and 3.3). Zooplankton samples collected during the March 1976 cruise of *Marion Dufresne* to the Prince Edward Islands also showed the tendency of biomass to increase with station bottom depth (Grindley and Lane, 1979). Unfortunately the number of stations occupied on that occasion was too small to allow any testing for a diurnal pattern. However, a larger set of data collected during the May 1983 cruise of *SA Agulhas* (Allanson *et al.*, 1985; Boden and Parker, 1986) did provide this opportunity. In Figure 3.4 the zooplankton biomass of samples collected in May 1983 during daylight and within the 1000 m isobath is plotted *versus* bottom depth. The low biomass levels per unit volume in shallow waters increase steadily to higher values with depth, up to about 50 mg m^{-3} , showing then a tendency to remain stable. Nonlinear regression analysis shows that biomass and depth are significantly related, the best fit to the data being given by the equation $Y = 49.3 [1 - \exp(-0.0054 \times X)]$ ($r = 0.809$, $p < 0.05$). This relationship clearly substantiates the evidence obtained from the time-course experiments.

What are the possible mechanisms responsible for this marked decrease of zooplankton biomass on the shelf during daytime? The number of observations available for the Prince Edward Islands is still too limited to draw many conclusions, but the results obtained so far and theoretical considerations suggest the following working hypothesis. The interaction of migrating zooplankton with shallow topog-

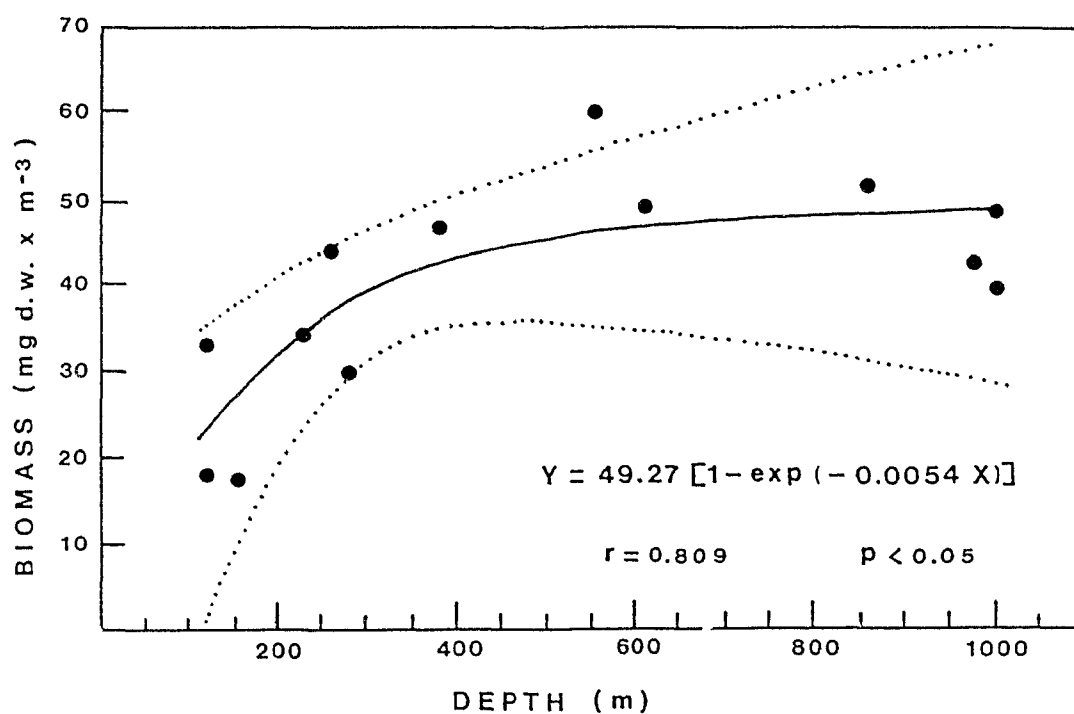


FIGURE 3.4. Regression of biomass versus depth data from the April 1983 cruise. Zooplankton biomass was measured from samples collected by WP-II hauls from the bottom over the shelf (depth ≤ 200 m) and from 200 m at off-shore stations.

raphy may result in a block to the diurnal descent of the migrators which had been advected above the shallow shelf while at near-surface depths during the preceding night. While trapped at shallow and relatively illuminated depths, this plankton would be vulnerable to predation by visual predators such as fish, squid, birds and seals that are plentiful around these islands (Skinner *et al.*, 1978; Berruti and Harcus, 1978; Williams *et al.*, 1979; Gon and Klages, 1988). This kind of mechanism has been observed by Isaacs and Shwartzlose (1965) over some shallow banks along the coast of Baja California, and by Genin *et al.* (1988) in the southern California Bight. It is quite possible that this process occurs in the area under consideration as well. As the radial length scale of the shallow inter-island region is of the order of about 10 km, then even assuming that the zooplankton swim at the fastest cruising speeds observed, *i.e.*, $2.5\text{--}5\text{ cm s}^{-1}$ (Enright, 1977; Angel and Fasham, 1983), the time scale for crossing the shallow zone would be about 2.3–4.6 days. Thus, this calculation shows that vertical migrators can descend to their daylight depth (200–500 m) but cannot escape daylight exposure and visual predation horizontally if they are trapped over a shallow area.

Most of the land-based predators in the Prince Edward Archipelago are surface and sub-surface pelagic feeders (Condy, 1981; Abrams, 1985; Adams, 1987; Brown and Klages, 1987). Investigations on the composition of their diet have indicated that crustacean zooplankton, especially euphausiids, are the main food item of many seabirds (Croxall, 1984; Brown and Klages, 1987) and of the Antarctic fur seal (Condy, 1981). Zooplankton are also the dominant components of the stomach contents of benthic fish inhabiting the island shelves of the Southern Ocean (Duhamel and Hureau, 1985). Of this fish, nototheniids and congipodids are particularly abundant around the Prince Edward Islands (Gon and Klages, 1988). Thus, the potential impact of the community of visual predators on the local zooplankton stock is expected to be substantial and measurable on a short time-scale. The most favourable period of the day for visual predation seems to coincide with the early dusk and dawn hours, when a combination of light conditions and high densities of

vertical migrators in the upper layer results in optimal energetic advantages for the predators (Croxall *et al.*, 1985).

But how would the shelf of the Prince Edward Archipelago be replenished with zooplankton during the night? Off-shore zooplankton that migrate into the upper layer during nighttime are subjected to mass advection towards the archipelago by the free-stream current ($u \approx 0.35 \text{ m s}^{-1}$). Recent investigations in the area have shown the periodical occurrence of anticyclonic eddies in the saddle between the islands which are associated with the formation of phytoplankton blooms (Allanson *et al.*, 1985; Boden, 1988; Chapter 1; Perissinotto and Duncombe Rae, 1990). Anticyclonic eddies in the Southern Ocean are characterized by convergent lateral flux of water due to the Coriolis force. This radial advection alone is probably not enough to entrain a substantial proportion of the advected zooplankton on a time-scale of the order of 10–12 hours. However, zooplankton are likely to spread across the front into the eddy at a considerable faster rate because of independent swimming motion and wind-driven surface Ekman drift (Angel and Fasham, 1983). At the Prince Edward Islands the prevailing wind blows from the north-western quadrant with an average velocity of 10 m s^{-1} (South African Weather Bureau, pers. comm.). Thus, as the surface current induced by the wind stress is approximately 3% of the wind speed (Knauss, 1978), this would result in a surface Ekman drift of about 30 cm s^{-1} . This motion is substantial only in a very thin layer of the upper water column (10–20 m). However, the time scale required for a surface front of zooplankton to be advected along the whole radial distance of the eddy by this mechanism would be of only 9 hours. It appears, therefore, that the flux of vertical migrators within the eddy field is likely to replenish the interisland area during nighttime with allochthonous zooplankton. It is reasonable to assume that zooplankton entrained in the eddy would stay because of retention by the physical forces within the system, and their foraging activities. During daytime, when the migrators descend to the bottom, there would not be any significant current to advect them downstream of the eddy since the Ekman velocity falls off exponentially with depth.

Isaacs and Schwartzlose (1965) suggested that surface advection of zooplankton by night may represent a potential input of energy of the order of several times the local primary production rates. Phytoplankton production in the area can reach maximum values of about $175 \text{ mg } C \text{ m}^{-2} \text{ h}^{-1}$ (Table 3.1). Multiplying this value by a 12 hours daylength a rate of $2.1 \text{ g } C \text{ m}^{-2} \text{ d}^{-1}$ is obtained. Given the estimated magnitude of the advection speed ($u = 0.30 \text{ m s}^{-1}$), the vertical section ($S = 4 \times 10^5 \text{ m}^2$) and the surface of the shallow inter-island region ($A = 4 \times 10^8 \text{ m}^2$), an estimate of the maximum flux of zooplankton biomass into the area can be obtained (assuming that all zooplankton advected at night by the free-stream current is retained in the eddy field):

$$S/A(u \times C_z) = 4 \times 10^5 / (4 \times 10^8) \times (0.30 \times 40) = 518 [\text{mg } DW \text{ m}^{-2} \text{ d}^{-1}]$$

where C_z ($= 40$, Table 3.1) is the concentration of zooplankton in the water column at night, expressed as $\text{mg}(\text{dry weight})\text{m}^{-3}$. To compare this amount with the local primary production rate, the dry weight biomass units (DW) can be converted into carbon units (C) by employing the regression equation derived by Wiebe *et al.*, (1975):

$$\log(DW) = 0.508 + 0.977 \log(C)$$

Thus: $\log(C) = [\log(518) - 0.508] / 0.977 = 2.27$, and $C = 186 \text{ mg}$

As during bloom conditions the maximum phytoplankton production is about $2.1 \text{ g } C \text{ m}^{-2} \text{ d}^{-1}$, the grazing impact of this advected zooplankton would be negligible and in the range of 1–5% of the local daily primary production (assuming that zooplankton ingests phytoplankton at a rate of 5–20% of its own biomass each day). However, zooplankton biomass represents carbon units that have been elaborated from at least 10 times the same quantity of phytoplankton. Then, the advected zooplankton is equivalent to a steady-state phytoplankton productivity of at least $1.86 \text{ g } C \text{ m}^{-2} \text{ d}^{-1}$. Hence, the carbon flux into the area due to advection of allochthonous zooplankton *stocks from other areas* (Brown, 1989; Adams and Brown, 1989).

While this hypothetical mechanism may explain the spatio-temporal variations of the zooplankton community in the upstream off-shore region and over the plateau, its effects on the downstream side of the archipelago are not sufficiently resolved because of sampling deficiency in this area. Theoretically, within a time scale larger than the advective time (L/U), the downstream community of vertical migrators should be depleted as a result of the constant predation pressure above the plateau. This is an important hypothesis that needs badly to be tested and could prove decisive in confirming or rejecting the proposed mechanism of nocturnal replenishment/diurnal depletion of zooplankton biomass in the island seas.

Another, and perhaps more important, problem related to this mechanism is represented by the consequences of the Ekman drift on the phytoplankton blooms and the nutrient-rich freshwater retained in the eddy system above the plateau. Even though the wind-induced motion appears to affect only the top 10-20 m of the mixed layer, the removal of phytoplankton biomass and freshwater from the shelf area by this advection may be substantial. Assuming that complete mixing occurs in the upper layer ($Z_{mix} \approx 50$), then about 20-40% of the freshwater run-off (and phytoplankton biomass) would be dissipated downstream of the archipelago within the Ekman advection time-scale ($\approx 0.7 d$). This implies that, to account for the observed level of freshwater and phytoplankton accumulation, the residence time of the water mass above the plateau must be longer than the estimated 12-15 days period, *i.e.*, about 17-25 days. Alternatively, the regular nocturnal invasion of the shelf area by zooplankton must be controlled by a mechanism that does not involve advection in the surface layer.

CHAPTER 4

MESOOZOOPLANKTON SIZE-SELECTIVITY AND GRAZING IMPACT ON THE PHYTOPLANKTON COMMUNITY OF THE PRINCE EDWARD ARCHIPELAGO

4.1 Introduction

The marine ecosystem of the Prince Edward Archipelago (47° S, 38° E) exhibits repeated, seasonal occurrences of phytoplankton blooms, with enhanced primary productivity relative to the surrounding ocean (Allanson *et al.*, 1985; Boden 1988; Perissinotto *et al.*, in press). This high production is related to a form of island mass effect that involves the stability of the surface mixed-layer and the availability of reduced forms of nitrogen nutrients (Perissinotto *et al.*, in press; Chapter 2; Perissinotto *et al.*, 1990). Both features are locally enhanced by high levels of freshwater run-off from the islands.

The fate of these phytoplankton blooms is largely unknown. However, the presence of a rich benthic community in the inter-island plateau, and the abundance of resting spores in the phytoplankton collections (Fryxell *et al.*, 1981), suggests that most of its biomass may be transferred to the benthic subsystem via sedimentation. Another likely pathway, by which the bloom biomass can be utilised by higher trophic levels, is represented by zooplankton grazing in the upper mixed layer. The zooplankton community of the Prince Edward Archipelago is relatively rich and comparable in biomass to that of the Antarctic Polar Front (Boden, 1988; Chapter 3; Perissinotto, 1989). However, in the inter-islands plateau, where most of the phytoplankton blooms are concentrated, the zooplankton is exposed to high predation pressure by part of the large community of marine and land-based visual predators. This results in zooplankton mass depletion (up to 50% decrease in biomass), especially during daytime when the descent of the vertical migrators is

blocked by interaction with the shallow bottom topography of the area (Chapter 3; Perissinotto, 1989).

Preliminary investigations on the zooplankton-phytoplankton relationships in the Prince Edward Archipelago have suggested that utilization of the rich phytoplankton blooms by the pelagic herbivores may be poor or negligible (Perissinotto and Boden, 1989). The present study was designed to test this hypothesis by means of size selectivity experiments and by estimating the grazing impact of the local community of zooplankton on the naturally occurring phytoplankton assemblage.

4.2 Materials and methods

Size selectivity. Naturally occurring phytoplankton was collected with a submersible pump during the MOES-2 (Marion Off-shore Ecosystem Study) cruise of *SA Agulhas* to the Prince Edward Archipelago in autumn 1989 (April/May). As chlorophyll-*a* concentrations were unusually low, phytoplankton collections were concentrated on 0.2 μm Nuclepore filters to an experimental concentration of about 1.5–3.0 $\mu\text{g Chl-}a\text{ l}^{-1}$ (*i.e.*, the normal concentration range for blooms in the area). Three experimental bottles with animals and two control bottles with no animals were filled with the phytoplankton mixture and rotated on a Plankton Wheel ($\approx 1\text{ rpm}$) in the dark, at 9–10 °C for 24 hours. Five euphausiids and 10 copepods were incubated in each 2 *l* or 1 *l* experimental bottle, respectively. Duplicate water samples (100 *ml*) were taken from each bottle at the beginning and end of the incubation for chl-*a* and phaeopigment analysis. Four size fractions of phytoplankton were obtained by multiple serial filtration on a Sartorius Membranfilter column. The fractionation into 200–20, 20–5, 5–1 and 1–0.2 μm was employed for the copepod grazing experiments whereas a fractionation into 200–37, 37–20, 20–1 and 1–0.2 μm was used in the experiments with euphausiids. Pigments from the different filters were extracted overnight at 4 °C in 10 *ml* 90% acetone and concentrations were calculated from the fluorescence readings on a Turner Model 111 fluorometer (Strickland and Parsons, 1968; Conover *et al.*, 1986).

Grazing impact. The estimation of zooplankton community grazing was made by using the eight most important taxa (in terms of biomass) encountered in the area. These included the pteropod *Limacina* sp., the ostracod *Conchoecia* sp., the copepods *Calanus simillimus*, *Clausocalanus brevipes* and *Metridia gerlachei*, and three developmental stages of the euphausiid *Euphausia vallentini* (i.e., adult, calyptopis and furcilia). Two stations of 30 and 36 hours were occupied in the Prince Edward Archipelago during April 1985: station A, located over the Natal Bank, and station B, located midway between Prince Edward and Marion Island (Fig 4.1). In April/May 1989 two other stations (E and F), each of 24 h and corresponding approximately to the sites of 1985, were investigated. Stations A and E are representative of the islands' shelf as they lie within the 100 m isobath, while stations B and F are situated off-shore where the slope falls off very rapidly (Fig 4.1). During 1989, depth profiles of conductivity and temperature were measured at six hour intervals using a Neil Brown MK. III probe, while only XBT profiles were obtained during April 1985. Discrete samples for chlorophyll-*a* analysis were taken every 6–12 h at standard depths (Figs 4.2 and 4.3) with 5 l Niskin bottles. Chlorophyll-*a* concentrations were obtained by the spectrophotometric method of SCOR/UNESCO (1966). Primary production rates were estimated by on-deck incubation (4.5 h) at different light levels of 300 ml samples inoculated with 20–25 μCi of $\text{NaH}^{14}\text{CO}_3$.

The estimation of the community feeding impact (F_I) can be calculated from the equation:

$$F_I = \sum_{i=1}^n (A_i \times I_i), [\text{ng pigm } m^{-3} d^{-1}]$$

where A is the zooplankton abundance in $\text{ind } m^{-3}$, I the ingestion rate in $\text{ng pigm ind}^{-1} d^{-1}$ and the suffix i represents the i^{th} taxon of the zooplankton community. Under the assumption of steady state ($dP/dt = 0$), the ingestion rate is given by the product of ingested pigment, $P(\text{ng pigm ind}^{-1})$, and the gut evacuation rate, $K(d^{-1})$. P is the sum of the pigment measurable in the gut, G , and the undetectable fraction of the pigment that has been absorbed (digested), b . Since

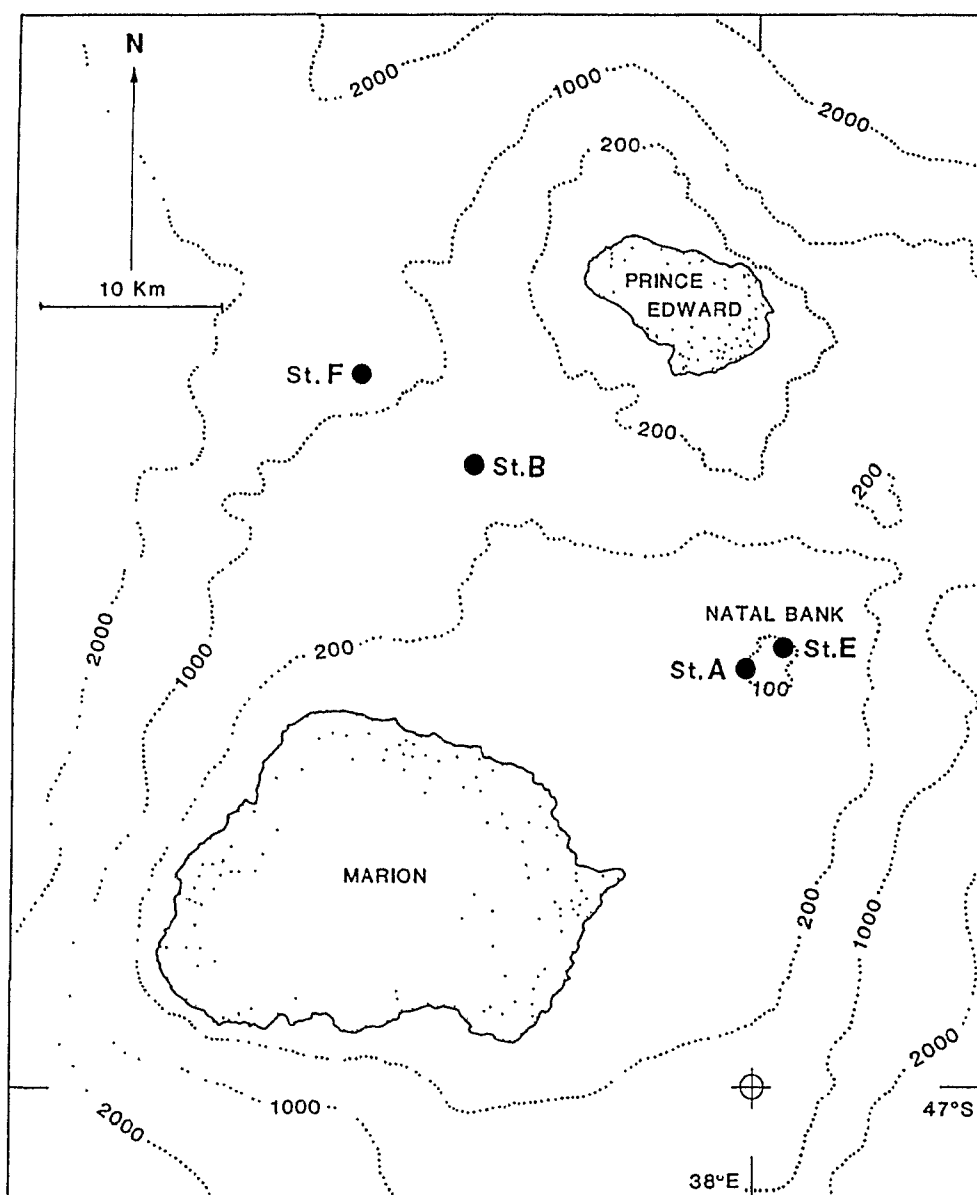


FIGURE 4.1. Position of the sampling stations in the Prince Edward Archipelago. Stations A and B were occupied in April 1985, stations E and F were occupied in April/May 1989. Depth contours are in metres.

b can be expressed as: $b = b' P$, where b' represent a non-dimensional index for the loss of pigment in the digestive process, then substituting the ingestion rate equation can be written as (Wang and Conover, 1986):

$$I = KG/(1 - b')$$

Due to the large variability in zooplankton abundance and feeding activity during a diurnal cycle, integrated values (over a 24 h period) of both gut pigment contents and abundance are probably the most appropriate for the calculation of daily impact:

$$G = 1/t \int_0^{24} g \, dt, \quad A = 1/t \int_0^{24} a \, dt$$

The community feeding impact can then be rewritten as:

$$F_I = \sum_{i=1}^n \frac{(K_i/t)}{(1-b'_i)} \int_0^{24} (a_i \times g_i) \, dt$$

The following is a description of the methods used to estimate the parameters A , G , K , and b' .

Zooplankton abundance (A). Zooplankton was collected at 3 hour intervals by means of oblique Bongo (200 μm mesh) tows to depths of about 200–300 m during the day and 100 m during the night. This sampling schedule was adopted because previous investigations in the area have shown that most of the zooplankton live at depths ≥ 100 m during daytime and migrate to the surface layer during the night (Chapter 3; Perissinotto, 1989; Boden and Parker, 1986). One sample from each tow was preserved with 5% formalin for quantitative abundance analysis, while the second sample was used for measurements of gut pigment content. A closed, 2 litre volume cod-end was fitted to the net selected for the collection of material for gut pigment analysis.

From the preserved samples the major zooplankton taxa were counted in subsamples of 0.1–0.2 of the original samples obtained with the Wiborg's modified whirling apparatus (Kott, 1953). The biomass of individual taxa was estimated from the dry weight (60 °C) of three replicate sets of 50–300 specimens each (depending

upon the size of the taxon considered). The discrete abundance and biomass values were integrated over the 24 h periods by using the trapezoidal approximation.

Gut pigment content (G). Zooplankton for measurement of gut pigment content were sorted immediately after capture. The cod-end content was poured onto a 200 μm sieve from which individuals were gently picked using jewellers forceps (Peterson *et al.*, 1990). Picking was carried out during a period of time of 5–10 min and Peterson *et al.* (1990) have shown that defecation on the sieve does not occur within this time scale. Five to 10 individuals were picked per taxon, placed in a plastic centrifuge tube with 5 ml 90% acetone, homogenised with a glass rod, and stored at -20°C for 12 h. After centrifugation (5000 rpm) the pigment content of the acetone extract was measured with a Turner 111 fluorometer, before and after acidification (Mackas and Bohrer, 1976). The chlorophyll-*a* and phaeopigment contents per animal were calculated using the formulas of Strickland and Parsons (1968) modified by Conover *et al.* (1986):

$$[\mu\text{g Chl-}a \text{ ind}^{-1}] = \{F_d [\tau/(\tau - 1)] (R_b - R_a)\}/n$$

$$[\mu\text{g Phaeo ind}^{-1}] = \{\tau F_d [(\tau R_a - R_b)/(\tau - 1)] \times 0.66\}/n$$

Where F_d is the fluorometer door factor, R_b and R_a are the fluorescence readings before and after acidification respectively; τ is the ration R_a/R_b for pure chlorophyll, n the number of animals per sample and 0.66 is the molecular weight ratio of phaeophorbide-*a* to chlorophyll-*a*.

The gut pigment levels for *C. brevipes*, *M. gerlachei*, *E. vallentini* (adults and furcilia) and *Limacina* sp. were not measured in 1985. However, for the other taxa (*C. similis*, *E. vallentini* calyptopis and *Conchoecia* sp.) data of gut pigment contents were available in both years. For these taxa, differences in pigment levels between the bloom (1985) and non-bloom conditions (1989) were constant, with values always much higher in 1985 than in 1989. Therefore, to estimate gut pigment contents for the species for which these were not available in 1985, conversion factors were used. The community grazing impact for Apr. 1985 was then obtained by

multiplying the gut pigment levels of *C. brevipes*, *M. gerlachei*, *E. vallentini* and *Limacina* sp. measured in 1989 by an average factor of 8.9 for the Natal Bank and 11.7 for the off-shore samples.

Gut evacuation rate (K). Estimates of this parameter were obtained only during April/May 1989. Freshly caught zooplankton was placed into 10 l containers filled with 0.2 μm filtered seawater. As temperature is a very important factor affecting evacuation rate (Dam and Peterson, 1988), containers with experimental animals were kept in a cold room (9–10 °C), at ambient temperature. Gut pigment contents of zooplankton were then monitored throughout time. For all copepods, the ostracod *Conchoecia* sp. and the gastropod *Limacina* sp. measurements were taken for one hour at intervals of 0, 5, 10, 20, 30, 40, and 60 min. The choice of estimating K from frequent measurements during the first hour of starvation was made because it is becoming evident that after this period there are significant differences in gut evacuation rate between starved and continuously feeding animals (Baars and Helling, 1985; Kiørboe and Tiselius, 1987; Dam and Peterson, 1988). Euphausiids tend to retain food in their guts for periods of up to 2 days, unless they are kept under continuous feeding conditions (Willason and Cox, 1987). Thus, to determine their gut evacuation rate, charcoal particles (< 100 μm) were added to the filtered seawater in the experimental containers. The role of these particles is to displace previously ingested food. Gut pigment contents were then monitored for 12 hours at intervals of 0, 0.5, 1, 2, 4, 8 and 12 h after collection. With a constant evacuation rate, the amount of pigment in the gut of zooplankton grazers is related to time without food as:

$$G_t = G_0 \exp(-Kt)$$

Here G_0 and G_t represent the amount of gut pigment measured at the beginning of the starvation period and at time t , respectively. Taking the logarithms, K can be calculated from the plot of gut pigment concentration against time of incubation:

$$K = \ln(G_0/G_t)/t, \quad [h^{-1}]$$

Since no gut evacuation rate measurements were made in April 1985, the values obtained during 1989 were used to calculate the grazing impact for both periods.

Absorbed pigments (b'). Loss of pigments by absorption/destruction was estimated from measurements of decrease in pigment content of grazing bottles and increase in gut pigment levels of animals incubated in these bottles. Animals starved for 6 to 12 h were fed concentrated phytoplankton mixtures ($1.5\text{--}3.0 \mu\text{g l}^{-1}$) in 1 l bottles. Pigments may be lost from the grazing bottles either by digestion to non-fluorescent residues or by disintegration and leakage of faecal pellets. To exclude losses due to disintegration of faeces, incubations were carried out over short times ($< 30 \text{ min}$ for copepods and $< 60 \text{ min}$ for euphausiids) and pigment levels measured before defecation (Dagg, 1983; Kiørboe and Tiselius, 1987). At the end of the incubation, the grazing bottle contents were filtered onto a $60 \mu\text{m}$ Nitex filter to check for faecal production. On no occasion were faeces recorded. Four replicate samples (100 ml) from both experimental and control bottles were filtered onto $0.2 \mu\text{m}$ Nuclepore filters from which pigment levels were measured using the technique outlined above.

Calculations of the fractional loss of pigment, for each taxon examined, were made using the relation:

$$b' (\%) = \{[(G_t - P_b)/P] - 1\} \times 100$$

Where G_t is the gut pigment content ind^{-1} at the end of the incubation, P_b the background fluorescence ind^{-1} and P the total amount of pigment ingested ind^{-1} . P is derived from the difference between control (C_t) and experimental (E_t) bottles, at the end of the incubation, divided by the number of animals in the grazing bottles (n): $P = (C_t - E_t)/n$.

Experiments were carried out with *C. simillimus*, *M. gerlachei* and the three stages of *E. vallentini*. The percentage of pigments absorbed (digested) during the digestive process in *C. brevipes*, *Conchoecia* sp. and *Limacina* sp. was assumed to be equal to the average of the values derived from the conversion efficiency

measurements on the other four taxa (Table 4.4). This assumption was based on the fact that the percentage of lost pigments seems to be independent of the type of grazer (Dam and Peterson, 1988).

4.3 Results

Size selectivity. During April/May 1989 the phytoplankton community of the Prince Edward Archipelago was dominated by the nano-size fraction ($20-100 \mu\text{m}$), which represented $50.2 \pm 2.8\%$ of the total Chlorophyll-*a*. The net- ($200-2000 \mu\text{m}$) and picoplankton ($1-0.2 \mu\text{m}$) constituted 35.8 ± 6.3 and $14.3 \pm 3.1\%$ of the total, respectively. The major components of the zooplankton community showed a preferential selection for the nano-size fractions (Table 4.1).

Of the five zooplankton species used in the experiments (the copepods *Calanus simillimus* and *Metridia gerlachei* and the euphausiids *Euphausia vallentini*, *E. similis* var. *armata* and *Thisanoessa vicina*) only two euphausiids, *E. vallentini* and *T. vicina*, appeared to have a significant impact on the smaller net-phytoplankton ($37-200 \mu\text{m}$).

Grazing impact. In April/May 1985, Chlorophyll-*a* concentrations attained values that are indicative of bloom conditions in the area. Typically, on the Natal Bank, surface levels were $> 2 \text{ mg m}^{-3}$, while at the off-shore station the highest values were about half of this amount (Fig 4.2). Such a difference between the two stations is reflected in the depth of the thermocline, $\approx 30-40 \text{ m}$ and $\approx 80-100 \text{ m}$ on the Natal Bank and offshore, respectively (Fig 4.2). Conversely, no difference in chlorophyll-*a* concentration between the two stations was evident during April/May 1989 and low values ($< 0.3 \text{ mg m}^{-3}$) were recorded at both sites (Fig 4.3). The thermocline was deeper than in 1985 and positioned at $\approx 60-70 \text{ m}$ on the Natal Bank and at $\approx 90-110 \text{ m}$ off-shore (Fig 4.3). Phytoplankton production during the two investigations followed the same pattern described for chlorophyll-*a*. In 1985, maximum values of ^{14}C uptake by the phytoplankton community was between 0.7

Table 4.1. t-Test (independent samples) on the size selectivity of naturally occurring phytoplankton by the most important components of the zooplankton community of the Prince Edward Island seas (April 1989). Control and experimental values are expressed as mean $\pm$ standard deviation. n.s. = not significant.

Size Fract. (μm)	Control ($\mu\text{g pigm l}^{-1}$)	Experim. ($\mu\text{g pigm l}^{-1}$)	t-Stat.	Signif. (p)	N (<i>pooled</i>)
<i>Thysanoessa vicina</i>					
200-37	0.56 ± 0.16	0.50 ± 0.17	0.45	n.s.	12
37-20	0.45 ± 0.03	0.27 ± 0.05	7.01	0.001	12
20-1	3.19 ± 0.54	1.69 ± 0.88	2.74	0.021	12
1-0.2	0.43 ± 0.21	0.60 ± 0.34	1.83	n.s.	12
<i>Euphausia vallentini</i>					
200-37	0.47 ± 0.03	0.33 ± 0.09	3.06	0.012	12
37-20	0.33 ± 0.08	0.17 ± 0.08	3.17	0.001	12
20-1	1.85 ± 0.35	1.13 ± 0.34	3.43	0.003	12
1-0.2	0.54 ± 0.32	0.32 ± 0.29	1.20	n.s.	12
<i>E. similis</i> var. <i>armata</i>					
200-20	0.29 ± 0.12	0.30 ± 0.05	0.38	n.s.	16
20-5	0.30 ± 0.09	0.16 ± 0.07	3.35	0.009	16
5-1	0.29 ± 0.15	0.31 ± 0.18	0.31	n.s.	16
1-0.2	0.22 ± 0.10	0.19 ± 0.07	0.61	n.s.	15
<i>Calanus simillimus</i>					
200-20	0.52 ± 0.07	0.50 ± 0.06	0.56	n.s.	16
20-5	0.45 ± 0.08	0.21 ± 0.17	3.66	0.048	16
5-1	0.26 ± 0.05	0.16 ± 0.04	4.15	0.001	16
1-0.2	0.18 ± 0.06	0.14 ± 0.07	1.18	n.s.	16
<i>Metridia gerlachei</i>					
200-20	0.55 ± 0.04	0.47 ± 0.14	1.52	n.s.	18
20-5	0.39 ± 0.12	0.20 ± 0.11	3.38	0.018	18
5-1	0.38 ± 0.24	0.35 ± 0.27	0.21	n.s.	18
1-0.2	0.13 ± 0.07	0.23 ± 0.16	1.61	n.s.	18

(off-shore) and $1.2 \text{ mg C m}^{-3} \text{ h}^{-1}$ (Natal Bank), while in 1989 values never exceeded $0.4 \text{ mg C m}^{-3} \text{ h}^{-1}$ (Figs 4.2 and 4.3).

Zooplankton abundance. The eight mesozooplankton taxa considered in the estimation of the community grazing impact are usually among the most abundant in the area (Boden and Parker, 1986; Chapter 3; Perissinotto, 1989). During the investigations these eight taxa together constituted 25–50% in number, and 62–78% by weight (*DW*) of the total catch (Table 4.2). On both occasions the group was numerically dominated by *C. simillimus*, while *E. vallentini* (all stages combined) was always the largest contributor to total biomass. During April 1989, abundances were generally higher than in 1985. Values recorded on the former investigation were up to 3.5 times (*C. simillimus*) those found in April 1985. Apart from *Limacina* sp. and *C. brevipes*, all the other taxa were present in higher concentrations at the off-shore stations than on the Natal Bank (Table 4.2).

Gut pigment content. All zooplankton taxa showed diel feeding rhythms at both stations and during both years (Figs 4.4 and 4.5). The pattern of variation in gut pigments during the 24 h cycles appeared to be predominantly unimodal, but in a few cases (*Conchoecia* sp., 1985; *E. vallentini*-adults, 1989; *Limacina* sp., 1989) some evidence of bimodality was also recorded. The highest gut pigment levels were always found at night, but while on the Natal Bank the peak values occurred in the earlier night hours (18.00–22.00), in off-shore waters there was a consistent time-lag and gut pigment maxima were shifted to the pre-dawn period (01.00–04.00 h). In most cases during 1989, zooplankton had higher average gut pigment contents on the Natal Bank than in off-shore waters (Fig 4.5). This pattern however, was not evident in the results of the 1985 investigation (Fig 4.4). Within the same taxa, large differences were observed in the levels of gut pigment between the period of phytoplankton bloom (April 1985) and the non-bloom conditions (April/May 1989). The largest difference was recorded for the ostracod *Conchoecia* sp. which during 1985 showed pigment concentrations 16–22 times higher than in 1989. For *C. simillimus* and *E. vallentini*-calyptopis differences between the two periods ranged

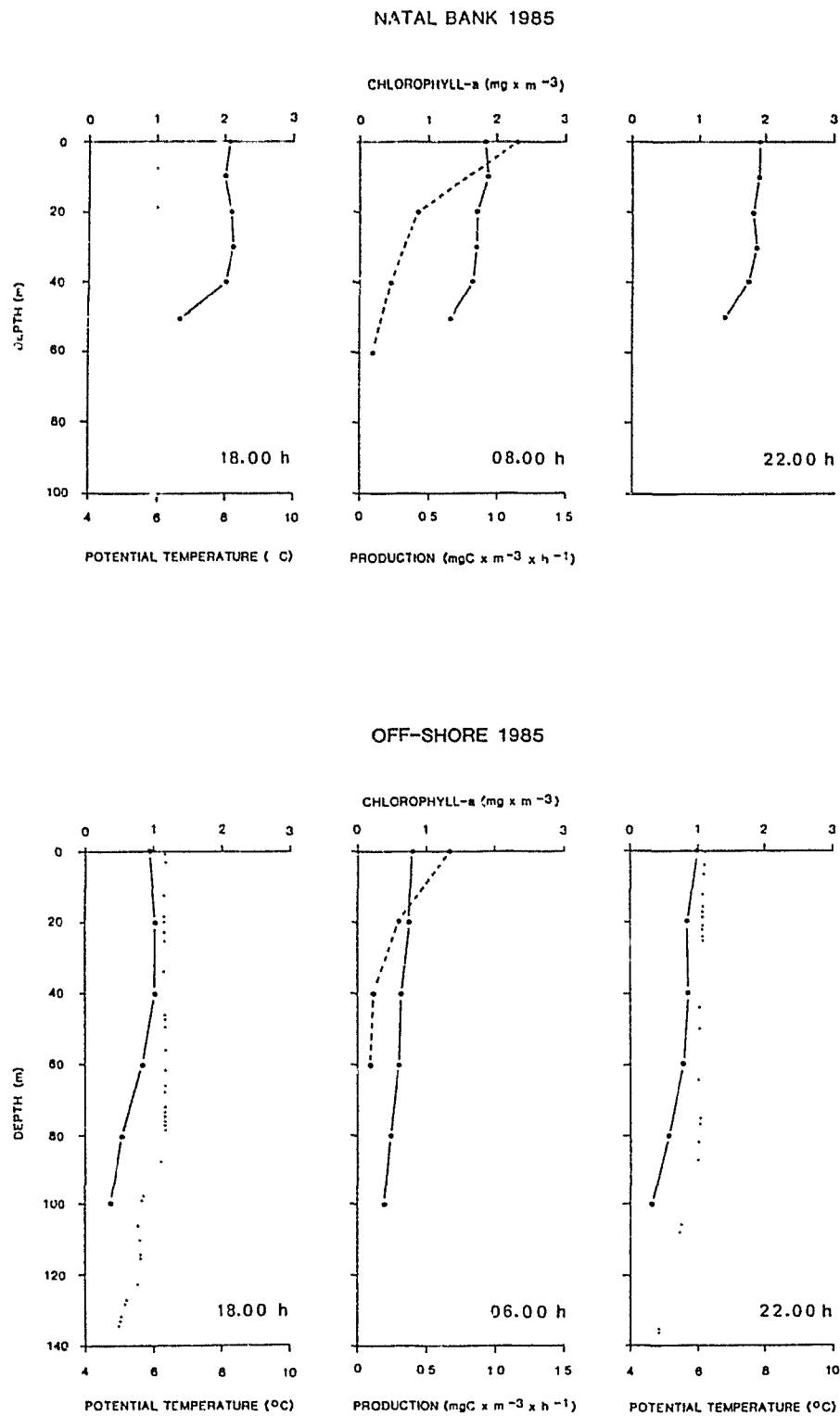
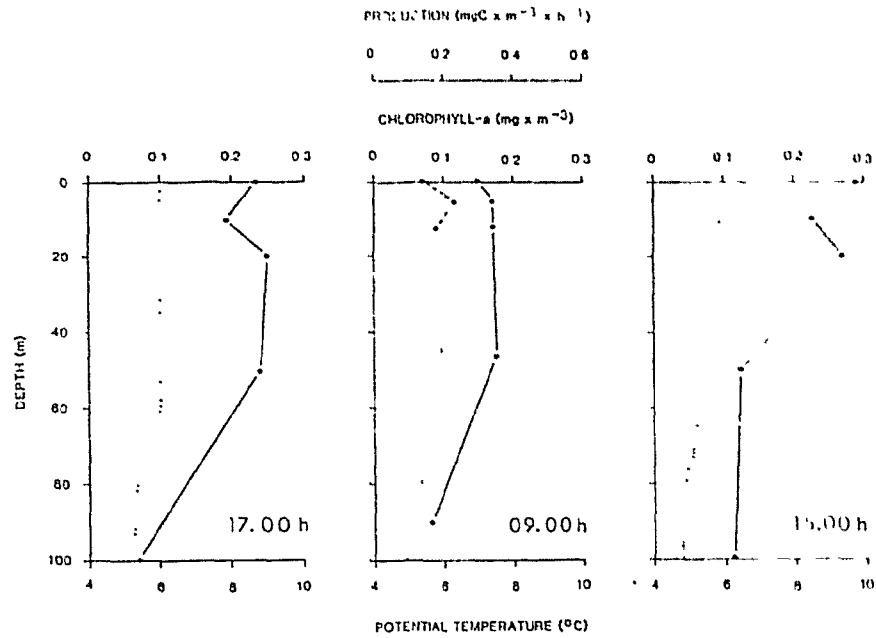


FIGURE 4.2. Vertical profiles of temperature (dotted line), chlorophyll-*a* (solid line) and phytoplankton production (broken line) for the April 1985 survey.

NATAL BANK 1989

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OFF-SHORE 1989

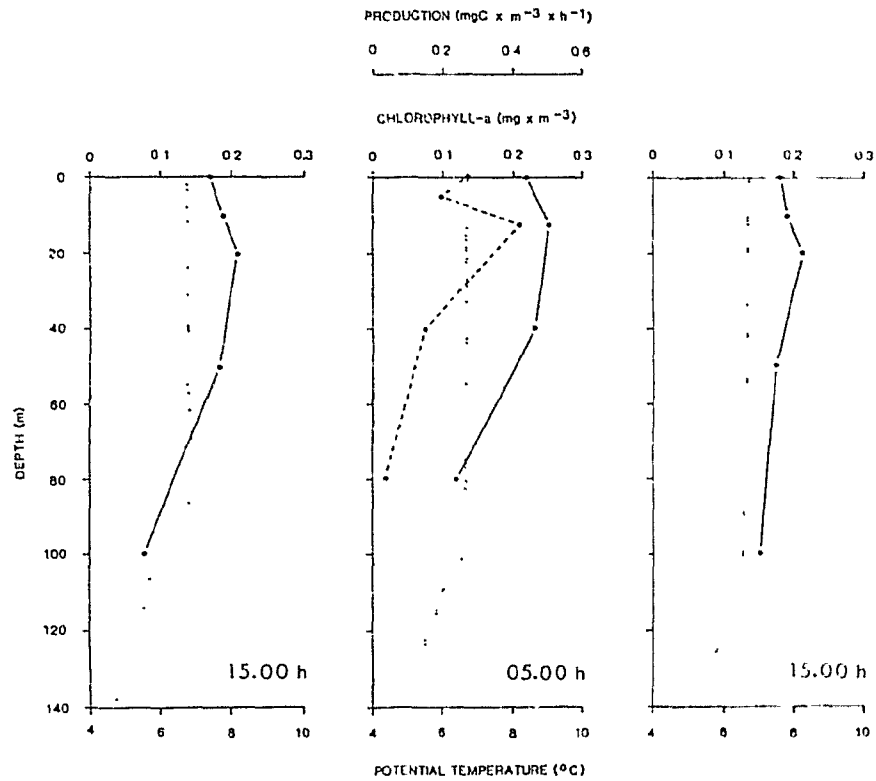


FIGURE 4.3. Vertical profiles of temperature (dotted line), chlorophyll-*a* (solid line) and phytoplankton production (broken line) for the April/May 1989 survey.

Table 4.2. Abundance estimates of the most important components of the mesozooplankton community during the two periods of investigation. All values are integrated over a period of 24 h. DA = daily numerical abundance ($ind\ m^{-3}\ d^{-1}$), DB = daily biomass ($mg\ DW\ m^{-3}\ d^{-1}$), %A = percentage by number of the total, %B = percentage by weight (DW) of the total.

Taxon	Natal Bank 1985				Off-shore 1985				Natal Bank 1989				Off-shore 1989			
	DA	%A	DB	%B	DA	%A	DB	%B	DA	%A	DB	%B	DA	%A	DB	%B
<i>Sagitta</i> sp.	221	6.1	66	15.8	346	6.3	104	14.5	181	4.4	54	7.0	328	7.1	98	7.2
<i>Calanus simillimus</i>	273	7.6	76	18.2	402	7.3	113	15.7	862	20.9	241	31.1	1055	23.0	295	21.6
<i>Rhincalanus gigas</i>	25	0.7	13	3.1	77	1.4	39	5.4	17	0.4	9	1.2	67	1.5	34	2.5
<i>Clausocalanus brevipes</i>	213	5.9	38	9.1	124	2.3	22	3.1	130	3.1	23	3.0	96	2.1	18	1.3
<i>Microcalanus pygmaeus</i>	1032	28.7	18	4.3	2865	52.0	52	7.2	883	21.4	16	2.1	1559	34.0	28	2.0
<i>Eucalanus longipes</i>	14	0.4	5	1.2	32	0.6	10	0.1	8	0.2	3	0.4	44	1.0	14	1.0
<i>Metridia gerlachei</i>	121	3.4	36	8.6	270	4.9	81	11.3	139	3.4	42	5.4	187	4.1	56	4.1
<i>Oithona</i> spp.	1341	37.3	21	5.0	806	14.6	13	1.8	241	5.8	4	0.5	151	3.3	3	0.2
<i>Euphausia vallentini</i> ad.	12	0.3	22	5.3	29	0.5	53	7.4	38	0.9	69	8.9	96	2.1	176	12.9
<i>E. vallentini</i> calypt.	47	1.3	46	11.0	88	1.6	86	12.0	114	2.8	112	14.5	194	4.2	190	13.9
<i>E. vallentini</i> furc.	38	1.1	17	4.1	76	1.4	35	4.9	116	2.8	53	6.8	210	4.6	97	7.1
<i>E. similis</i> var. <i>armata</i>	3	0.1	6	1.4	12	0.2	25	3.5	12	0.3	25	3.2	72	1.6	152	11.1
<i>Thisanoessa vicina</i>	6	0.2	10	2.4	18	0.3	30	4.2	37	0.9	61	7.9	80	1.7	133	9.7
<i>Conchoecia</i> sp.	113	3.1	15	3.6	255	4.6	33	4.6	124	3.0	16	2.1	302	6.6	39	2.9
<i>Limacina</i> sp.	134	3.7	28	6.7	107	1.9	23	3.2	221	5.4	46	5.9	138	3.0	30	2.2

from 5 to 9 and from 3 to 5 times, respectively (Figs 4.4 and 4.5). The average difference for the three pooled taxa was between 8 and 12 times for the Natal Bank and the off-shore stations, respectively.

Gut evacuation rate. In all cases, negative exponential models (Table 4.3) provided the best fit to the decline in gut pigment contents during the non-feeding period. The highest evacuation rate constants (K) were found for the three copepod species with values of 1.96, 1.75 and 1.41 h^{-1} for *C. simillimus*, *M. gerlachei* and *C. brevipes*, respectively. The corresponding gut turnover times (reciprocal of K) were 0.51, 0.57 and 0.71 h . All the other taxa had much longer gut turnover times (i.e., $K < 1$, Table 4.3).

Absorbed pigments. Percentage-conversion efficiency calculated for the three developmental stages of *E. valleritini*, and the copepods *C. simillimus* and *M. gerlachei*, ranged from a minimum of $\approx 52\%$ to a maximum of $\approx 70\%$ of total pigment ingested (Table 4.4). Therefore, the amount of pigment lost during the digestive process was between 30 and 48% of the total. The copepods had the lowest while all stages of *E. valleritini* had the highest levels of digestive loss (Table 4.4). Differences were however not significant (t-test, $p > 0.05$).

Community grazing impact. During the phytoplankton bloom of April 1985 the ingestion rate of the zooplankton community investigated varied between 86.2 (Natal Bank) and 123.6 (off-shore) $\mu g \text{ pigm } m^{-3} d^{-1}$ (Table 4.5). Contributions of individual taxa (for Natal Bank and off-shore, respectively) were highest for *Limacina* sp.: 27.4 and 26.1%. The second most important grazer was *C. simillimus* with 25.0 and 21.2% of total pigment ingested. The whole community examined had a grazing impact of only 4.9% and 9.9% of the euphotic zone-integrated phytoplankton biomass (Table 4.5). For the same stations, the impact on the integrated phytoplankton production was 8.8 and 17.4%, respectively. The community grazing impact was much higher during April/May 1989 (Table 4.5). On this occasion the eight zooplankton taxa consumed 33.4 (Natal Bank) to 47.7% (off-shore) of the

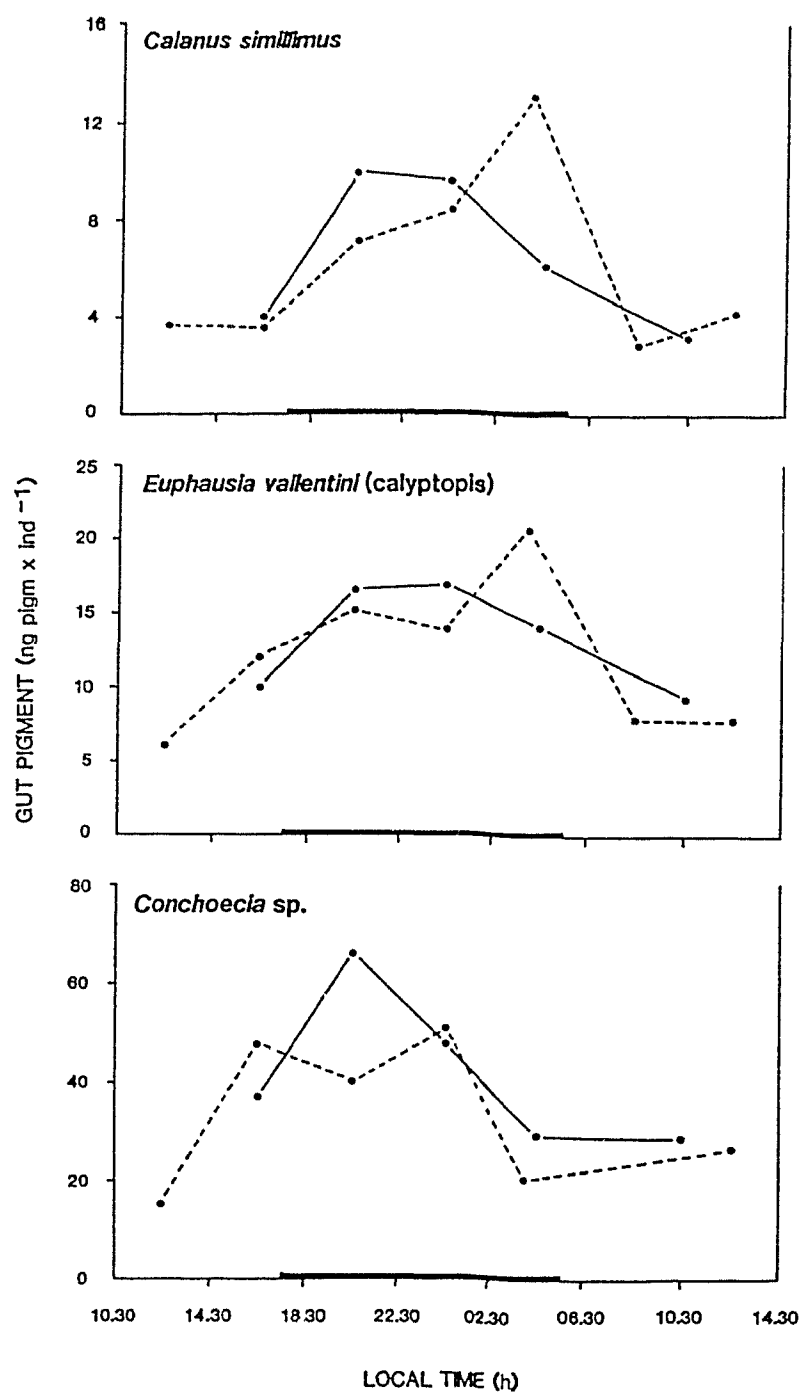


FIGURE 4.4. Diurnal variations in total gut pigment levels per individual zooplankter on the Natal Bank (solid line) and off-shore (broken line) during April 1985. Period of darkness is indicated by thickening of the horizontal axis.

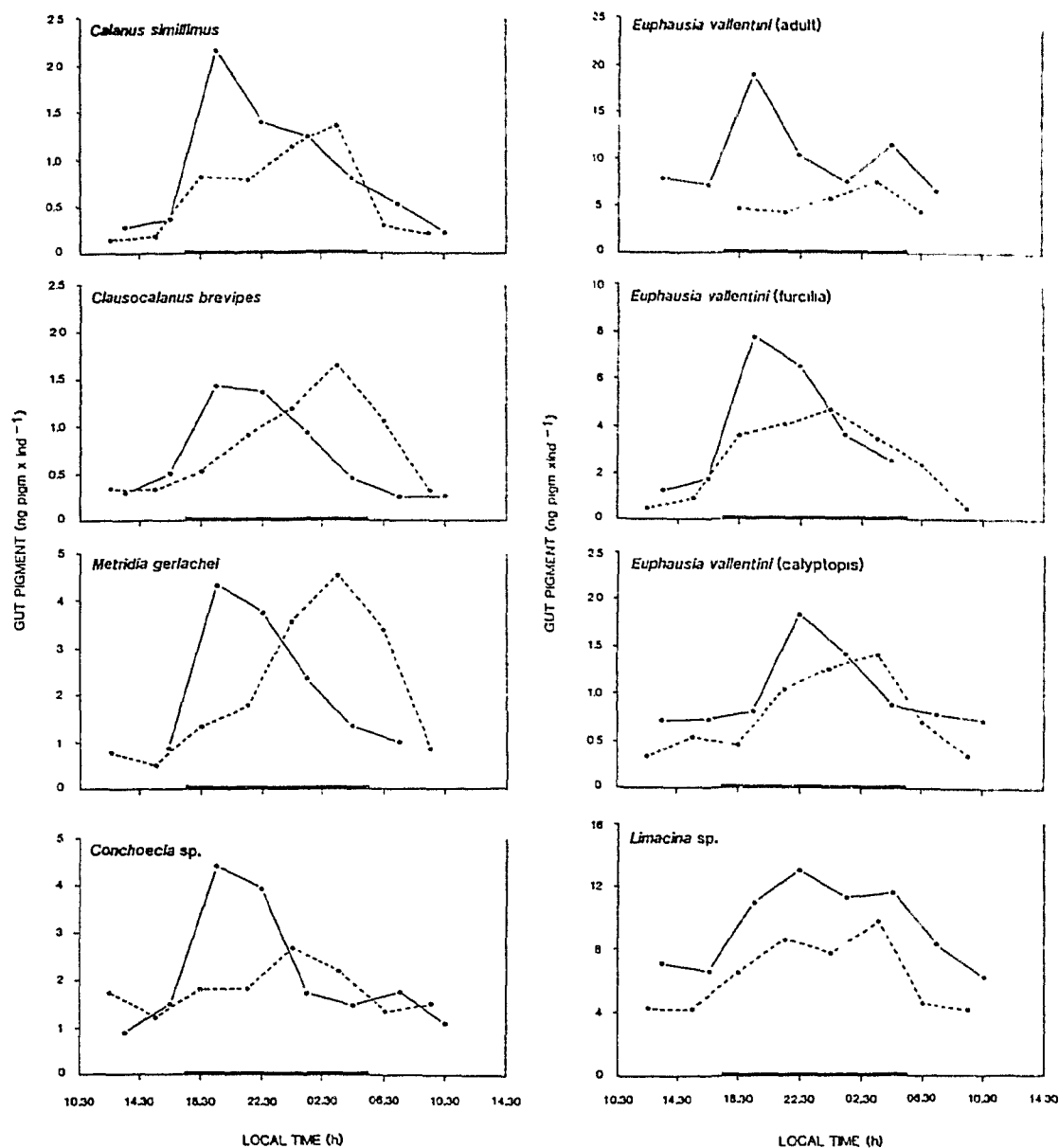


FIGURE 4.5. Diurnal variations in total gut pigment levels per individual zooplankter on the Natal Bank (solid line) and off-shore (broken line) during April/May 1989. Period of darkness is indicated by thickening of the horizontal axis.

Table 4.3. Exponential models of the gut evacuation rate for the zooplankton taxa investigated at the Prince Edward Islands (April/May 1989). K = gut evacuation rate constant.

Taxon	Model fit	N	R^2	$K(h^{-1})$
<i>Calanus simillimus</i>	$Y = \exp(0.77 - 0.03)$	14	0.85	1.96
<i>Clausocalanus brevipes</i>	$Y = \exp(-7.67 - 0.02)$	14	0.77	1.41
<i>Mutridia gerlachei</i>	$Y = \exp(2.17 - 0.03)$	14	0.93	1.75
<i>Euphausia vallentini</i> ad.	$Y = \exp(1.35 - 1.70)$	14	0.91	0.59
<i>E. vallentini</i> cal.	$Y = \exp(1.30 - 1.24)$	14	0.91	0.68
<i>E. vallentini</i> fur.	$Y = \exp(0.45 - 1.67)$	14	0.79	0.81
<i>Limacina</i> sp.	$Y = \exp(6.77 - 0.01)$	20	0.68	0.98
<i>Conchoecia</i> sp.	$Y = \exp(0.46 - 0.01)$	20	0.62	0.97

Table 4.4. Estimation of the molar conversion efficiency of chlorophyll-*a* to phaeophorbide-*a* for some of the taxa investigated during April/May 1989. All values are expressed as mean $\pm$ standard deviation.

Taxon	Gut pigm. content	Pigm. ingested	Conversion
	<i>ng pigm ind</i> ⁻¹	<i>ng pigm ind</i> ⁻¹	efficiency (%)
<i>Calanus simillimus</i>	1.69 $\pm$ 0.34	2.38 $\pm$ 0.19	70.3 $\pm$ 8.7
<i>Metridia gerlachei</i>	1.87 $\pm$ 0.55	2.82 $\pm$ 0.31	65.0 $\pm$ 12.4
<i>Euphausia vallentini</i> ad.	3.15 $\pm$ 1.18	5.62 $\pm$ 0.48	54.7 $\pm$ 16.3
<i>E. vallentini</i> cal.	2.73 $\pm$ 0.73	5.17 $\pm$ 0.93	51.8 $\pm$ 5.7
<i>E. vallentini</i> fur.	2.87 $\pm$ 0.84	4.87 $\pm$ 0.58	57.7 $\pm$ 10.4

phytoplankton biomass and 75.6 to 81.3% of primary production per day. The most important contributor to the daily ingestion in this case was *C. similis* which alone accounted for 40.2 and 33.0% of the total.

4.4 Discussion

The results of the size-selectivity experiments show that all zooplankton taxa select preferentially the nanoplankton, while only the euphausiids *Euphausia valleroni* and *Thysanoessa vicina* also have positive selection for the net size-class (Table 4.1). These experiments were carried out in April/May 1989, when no phytoplankton blooms occurred in the area. During this period the nanoplankton was also the dominant fraction of the phytoplankton biomass with $\approx 50\%$ of the total, followed by net- ($\approx 36\%$) and picoplankton ($\approx 14\%$). Therefore, the observed positive selection of zooplankton for the nano size-class may suggest a case of preferential feeding on the biomass peak. However, feeding models of passive selection based on particle size and abundance have been largely dismissed (Koehl and Strickler, 1981; Huntley *et al.*, 1983; Stuart, 1989) and seem to apply only to mixtures where there are no differences in food quality between particles (Conover and Mayzaud, 1984). Also, other investigations in the Prince Edward Islands area have suggested that even during phytoplankton blooms, when the net-phytoplankton constitutes the biomass peak, a positive selection for the smaller size fractions persists (Perissinotto and Boden, 1989). The typical size structure of the cells during a bloom, such as the one investigated in 1985, shows that $\approx 80\%$ of total biomass is represented by net-plankton, while nanoplankton accounts for only $\approx 20\%$ of the total (El Sayed *et al.*, 1979; Perissinotto and Boden, 1989).

Inefficient utilization of bloom phytoplankton is corroborated by the comparative study of zooplankton grazing during bloom and non-bloom conditions. Estimated grazing rates, for the eight zooplankton taxa here examined, show that when phytoplankton biomass is low zooplankton ingests an amount of chlorophyll-*a* per day equivalent to 33–48% of the average concentration in the euphotic zone,

Table 4.5. Feeding impact of the mesozooplankton community at the Prince Edward archipelago. DI = daily ingestion rate ($\mu\text{g pigm m}^{-3} \text{ d}^{-1}$), PB = phytoplankton biomass, PP = phytoplankton production.

Taxon	Natal Bank 1985			Off-shore 1985			Natal Bank 1989			Off-shore 1989		
	DI	%PB	%PP	DI	%PB	%PP	DI	%PB	%PP	DI	%PB	%PP
<i>Calanus simillimus</i>	21.8	1.2	2.2	26.2	2.1	3.7	19.6	13.4	30.4	26.0	15.7	26.7
<i>Clausocalanus brevipcs</i>	2.9	0.2	0.3	3.2	0.3	0.5	1.0	0.7	1.6	2.2	1.3	2.3
<i>Metridia gerlachei</i>	11.1	0.6	1.1	17.1	1.4	2.4	6.4	4.4	9.9	14.3	8.6	14.7
<i>Euphausia vallentini</i> ad.	11.7	0.7	1.2	18.6	1.5	2.6	8.3	5.7	12.9	10.3	6.2	10.6
<i>E. vallentini</i> calypt.	4.7	0.3	0.5	10.5	0.8	1.5	2.8	1.9	4.3	4.0	2.4	4.1
<i>E. vallentini</i> furc.	3.8	0.2	0.4	3.7	0.3	0.5	2.1	1.4	3.3	1.6	1.0	1.6
<i>Conchoecia</i> sp.	6.6	0.4	0.7	11.9	0.9	1.7	1.6	1.1	2.5	2.3	1.4	2.4
<i>Limacina</i> sp.	23.6	1.3	2.4	32.3	2.6	4.6	6.9	4.7	10.7	18.5	11.2	19.0
Total community	86.2	4.9	8.8	123.6	9.9	17.4	48.7	33.4	75.6	79.0	47.7	81.3

or 76–81% of daily primary production (Table 4.5). However, during conditions of phytoplankton bloom the zooplankton grazing impact becomes small and only 5 to 10% of the chlorophyll-*a* concentration, or 9 to 17% of daily primary production, is consumed per day.

Although not all numerically dominant zooplankton taxa were included in this grazing budget, the proportion examined accounts for ≈ 75 –85% of the total biomass of the community of herbivores and omnivores of the Prince Edward Archipelago (Table 4.2). The tiny *Microcalanus pygmaeus* and *Oithona* spp. were the most numerous copepods, especially during April 1985, but in terms of biomass they represented together only 3–10% of the total. Also, their size suggests that they would, in any event, be unable to ingest the large phytoplankton cells and chains that form the bulk of the blooms.

It could be argued that a more serious source of error, affecting the calculated grazing impact, may be due to the lack of measurements of clearance rate constants in the zooplankton of April 1985. Indeed, while in April/May 1989 estimates of grazing impact were made by *in situ*, simultaneous determination of zooplankton gut evacuation rates, pigment contents and absorption levels (as recommended by Wang and Conover, 1986 and Daggs and Walser, 1987), no measurements of gut evacuation rates were carried out in 1985. The response of zooplankton gut evacuation rates to changes in ambient food concentration is still largely undetermined (Wang and Conover, 1986; Head and Harris, 1987). However, there is some evidence that the residence time of food in the gut may decrease (*i.e.*, evacuation rate increases) as food concentration increases (Daggs and Walser, 1987; Tsuda and Nemoto, 1987). Thus, in this study, by using the clearance rate constants obtained in 1989 (low chl-*a* levels) to calculate the grazing rates for April 1985 (bloom conditions), the values of community impact for the latter occasion could have been significantly underestimated. Nevertheless, even by assuming that the gut evacuation rates during the bloom were twice as high as during the non-bloom conditions (*i.e.*, feeding rate values were doubled), the resulting community grazing impact would

still be low.

Another aspect that must be considered, in the comparison between bloom and non-bloom conditions, is the variation in zooplankton abundance and biomass between the two different occasions. During 1989, when chlorophyll-*a* concentration was very low, the biomass of the eight zooplankton taxa examined was approximately two times higher than during the bloom of 1985. Year to year variations in zooplankton biomass of this magnitude have been recorded on several occasions in the Prince Edward Archipelago (Allanson *et al.*, 1985; Boden and Parker, 1986). Thus, the low grazing impact measured during the bloom condition may have been partly due to an unusually poor zooplankton abundance. Then, standardizing the grazing rates measured during April 1985 by the zooplankton biomass of 1989 (*i.e.*, multiplying the grazing impact by a factor of two), the community impact during the bloom would increase to ≈ 10 –20% of chl-*a* concentration and 18–34% of daily primary production. Therefore, even in this case it appears that the major portion of the blooms would not be utilized by the pelagic herbivores.

Thus, both size-selectivity results and estimates of community grazing indicate that the phytoplankton blooms occurring in the Prince Edward Archipelago may not represent a favourable food environment for the local zooplankton. This apparent paradox requires some considerations on the structure of the phytoplankton community of these blooms and on the feeding habits of the major zooplankton groups found in the area.

The dominance of net size cells in the phytoplankton blooms of the island seas is due to the presence of large concentrations of chains of *Chaetoceros* spp. or long cells of *Rhizosolenia* spp. (Table 4.6). Blooms of *C. radicans* in the Prince Edward Archipelago have been repeatedly found during April 1976 (El Sayed *et al.*, 1979), May and November 1983 (Allanson *et al.*, 1985) and April/May 1987 (Boden, 1988). A bloom of *C. neglectum* was recorded in March 1981 (Fryxell *et al.*, 1981) while *R. curvata* was found in bloom stage during May 1983 (Allanson *et al.*, 1985). Bloom concentrations of the silicoflagellate *Dictyocha speculum* were also

found in November 1983 (Boder, 1988). This typical composition is well reflected in the structure of the phytoplankton bloom investigated in April 1985 (Table 4.6). An account of the available information on zooplankton feeding response to the qualitative characteristics of this food source is given below.

Limacina sp. like all thecosomatous pteropod molluscs is a ciliary-mucus feeder ingesting primarily phytoplankton, although larger species also capture planktonic protozoa including tintinnids, foraminifera and radiolarians (Gilmer, 1974). Particles less than 5 μm account for the largest percentage by number of all food particles. Ingestion of larger particles appears to be limited by the dimensions of the ciliated grooves through which the food must pass to enter the mouth (Gilmer, 1974). Thus, it seems unlikely that *Limacina* sp. can effectively ingest large cells like *Rhizosolenia* spp. or the long, spiny chains of *Chaetoceros* spp. that dominate the phytoplankton community of the Prince Edward Islands. Indeed, Morton (1954) reported that large cells of *Chaetoceros* with long bristles were rejected as unwieldy by *L. helicoidea* in Antarctic waters.

The most important copepods of the zooplankton community of the Prince Edward Island seas are *Calanus simillimus*, *Clausocalanus brevipes* and *Metridia gerlachei* (Table 4.2). *C. simillimus* and *C. brevipes* belong to families (Calanidae and Pseudocalanidae) which are well known for their ecological importance as phytoplankton grazers, while *M. gerlachei* is an omnivorous feeder (Schnack, 1983). In incubation experiments, copepods feeding on naturally occurring phytoplankton tend to ingest preferentially the dominant size-class (biomass peak) regardless of size (Poulet, 1974; Conover, 1978; Huntley, 1981). Selective feeding on the larger particles has also been observed, especially in artificial mixture of particles (Haq, 1967; Frost, 1977; Gifford *et al.*, 1981). However, it has been shown that copepods are able to select particulate food according to its quality and can discriminate particles after collection by either ingesting or rejecting them (Poulet and Marsot, 1978; Donaghay and Small, 1979; Koehl and Strickler, 1981; Huntley *et al.*, 1983). A number of studies have indicated that the phytoplankton taxa which dominate

Table 4.6. Phytoplankton taxa encountered during April 1985 in the Prince Edward Archipelago. D: dominant, A: abundant, C: common, R: rare. NB = Natal Bank, OS = Off-shore.

Taxon	NB	OS	Taxon	NB	OS
Diatoms			<i>Navicula distans</i>	R	-
<i>Psammodiscus nitidus</i>	R	-	<i>Pleurosigma directum</i>	C	C
<i>Thalassiosira eccentrica</i>	C	A	<i>Trepidoneis antarctica</i>	R	
<i>T. leptopus</i>	R	-	<i>Pseudoeunotia doliolus</i>	R	-
<i>Corethron criophilum</i>	C	C	<i>Cylindrotheca closterium</i>	C	R
<i>Leptocylindrus danicus</i>	C	R	<i>Nitzschia seriata</i>	C	C
<i>Coscinodiscus</i> sp.	A	A	<i>N. pelagica</i>	R	
<i>Asteromphalus heptactis</i>	R	-	<i>N. delicatissima</i>	C	R
<i>Dactyliosolen antarcticus</i>	C	R	<i>N. lineata</i>	A	R
<i>Guinardia flaccida</i>	-	C	<i>N. kerguelensis</i>	C	
<i>Rhizosolenia alata</i>	C	A			
<i>R. alata</i> f. <i>indica</i>	R	R	Dinoflagellates		
<i>R. alata</i> f. <i>gracillima</i>	-	C	<i>Prorocentrum micans</i>	C	C
<i>R. curvata</i>	A	A	<i>P. dentatum</i>	C	R
<i>R. delicatula</i>	R	C	<i>P. scutellum</i>	C	R
<i>R. stolterfothii</i>	R	A	<i>P. gracile</i>	R	-
<i>Bacteriastrum</i> sp.	R	-	<i>Dinophysis ovum</i>	R	-
<i>Chaetoceros affinis</i>	-	R	<i>Dinophysis</i> sp.	-	C
<i>C. atlanticus</i>	A	C	<i>Gymnodinium</i> sp.	C	C
<i>C. criophilus</i>	R	-	<i>G. arcticum</i>	R	
<i>C. didymus</i>	C	R	<i>Protoperidinium breve</i>	-	R
<i>C. didymus</i> v. <i>protuberans</i>	R	-	<i>P. depressum</i>	R	R
<i>C. peruvianus</i>	C	A	<i>Ceratium fusus</i>	R	
<i>C. radicans</i>	D	A	<i>C. tripos</i>	R	C
<i>C. socialis</i>	R	-	<i>C. pentagonum</i>	R	R
<i>Dytilum sol</i>	R	C	<i>C. furca</i>	C	C
<i>Delphineis karstenii</i>	R	-	<i>Oxytoxum mitra</i>	R	R
<i>Fragilaria granulata</i>	C	C	<i>O. variabile</i>	R	-
<i>Striatella delicatula</i>	-	R	<i>Poella ampas bipes</i>	R	-
<i>Synedra indica</i>	R	C	<i>P. elegans</i>	R	
<i>S. ossiformis</i>	R	-			
<i>Thalassionema nitzschioides</i>	-	C	Silicoflagellates		
<i>Thalassiotrix longissima</i>	A	A	<i>Dictyocha speculum</i>	A	R

the blooms in the Prince Edward Islands are usually rejected by pelagic copepods. Although some degree of copepod grazing on *Chaetoceros* spp. has been shown (Longhurst, 1967; Poulet, 1974; Schnack, 1979, 1985), these diatoms are often not readily consumed because their thick spiny filaments act as a deterrent (Parsons *et al.*, 1967; Hargrave and Geen, 1970; Corkett and McLaren, 1978; Voronina and Sukhanova, 1977; Schnack *et al.*, 1985). *C. radicans*, the most common species around the Prince Edward Islands, forms long chains (up to 2000 μm) and even mats, and has one of the thickest spine structure in the genus. Similarly, although some small species of *Rhizosolenia* can be ingested (Conover, pers. comm.), these diatoms are usually poorly represented in the gut contents of pelagic copepods and not eaten in selective feeding experiments (Haq, 1967; Bogorov, 1967; Marshall, 1973). Cells of *R. curvata* are very long (up to 700 μm), cylindrical and often aggregate in chains or "rafts" of individuals of varying size. The cell wall is robust and moderately silicified (Boden and Reid, in press). The silicoflagellate *D. speculum* has an internal skeleton of conspicuous siliceous spicules and like all silicoflagellates is not known to be a staple component of copepod diets (Marshall, 1973; Raymont, 1983).

During April/May 1989, the euphausiids were the only group among the zooplankton examined to show a preferential selection for net-phytoplankton, as well as nanoplankton (Table 4.1). The sub-Antarctic *E. vallentini* is the dominant species in the area and, like the Antarctic krill *E. superba*, is regarded as a typical herbivorous filter-feeder with well-developed maxillary setae (Mauchline, 1980). *Euphausia* species are known to ingest efficiently particles in a wide size range because of the peculiar structure of their feeding basket (see McClatchie and Boyd, 1983 for *E. superba*). They graze moderately on large *Rhizosolenia* cells and on chains of *Chaetoceros* (Parsons *et al.*, 1967; Pavlov, 1971; Kawamura, 1981), but Stuart (1989) has recently shown that in a diatom-dominated upwelling system *E. lucens* prefers the less abundant dinoflagellates. These euphausiids also have the ability to switch to carnivorous feeding when sufficient zooplankton prey is available (Mauchline, 1980;

Price *et al.*, 1988). Foraminifera were a staple component in the guts of *E. valentini* in April/May 1989 at the Prince Edward Islands (Stuart, pers. comm.). Diatom fragments along with tintinnids and radiolarians were poorly represented in the gut samples. Species of the genus *Thisanoessa*, represented in the Prince Edward Archipelago by *T. vicina*, have elongated 2nd thoracic legs of use in predatory feeding and are mixed feeders, but mainly carnivorous (Mauchline, 1980).

Similarly, the morphology of the mouthparts of the ostracods *Conchoecia* spp. suggests that they are generally predatory or detritivores. Copepod remains are often predominant in their stomachs but phytoplankton is also ingested and is probably collected by sticky secretions of the marginal glands of the carapace, or by the mandibular palps (Iles, 1961; Angel, 1981). Diatoms and silicoflagellates have been recorded in abundance in the stomach contents and faecal pellets of some species (Angel, 1968). Very high levels of plant pigments were found in the gut of *Conchoecia* sp. during the 1985 phytoplankton bloom (Fig 4.4). However, due to the scarce representation of this ostracod within the zooplankton community, its grazing impact was very limited both during the 1985 and the 1989 surveys (Table 4.5).

Poor utilization of diatom blooms by the zooplankton of the Prince Edward Archipelago may also be related to the biochemical composition of this food source. Recent studies report that diatoms in general do not represent a food source of high nutritional value, relative to other planktonic groups. Hitchcock (1982) has shown that dinoflagellates contain 3–5 times more calories than diatoms per unit volume. Furthermore, comparative analyses on the presence of unsaturated fatty acids in species of dinoflagellates, diatoms, ciliates and autotrophic nanoflagellates (Ben-Amotz *et al.*, 1987; Claustre *et al.*, 1989) have indicated that some diatoms (*Chaetoceros* sp. and *Nitzschia* sp.) have the lowest levels among the taxa examined. Unsaturated fatty acids apparently play a dominant nutritional role for zooplankton grazers (Holz, 1981; Claustre *et al.*, 1989). Thus, the observed negative selection of most zooplankton for the large diatoms, and their preference for nanoplankton,

could have a sound energetic basis. Nanoplankton largely dominates the phytoplankton biomass of the Southern Ocean where usually it constitutes 60–85% of the total (Weber and El Sayed, 1987). Also, the biomass contribution of diatoms to the nanoplankton decreases dramatically, compared to the netplankton. Indeed, the use of sequential epifluorescence and electron microscopy techniques has demonstrated that most of the nano-phytoplankton is composed of autotrophic flagellates (Estep *et al.*, 1984; Hoepffner and Haas, in press). Then, the ability of zooplankton to select preferentially the smaller cells may result in an increase in their conversion efficiency by ingesting food of higher nutritional value.

It is also possible that the phytoplankton species (diatoms) in the island blooms may be endemic to the islands (especially since they produce spores) and the largely allochthonous zooplankton may not be adapted to consuming them. This seems particularly likely for *C. radicans*, which is the dominant diatom species in the blooms but is only scarcely represented in the surrounding oceanic region (Boden *et al.*, 1988).

The potential significance of the poor utilization of phytoplankton blooms by the mesozooplankton of the Prince Edward Island seas cannot be overemphasized. Any primary production that is not consumed by these grazers is available to the other parts of the marine ecosystem, like the microheterotrophic food web and the benthic filter-feeders. Phagotrophic protozoa can graze most of the primary production in open oceanic waters dominated by pico- and nanoplankton (Sherr *et al.*, 1986). But, on account of size differences, it is unlikely that the bulk of these neritic blooms of large diatoms are significantly consumed by microheterotrophs. Their most probable fate is to sink out of the photic zone, thus providing an important input of biomass into the benthic subsystem. Sedimentation of the spring diatom blooms, in absence of overwintering populations of zooplankton grazers, is well documented for many coastal areas (Smetacek *et al.*, 1978; Conover and Mayzaud, 1984; Kuparinen *et al.*, 1985). There is also evidence that large portions of phytoplankton biomass sediment even in the presence of large overwintering zoo-

plankton populations (Dagg *et al.*, 1982; Smetacek, 1984). In Antarctic waters, mass sinking of diatom blooms has been shown by means of moored sediment traps in the Bransfield Strait (Bodungen *et al.*, 1986) and in Breid Bay (Fukuchi *et al.*, 1988). Bodungen *et al.* (1986) found that mass sedimentation occurred in conjunction with formation of diatom resting spores, which contributed about two-thirds of the total phytoplankton cells in their trap collections. Resting spores, particularly of *C. radicans* in bloom stage, have often been found in the phytoplankton of the Prince Edward Islands (Fryxell *et al.*, 1981; Boden and Reid, in press). Spore concentrations of nearly 100 per chain of 8–9 cells of *C. radicans* have been recorded by Boden and Reid (in press). This, and the relatively high sedimentation rates of particulate organic matter observed in the area (Bailey, pers. comm.), appear to confirm the hypothesis that sedimentation in the Prince Edward Archipelago causes a greater loss of phytoplankton biomass from the surface layer than zooplankton grazing. This would also explain the large biomass of benthic filter-feeders observed on the islands' shelf (Perissinotto *et al.*, in press).

CHAPTER 5

THE ROLE OF THE SUB-ANTARCTIC SHRIMP *NAUTICARIS MARIONIS* IN COUPLING BENTHIC AND PELAGIC FOOD WEBS

5.1 Introduction

Like many islands in the Southern Ocean, the Prince Edward Archipelago (47° S, 38° E) supports enormous seasonal populations of predatory pinnipeds and marine birds, the two combined being estimated in excess of two million (Williams *et al.*, 1979; Condry, 1981). The seas around the islands are also characterized by an island mass effect which results in enhanced primary productivity levels and the repeated formation of dense phytoplankton blooms, with chlorophyll-*a* concentrations of 1.5–3.0 $mg\ m^{-3}$ (Boden, 1988; Chapter 2; Perissinotto *et al.*, 1990). Utilization of these blooms by the community of planktonic herbivores is poor (Perissinotto and Boden, 1989) and much of this production seems to be transferred to the rich benthic community by senescence and sedimentation. However, few of the island based predators feed directly on the benthos (Condry, 1981; Brown and Klages, 1987; Espitalier-Noel *et al.*, 1988; Adams and Klages, 1989). This study examines the link between phytoplankton production and the maintenance of large predator populations by investigating the position of the abundant caridean shrimp *Nauticaris marionis* in these food-webs.

N. marionis is a sub-Antarctic caridean shrimp with a distribution that ranges from southern New Zealand to the Prince Edward Islands. It is found in abundance at Auckland and Campbell islands, on the Campbell Plateau (Yaldwyn, 1965) and is present, though not abundant, at both the Crozet and Kerguelen archipelagos (Ledoyer, 1979). The Prince Edward Islands represent the westernmost limit of its distribution (Boden and Parker, 1986), and further west it is replaced by the congeneric *N. magellanica* which occurs at Gough Island, the Falkland Islands and in sub-Antarctic South America (Yaldwyn, 1965).

Since the earliest benthic surveys of the Prince Edward Island seas, the local population of *N. marionis* has been noted for its high abundance, compared to populations at other sub-Antarctic islands (Bate, 1888; Ledoyer, 1979). *N. marionis* is frequently found in the stomach contents of a variety of visual predators and constitutes the dominant component of the diet of the Gentoo penguins and Imperial cormorants inhabiting the archipelago (Adams and Klages, 1989; Espitalier-Noel *et al.*, 1988).

5.2 Materials and methods

Sampling procedure. The Prince Edward Archipelago lies between Africa and Antarctica and consists of two small islands, Marion (area $\approx 300 \text{ Km}^2$) and Prince Edward (area $\approx 100 \text{ Km}^2$), 22 Km apart on a shallow plateau of about 200 m depth. The plateau itself is roughly 1000 Km² in area and drops off sharply into deep waters (3000 m, Fig 5.1).

The benthic epifauna of the islands was sampled during four cruises of the *SA Agulhas* in November 1983, March 1984, April 1987 and 1989. 65 stations were dredged by means of a D-net (0.5 m² aperture) fitted with a depressor plate, towed at about 0.5 m s⁻¹, or using a scallop dredge towed at 2 knots. Net hauls in the suprabenthic layer were also made during April 1989, using 500 μm mesh Bongo and 4 mm mesh RMT-2 nets. The fishing depth of the nets was controlled by a Universal Underwater Unit (U^3) while the target layers were identified with a SIMRAD 120 KHz echo-sounder.

In addition, *in situ* photographs of the benthic community were taken at 30 stations along three transects between Marion and Prince Edward islands, using an underwater camera deployed from the ship.

Dredged samples were sorted into taxa and a determination of the biomass (expressed as g (wet weight) m⁻² of substratum) was carried out for the major components of the epibenthic community.

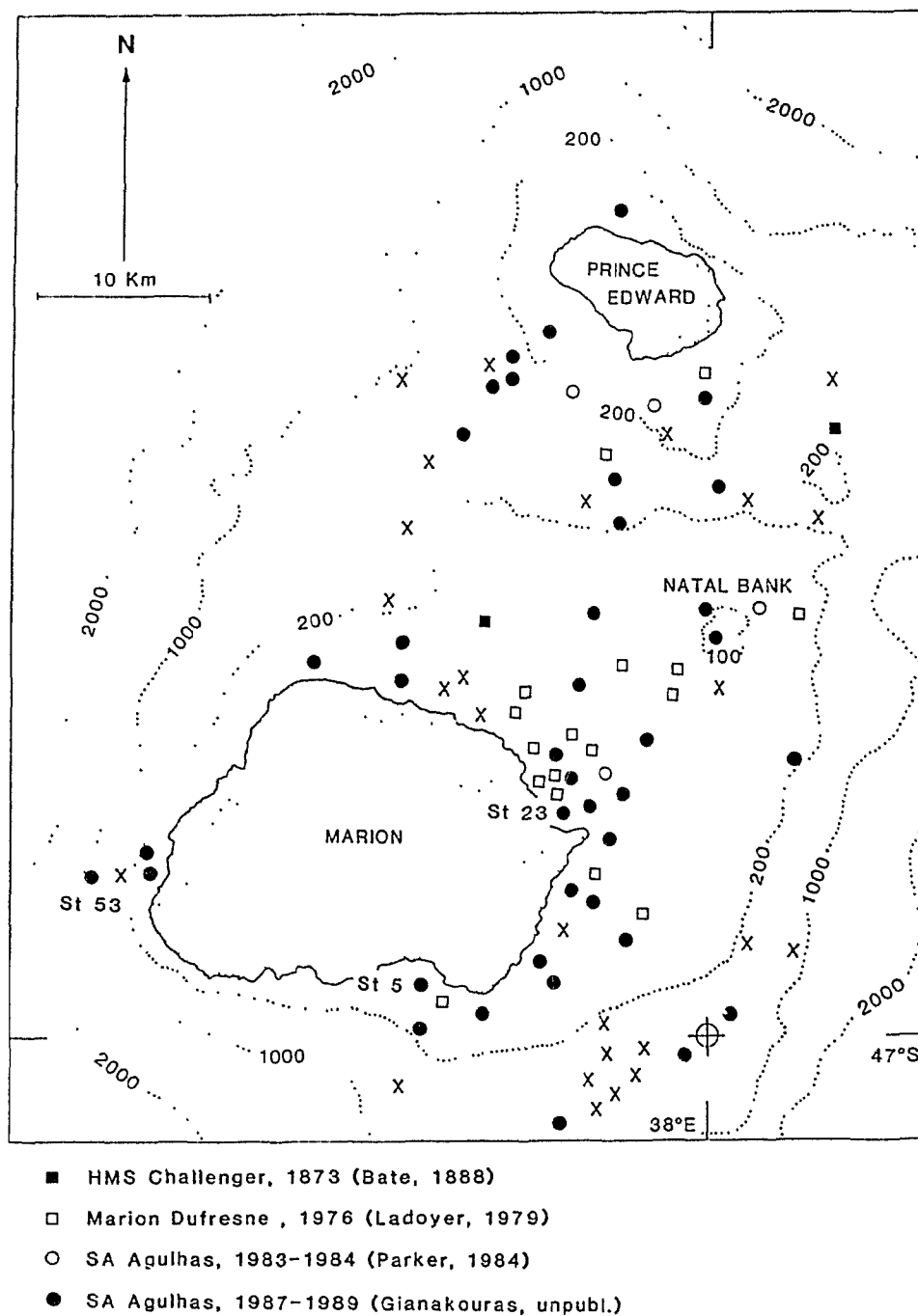


FIGURE 5.1. Occurrence of *Nauticar marionis* at the Prince Edward Archipelago based on four benthic surveys. X indicates dredge stations where no shrimps were found.

Feeding biology. Gut content analyses were performed on preserved adult *N. marionis* sampled in 1984, 1987 and 1989 at stations located on the inter-island plateau. The guts of 10 male and 30 female shrimps were removed and their contents examined under $400\times$ magnification.

Possible grazing of phytoplankton blooms by *N. marionis* was examined by size-selectivity grazing experiments. Naturally occurring phytoplankton was collected with a submersible pump and concentrated on $0.2\ \mu\text{m}$ Nuclepore filters to experimental concentrations of about $1.5\ \mu\text{g Chl-}a\ \text{l}^{-1}$. Three experimental 2 l bottles, each containing 3 shrimps, and two control bottles with no shrimps were filled with the phytoplankton mixture and rotated on a Plankton Wheel ($\approx 1\ \text{rpm}$) in the dark, in a cold room ($\approx 9\text{--}10\ ^\circ\text{C}$) for 24 hours. Duplicate water samples (100 ml) were taken from each bottle at the beginning and end of the incubation for chlorophyll-*a* and phaeopigment analysis. Five size-fractions of phytoplankton (200–37, 37–20, 20–5, 5–1, and $1\text{--}0.2\ \mu\text{m}$) were obtained by multiple serial filtration on a Sartorius Membranfilter column. Pigments from the different filters were extracted overnight at $4\ ^\circ\text{C}$ in 10 ml 90% acetone and concentrations were calculated from the fluorescence readings on a Turner Model 111 fluorometer (Strickland and Parsons, 1968).

Diurnal variations in gut pigment contents of *N. marionis* were measured for freshly caught megalope larvae at three hour intervals for 24 h. At each interval, three replicates of 3 individuals were placed in a plastic centrifuge tube with 90% acetone, homogenised with a glass rod, and stored at $-20\ ^\circ\text{C}$ for 12 h. The tubes were then spun in a centrifuge for 10 min at 5000 rpm and the pigment content of the acetone extract was measured with a Turner 111 fluorometer, before and after acidification (Mackas and Bohrer, 1976; Dagg and Walser, 1987). The daily grazing impact of megalope larvae on the local phytoplankton community was estimated following the procedure outlined in Chapter 4, according to the equation:

$$F_I = (K/t)/(1 - b') \int_0^{24} (a \times g) dt \quad [\text{ng pigm m}^{-3} \text{ d}^{-1}]$$

where: t = time (h), K = gut evacuation rate constant (h^{-1}), b' = fractional loss

of pigment (%) during the digestive process, a = numerical abundance of megalope larvae ($ind\ m^{-3}$) and g = gut pigment content ($ng\ pigm\ ind^{-1}$).

5.3 Results

Benthic community. Biomass data for Nov. 1983 and March 1984, show that *N. marionis* is a major component, being second in importance in terms of biomass only to the bryozoan suspensoid feeders (Fig 5.2). In epibenthic samples, the bryozoan component was dominated by erect, arborescent rather than encrusting colonies. Erect forms were almost exclusively composed of stoloniferan ctenostomes and cheilostomes bearing very large zooids.

Net tows and dredge samples show that *N. marionis* is widely distributed around the Prince Edward Islands and occurs mainly within the 200 m depth contours (Fig 5.1, Table 5.1). The shallowest depth at which the shrimp has been recorded is 30–33 m (stn. 23 on the east coast of Marion Island) while the deepest is between 606 and 775 m (stn. 53 on the west coast of Marion Island). On the inter-island plateau the shrimp forms a suprabenthic layer which extends 5–10 m above the bottom and can be detected as a distinct scatterer with an 120 KHz echo-sounder (Fig 5.3, Table 5.1).

Abundance estimates from dredge samples are as high as 25 $ind\ m^2$, but photographs of the bottom show much higher densities, with a maximum of about 80 $ind\ m^2$ at 61 m depth, on the southeast coast of Marion Island (stn. 5). However, as photos were taken from $\approx 2.2\ m$ above the bottom (*i.e.*, beneath the scattering layer), it is possible that even this figure represents a significant underestimation of the true population density.

The dredge samples collected in autumn (March/April) usually consisted of a mixture of adult shrimps and megalope larvae. A typical carapace size distribution of the population of *N. marionis* during this period is given in Fig 5.4. No larval stages have been recorded in early summer (Nov.). While adult shrimps are very

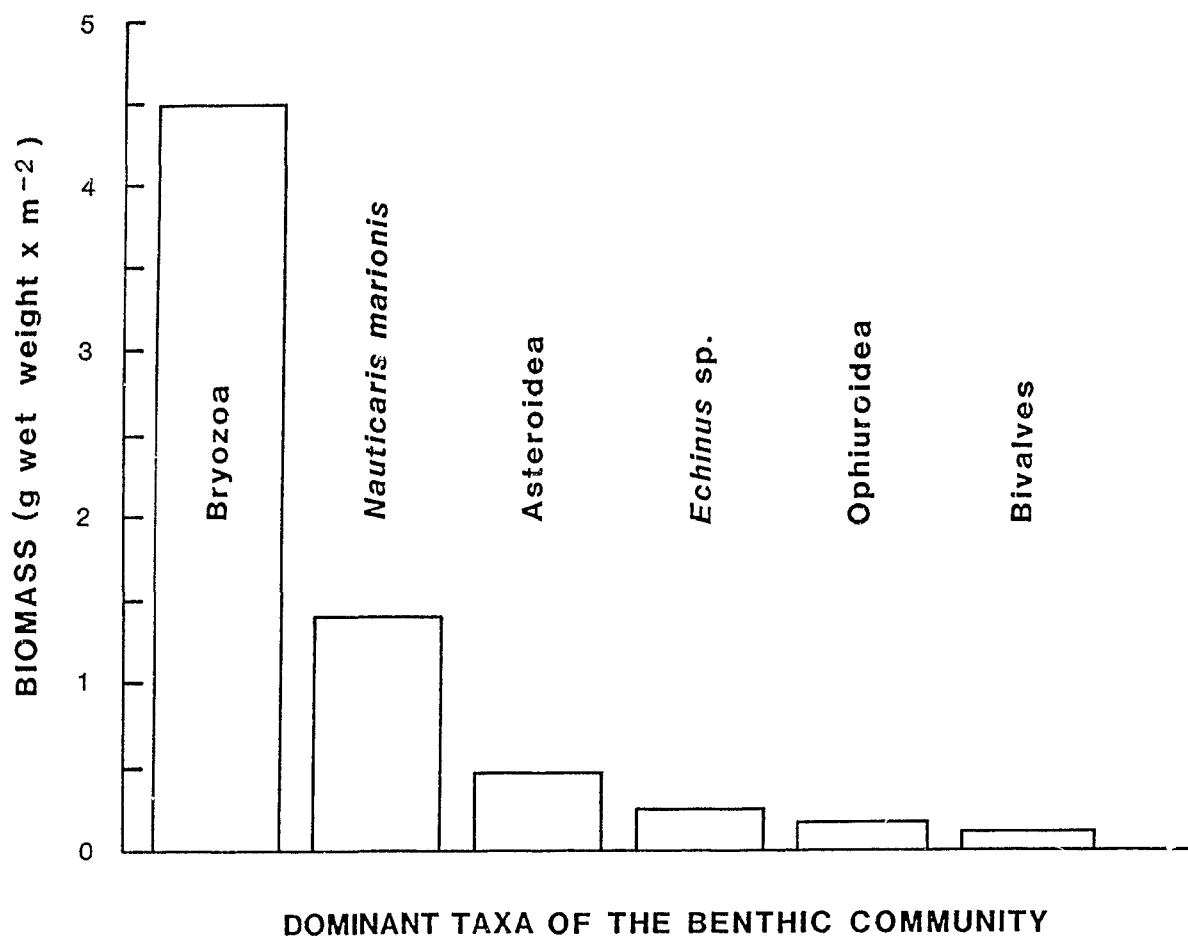


FIGURE 5.2. Biomass of the dominant taxa of the benthic community of the Prince Edward Archipelago estimated from dredge samples collected during Nov. 1983 and April 1984.

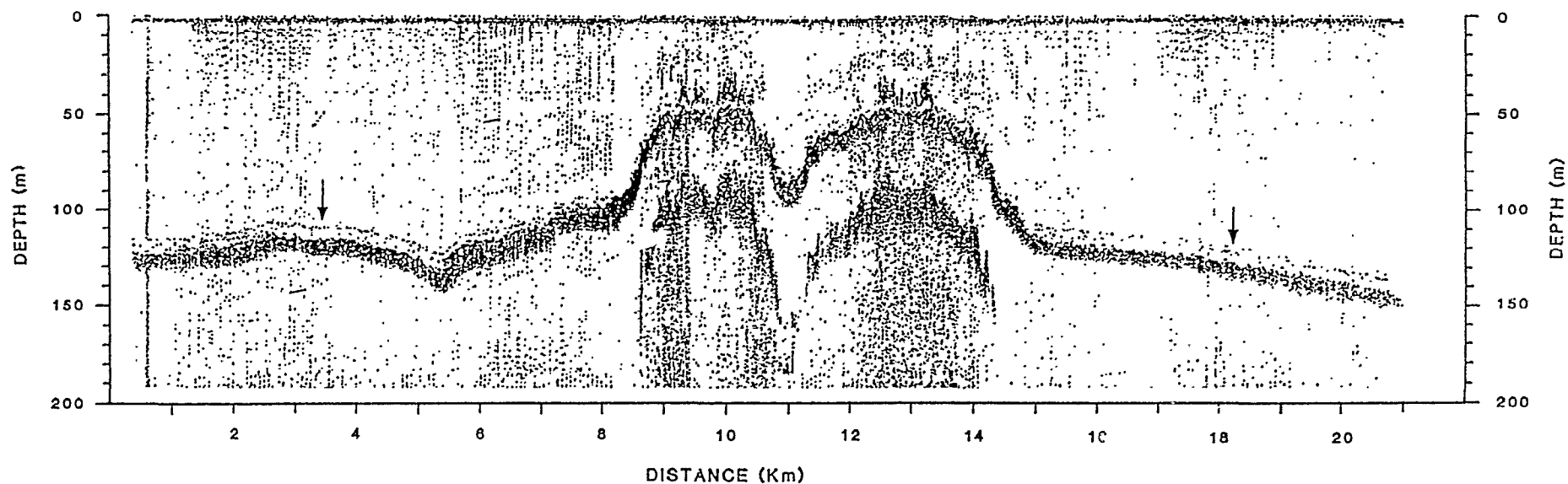


FIGURE 5.3. 120 KHz frequency acoustic record along an east-west transect in the inter-island region of the Prince Edward Archipelago. The scatterer indicated by the arrows represents a supra-benthic layer of *Nauticaris marionis* (time: 0700 h).

Table 5.1. Concentrations of the major macrozooplankton taxa (*ind* 100 m^{-3}) and micronekton (*ind* 1000 m^{-3}) on the islands' shelf and off-shore of the Prince Edward Archipelago. Samples were collected on the 26/04/89 by horizontal hauls with opening-closing RMT-2 nets.

Taxon	Day, Natal Bank			Night, Natal Bank			Day, Off-shore			Night, Off-shore		
	surf	midw	botw	surf	midw	botw	surf	midw	deep	surf	midw	deep
	10 m	70 m	140 m	10 m	70 m	140 m	10 m	150 m	400 m	10 m	150 m	400 m
<i>Rhincalanus gigas</i>	—	—	2.1	6.3	13.6	0.8	—	7.8	—	9.2	2.3	—
<i>Euphausia vallentini</i>	—	—	2.6	92.8	31.8	5.1	3.3	10.9	165.3	139.9	86.4	12.6
<i>Themisto gaudichaudii</i>	0.7	2.9	1.5	0.7	8.1	5.1	9.9	9.1	—	1.6	9.1	0.6
<i>Nauticaris marionis</i>	—	6.2	91.0	11.0	63.6	55.1	—	—	—	—	—	—
<i>Conchoecia</i> sp.	—	3.8	7.7	4.8	1.3	3.2	0.4	1.7	—	3.2	9.1	—
<i>Sagitta</i> sp.	51.5	34.4	25.1	18.8	106.3	85.9	19.0	31.8	35.0	32.9	94.1	61.4
<i>Salpa fusiformis</i>	—	3.3	5.6	1.1	—	5.9	9.1	14.8	—	3.9	15.9	0.6
<i>Lepidonotothen larseni</i>	—	—	3.6	—	—	7.3	—	—	—	—	—	—
<i>Krefftichtys anderssoni</i>	—	2.4	2.6	—	3.4	1.5	—	—	12.2	0.8	7.9	1.3

sparsely represented in net tows away from the benthic layer, the megalope larvae are regularly found in midwater HUIT-2 hauls (Table 5.1). This occurs mostly during nighttime, when megalope concentrations of up to 3 ind m^{-3} are recorded in the upper layer.

Feeding biology. The main prey items in the gut contents of *N. marionis* are benthic suspensoid feeders such as bryozoans, foraminifera, corals and harpacticoid copepods (Table 5.2). Bryozoans, the dominant prey, were represented in the guts by clusters of zooids most often still attached to stolon fragments. There is a significant difference in frequency and abundance of some items between the male and female stomach contents. In particular, males ingest more foraminifera and bryozoans and fewer copepods than females. Also, large prey species such as euphausiids and amphipods are found only in female stomachs. Guts contents of both sexes (adults) included a relatively small amount of unidentifiable amorphous material, but no recognizable plant fragments, either phytoplankton or macrophyte, could be found in this material.

Grazing experiments on phytoplankton suspensions show that none of the size fractions of the naturally occurring algal community are ingested by adult *N. marionis* (t-test, $p > 0.05$). However, phytoplankton pigments (Chlorophyll-*a* and phaeopigments) were detected in the gut content of megalope larvae. Larvae also exhibit strong diurnal feeding rhythms with night-time gut pigment peaks reaching maximum values of about $50 \text{ ng pigm ind}^{-1}$ between 2300 and 0200 hours (Fig 5.5). During April/May 1989, megalope larvae consumed $21 \text{ ng pigm m}^{-3} \text{ d}^{-1}$, representing about 10% of the euphotic zone-integrated phytoplankton biomass ($\approx 0.19 \text{ mg Chl-}a \text{ m}^{-3}$) and 18% of daily primary production ($\approx 0.09 \text{ mg Chl-}a \text{ m}^{-3} \text{ d}^{-1}$).

5.4 Discussion

The marine ecosystem of the Prince Edward Archipelago experiences repeated,

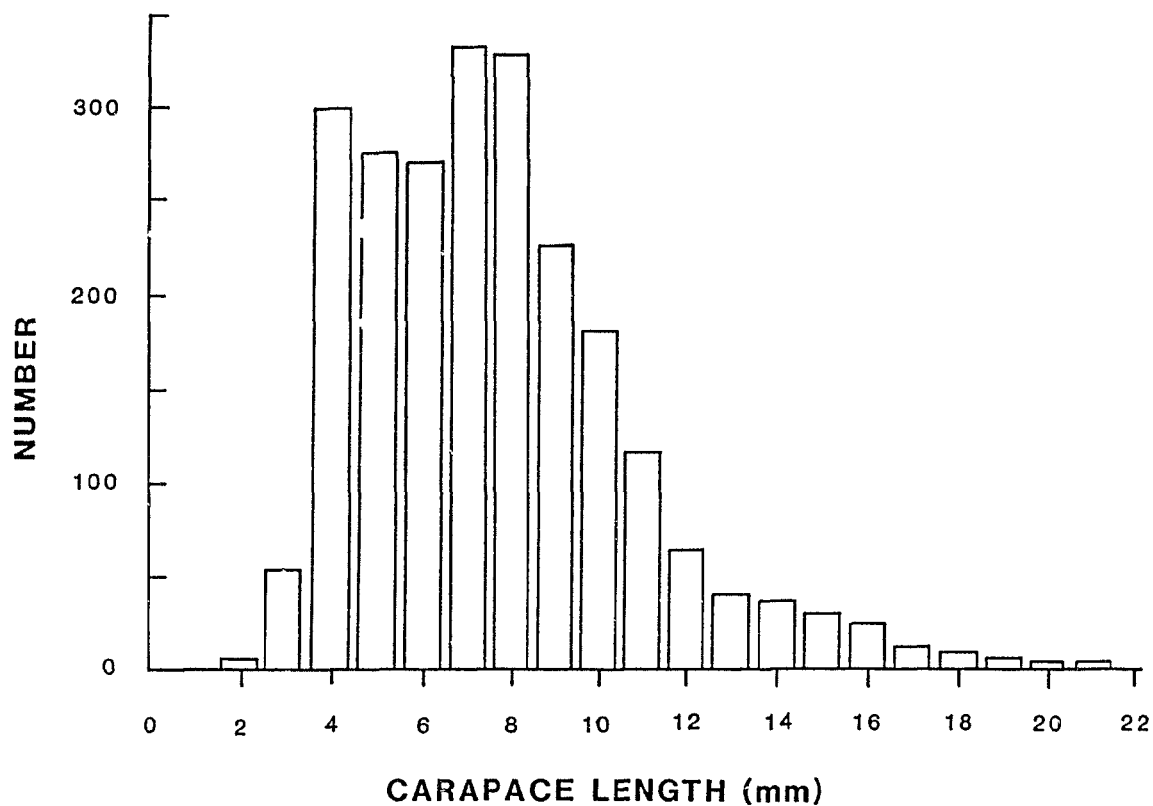


FIGURE 5.4. Size distribution of *Nauticaris marionis* (given as carapace length) from bottom samples collected in April 1984. Sample size, $N = 2295$. (After Parker, 1984). Carapace length range of adults: 7–21 mm, megalope larvae: 2–7 mm.

Table 5.2. Occurrence of prey items in the stomach contents of *Nauticaris marionis*. Frequency = number of stomachs in which the prey was found. Abundance = total number of prey found in the stomachs. t-test results represent differences in prey abundance between male and female gut contents. Significance levels: ** = 99%, * = 95%, n.s. = not significant.

Prey item	Male (n = 30)		Female (n = 30)		Signif. (t-test)
	Freq	Abund	Freq	Abund	
Foraminifera	27	256	24	125	**
Madreporaria (fragm.)	2	3	2	13	n.s.
Octocorallia (fragm.)	7	15	5	31	n.s.
Gastropod veligers	2	2	1	1	n.s.
Bivalve veligers	2	6	3	13	n.s.
<i>Limacina</i> sp.	7	7	2	2	n.s.
Ostracods	1	2	2	5	n.s.
Calanoid copepods	8	18	16	36	n.s.
Harpacticoid copepods	7	11	16	30	**
Cyclopoid copepods	2	3	3	5	n.s.
Amphipods	1	1	7	7	*
Euphausiids	0	0	6	6	**
Bryozoa(fragm.)	30	318	21	194	**
Echinoids (fragm.)	1	2	3	3	n.s.
Crinoids (fragm.)	0	0	1	1	n.s.
Tunicates (fragm.)	1	3	0	0	n.s.
Chaetognaths	0	0	2	2	n.s.

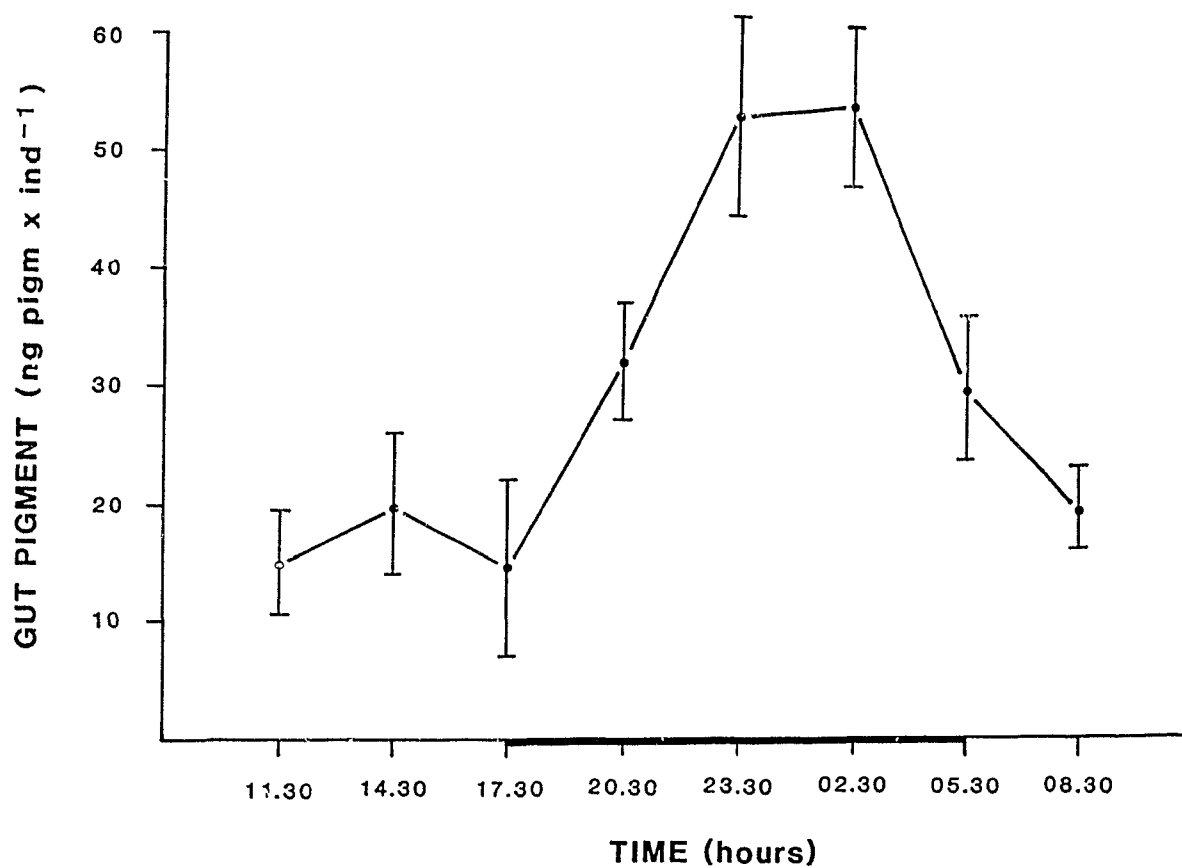


FIGURE 5.5. Diurnal variations in total gut pigment levels of the megalope larvae of *Nauticaris marionis* at the Prince Edward Archipelago during April/May 1989. Vertical bars represent standard deviation about the mean. Period of darkness is indicated by thickening of the horizontal axis.

seasonal occurrences of phytoplankton blooms concentrated in the inter-island region (Allanson *et al.*, 1985; Boden, 1988; Chapter 2; Perissinotto *et al.*, 1990). The bulk of the biomass of these blooms is composed of net-size phytoplankton ($200\text{ }\mu\text{m}$), while the contribution of the nano- ($20\text{--}1\text{ }\mu\text{m}$) and picoplankton ($1\text{--}0.2\text{ }\mu\text{m}$) to the local community is quite low, compared to other areas of the Southern Ocean and amounts to only $21.5 \pm 6.33\%$ of the total (El Sayed *et al.*, 1979). The diatoms *Rhizosolenia curvata* and *Chaetoceros radicans*, and the silicoflagellate *Dictyocha speculum* dominate the bloom communities of the Prince Edward Archipelago (Allanson *et al.*, 1985; Boden, 1988). None of these species is known to be a staple in zooplankton diets (Schnack, 1979; Perissinotto and Boden, 1989). Indeed, size-selectivity experiments, on zooplankton feeding on naturally occurring phytoplankton, show that the zooplankton community of the Prince Edward Island seas have very little grazing impact on the net-size phytoplankton (Perissinotto and Boden, 1989; Perissinotto *et al.*, in press). This implies that the rich food source stored in the phytoplankton blooms is scarcely exploited by the pelagic herbivores.

Although some degree of horizontal dispersion of the blooms does probably occur, it seems likely that most of this biomass sinks below the mixed layer in the form of senescent phytoplankton cells and/or resting spores. Recent measurements of the sedimentation rate of particulate matter in the area, by means of moored traps, indicate that relatively high values can occur, especially in the shallowest part of the inter-island region (up to 40 g of suspended solid $\text{m}^{-2}\text{ d}^{-1}$, Bailey, unpubl. data). Also, resting spores, particularly of *Chaetoceros radicans* in the bloom stage, have often been found in the phytoplankton of the Prince Edward Islands. Spores, like senescent phytoplankton cells, wind up mostly on the bottom. Therefore, their presence appears to corroborate a direct link between pelagic primary producers and benthic suspensoid feeders (Fryxell *et al.*, 1981; Perissinotto and Boden, 1989). The rich community of suspensoid feeders is largely composed of arborescent bryozoans. Gut contents and laboratory experiments have indicated that diatoms and dinoflagellates are important food items for bryozoans (Winston,

1977). Zooids are able to capture large cells by switching their feeding mode from ciliary currents (selection for small particles) to tentacular encagement (Okamura, 1987, 1990).

The megalope larvae of *N. marionis* exhibit both vertical diurnal migration in the water column and rhythms in gut pigment content (Fig 5.5) which clearly indicate nocturnal feeding and the ability to utilise phytoplankton as a food source. Their grazing impact account for about 18% of integrated daily primary production. Adult shrimps, however, do not graze on phytoplankton and the large resident population is maintained only indirectly by pelagic production. Gut contents of *N. marionis* reveal the overriding importance of benthic suspensoid feeders (Table 5.2) which are themselves maintained at high densities by imports from the upper mixed layer of the water column.

Differences between the gut contents of male and female shrimps are likely to be the result of size differences between sexes. Population mean size for females (32.3 ± 4.5 mm) is significantly higher than for males (25.6 ± 3.3 mm). Therefore, the greater proportion of amphipods and euphausiids, observed in the guts of the females, may be due to their ability to handle large preys more efficiently than the smaller males do. Combined abundance data for both sexes indicate that over 90% of gut contents is formed by bryozoans (54%) and benthic foraminiferans (40%), the former being a particularly important component of the benthic community (Fig 5.2; Parker, 1984; Gianakouras, unpubl. data).

A number of recent investigations on the ecology of the seabird community of the Prince Edward Archipelago, have revealed the importance of *N. marionis* as a prey item (Table 5.3). To our knowledge, in no other Southern Ocean ecosystem has *N. marionis* been found to be an important component of the diet of seabirds (see review by Croxall, 1987). At the Prince Edward Islands, *N. marionis* is the dominant prey item in the diet of the Gentoo penguin and of the Imperial cormorant, contributing respectively 26 and 19% by mass to their total annual food consumption (Adams and Klages, 1989; Espitalier-Noel *et al.*, 1988). In 1983-84

the shrimp was the most abundant crustacean in the diets of both Macaroni and Rockhopper penguins, constituting 40 and 60%, respectively, of all crustacean items identified in their stomachs (Brown and Klages, 1987). The shrimp has also been recorded in the stomach contents of the inshore fish *Paranotothenia magellanica* (Blankley, 1982) and of the starfish *Anasterias rupicola* (Blankley and Grindley, 1985 and Table 5.3). Thus, the local stock of *N. marionis* helps to support both the land-based and marine predators.

Enhancement of pelagic primary production by the island mass effect helps the archipelago to sustain high densities of visual predators, but only indirectly, through coupling with the benthic food web. Phytoplankton production appears to be transferred to the benthic community by sedimentation and on to higher trophic levels via the effects of benthic grazing by *N. marionis*. This indicates a key role for the shrimp in making pelagic production available to large visual predators.

Table 5.3. *Nauticaris marionis* in the diet of different predator groups at the Prince Edward Islands. n.a.= not available, Tr.= Trace only. N = sample size of predator stomachs examined.

Predator	% number	% mass	% occur.	N	Period	Source
BIRDS						
Gentoo penguin	12	26	33	144	March 84–March 85	Adams & Klages, 1989
King penguin	tr.	tr.	4	120	March 84–March 85	Adams & Klages, 1987
Macaroni penguin	5	n.a.	26	30	Dec. 83–Febr. 84	Brown & Klages, 1987
Rockhopper penguin	9	n.a.	24	34	Jan.–March 84	Brown & Klages, 1987
Imperial cormorant	87	19	47	47	April 84–March 85	Espitalier-Noel <i>et al.</i> , 1988
FISH						
<i>Paranotothenia magellanica</i>	2	4	5	129	May 79–May 80	Blankley, 1982
STARFISH						
<i>Anasterias rupicola</i>	tr.	tr.	n.a.	322	Sept. 79–May 80	Blankley & Grindley, 1985

CONCLUSIONS

It is concluded that the island mass effect in the Prince Edward Archipelago is dominated by the topographic generation of anticyclonic eddies, possibly stratified Taylor columns. Eddies prolong the residence time of the water in the island seas and entrain nutrient-rich freshwater run-off. High rainfall rates ($\approx 250 \text{ mm month}^{-1}$) on the islands provide an input of buoyancy into the surface waters, thereby increasing the vertical stability of the mixed layer. Also, rainwater dissolves the guano deposited on the coast and carries about $1.2 \times 10^6 \text{ mol}$ of reduced nitrogen (ammonia and urea) per day into shelf waters. Under normal flow conditions, the Antarctic Circumpolar Current ($u \approx 0.35 \text{ m s}^{-1}$) would advect this run-off energy downstream of the archipelago ($L \approx 2 \times 10^4 \text{ m}$) in about half a day. However, when the nitrogen-rich freshwater is retained on the plateau by anticyclonic anomalies for a sufficient period of time, phytoplankton blooms of up to $\approx 2.5 \text{ mg Chl-}a \text{ m}^{-3}$) can develop. Local primary production rates can reach maximum values that are one order of magnitude higher than those observed at the notably rich frontal zones of the Southern Ocean. The guano-based nitrogen flux into the island seas may support as much as 50–80% of this production.

The elevated phytoplankton standing stock appears to be channelled to the land-based predators in two different ways.

- a) A minor part of it (10–20%) is consumed by zooplankton and, therefore, passes directly from the pelagic subsystem to the predators (surface and sub-surface pelagic feeders) through their feeding on the meso- and macrozooplankton.
- b) A greater portion of the phytoplankton blooms probably sinks to the bottom and supports a rich community of benthic filter-feeders. This finally reaches the land-based predators (bottom feeders) indirectly, via their feeding on the benthic shrimp *Nauticaris marionis*.

The major components and their interactions within the Prince Edward Archipelago are presented in Figure 6.1.

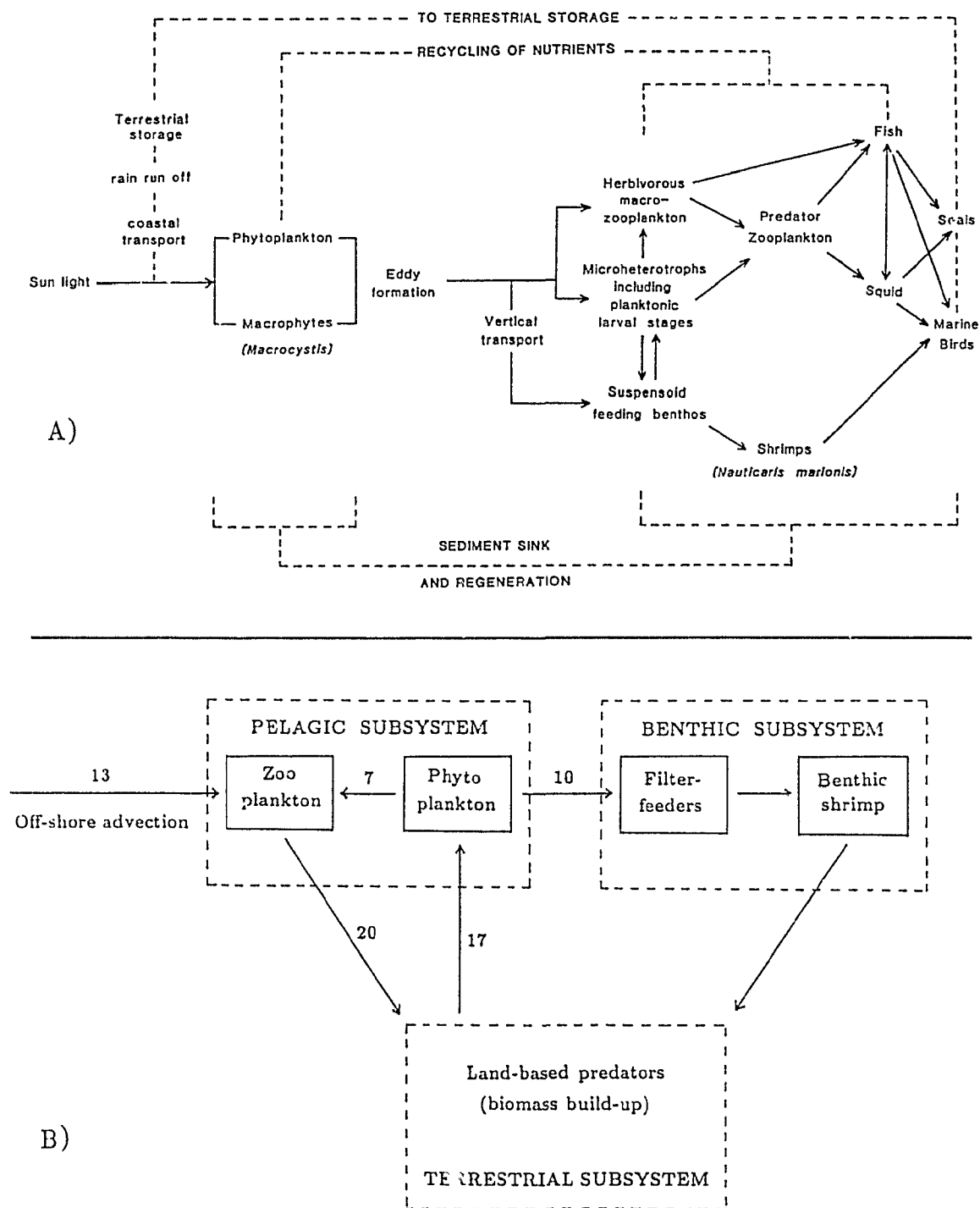


FIGURE 6.1. A) Some of the principal components and their interaction within the Prince Edward Archipelago marine ecosystem. B) Schematic representation of the daily nitrogen flux ($t N d^{-1}$) through the pelagic, benthic and terrestrial subsystems. Quantitative estimates of the flux within the benthic subsystem are not available.

Much of the food requirements of the predator community seems to be met by an allochthonous source. This results from the interaction between zooplankton vertical migrations and shelf topography. Off-shore zooplankton, advected above the plateau while at near-surface depths during the night, are trapped in relatively shallow and illuminated waters during their diurnal descent. Visual predators are thereby in a position to exploit this allochthonous resource which could represent a carbon input equivalent to the local maximum phytoplankton production. With an estimated nighttime advection of zooplankton into the islands' shelf (Area $\approx 4 \times 10^8 m^2$) of about $186 mg C m^{-2} d^{-1}$ (Chapter 3), a daily flux of ≈ 74 tonnes of carbon is obtained. Assuming a 10% efficiency of trophic transfer (ecological efficiency), a potential $7.4 t C d^{-1}$ of predator biomass would be produced. This represent approximately 185 t of wet weight, if it is assumed that carbon constitutes 4% of the living mass of seabirds (Croxall, 1987). Since penguins form the bulk of the land-based predator community of the Prince Edward Archipelago, and their total biomass is estimated to be about $11 \times 10^3 t$ of wet weight (Adams and Brown, 1989), then the allochthonous zooplankton would contribute a daily increase in this community equivalent to $\approx 1.6\%$ of its total biomass.

An important consequence of this input of external crustacean prey stocks lies in the role that guano, generated by the predators, plays in supporting local primary production. Guano nitrogen is supplied to the island seas in the form of two reduced nutrient species, ammonia and urea. To estimate the potential contribution of guano nitrogen to the total primary production, it is necessary to consider the flux of all major N nutrients into the archipelago. Ambient nitrate (NO_3) concentrations in the euphotic zone throughout the region are very high and typical of the Polar Front Zone (Lutjeharms *et al.*, 1985). Values range between 13 and $26 mmol N m^{-3}$. At steady state, the minimum flux of nitrate into the euphotic zone (depth $\approx 50 m$) of the islands' shelf is:

$$Q [NO_3] \approx S u [NO_3] \approx 2 \times 10^8 mol N d^{-1},$$

where: S = cross-sectional area ($\approx 5 \times 10^5 m^2$), u = advection speed ($\approx 0.35 m s^{-1}$)

and $[\text{NO}_3]$ = nitrate concentration ($\approx 13 \text{ mmol m}^{-3}$). Multiplying this flux by 6.8 (Redfield ratio for C:N) the potential new production is calculated (*i.e.*, assuming that all the available NO_3 is taken up by phytoplankton): $6.8 \times 2 \times 10^8 \text{ mol N d}^{-1} \approx 1.4 \times 10^9 \text{ mol C d}^{-1}$. Concerning the reduced N (ammonia and urea), the amount of fresh guano produced by the seabird community per year can be estimated by combining the data of Burger *et al.* (1978) and Fugler (1985). These give a total value of $\approx 3.6 \times 10^4 \text{ t y}^{-1}$ and, since the average N content of fresh guano is $\approx 17\%$ of its total weight (Burger *et al.*, 1978), the flux of N from this source is $\approx 6 \times 10^3 \text{ t y}^{-1}$. Oxidation of guano N is negligible during conditions of high rainfall when the excrements are washed away into the sea by freshwater run-off (Pietr *et al.*, 1983). Thus, in the island seas of the Prince Edward Archipelago guano N will be available almost exclusively in its reduced forms. The daily flux will be of the order of $\approx 17 \text{ t} \approx 1.2 \times 10^6 \text{ mol N}$ (Fig 6.1) and the total potential production from this source is calculated as above: $1.2 \times 10^6 \times 6.8 \approx 8.2 \times 10^6 \text{ mol C d}^{-1}$. This is three orders of magnitude lower than the potential new production levels (from NO_3 flux). However, given the preferential selection of phytoplankton for the reduced forms of N, and assuming that all ammonia and urea are utilized before any significant uptake of NO_3 occurs, the contribution of guano N to total primary production seems to be substantial. The measured average primary production in the islands' shelf during bloom conditions ranges between 50 and $80 \text{ mg C m}^{-2} \text{ h}^{-1}$. This is equivalent to ≈ 1 to $1.6 \times 10^7 \text{ mol C d}^{-1}$. Thus, the percentage contribution of the reduced N production would range between 51 and 82% of the total primary production. Whether this production must be considered regenerated or new depends upon the origin energy that supports the food requirements of the seabird community of the archipelago. Now given the estimated carbon flux, associated with the advection of allochthonous zooplankton, of 74 t C d^{-1} and a predator assimilation efficiency of 20–25% (range suggested by Brown, 1989 for *Eudyptes* penguins), a potential 15–18 t C d^{-1} of excrements would be generated by the land-based predators. Thus, since the in situ C:N ratio for seabird guano is ≈ 2.2 (Pietr *et al.*, 1983), the amount of

reduced nitrogen produced on the islands from the allochthonous source would be about $7\text{--}8 \text{ t N d}^{-1}$ (Fig 6.1). This accounts for 40–50% of the total guano-derived N measured in the area ($\approx 17 \text{ t d}^{-1}$). The estimation implies that the contribution of guano nitrogen to the local primary productivity may be largely in the form of new production.

Poor utilization of the excess NO_3 at the Prince Edward Archipelago is very obvious since, even during the highest phytoplankton bloom concentrations, changes in NO_3 levels were minimal and hardly detectable with high-resolution auto-analyser techniques. On no occasion was the available NO_3 measured in the area lower than 12.5 mmol m^{-3} (Allanson *et al.*, 1985; Boden, 1988; Duncombe Rae, 1989a). According to the recently-developed iron deficiency hypothesis for the Southern Ocean (Martin and Fitzwater, 1988; Martin, 1990; Martin *et al.*, 1990), the shallow shelf area of the islands is expected to be very rich in iron introduced from land and re-suspended sediments. Although no measurements of iron concentrations were made during the investigations in the Prince Edward Archipelago, the volcanic nature of the islands suggests that iron availability in the circuminsular waters must be very high and probably comparable to the levels recorded by Martin *et al.* (1990) in the neritic waters of the Gerlache Strait, *i.e.*, $\approx 7 \text{ nmol Fe Kg}^{-1}$. Using the phytoplankton Fe:N ratio of 1:5000 suggested by Martin *et al.* (1989), this iron availability would be more than enough to remove all the excess NO_3 in the island seas and to result in phytoplankton biomass of at least 20 mg m^{-3} (conversion factors from Holm-Hansen and Huntley, 1984).

However, as in most other neritic areas of the Southern Ocean (Sakshaug and Holm-Hansen, 1984; Holm-Hansen, 1985; Priddle *et al.*, 1986; El Sayed, 1988), bloom concentrations in the Prince Edward Archipelago are relatively low ($1.5\text{--}2.5 \text{ mg Chl-}a \text{ m}^{-3}$) and an order of magnitude lower than the expected levels. Also, local blooms do not persist throughout the austral summer/fall and their frequency of occurrence is largely unknown. On at least two occasions (March 1984 and April 1989) the island seas of the archipelago exhibited no enhancement

of chlorophyll-*a* and primary production levels, relative to the surrounding open ocean (Perissinotto and Duncombe Rae, 1990; Attwood and Lucas, in prep.). On the other hand, phytoplankton blooms and associated high production rates have been found repeatedly in off-shore waters of the Southern Ocean, near the main frontal systems (Allanson *et al.*, 1981; El Sayed and Weber, 1982; Yamaguchi and Shibata, 1982; Lutjeharms *et al.*, 1985; Bidigare *et al.*, 1986; El Sayed, 1988), where iron supplies are supposed to be severely limited (Martin, 1990).

Nevertheless, the iron deficiency hypothesis appears to be consistent with many features of Southern Ocean primary production and trace metal studies must be included in future research efforts in the area. Measurements of the variations in Fe concentrations at the Prince Edward Islands, and other similar systems, may help to explain an important part of the variance associated with phytoplankton production and biomass. However, the results of this study suggest that physical events in island shelves may play a dominant role in controlling the local primary production rates. Major progress in this field can be achieved only by focusing on the accurate estimation of the frequency of eddy formation and shedding in island seas, and therefore of their residence time in the area. Recent developments in satellite remote-sensing techniques appear to provide the best tools for these studies. In particular, the deployment of Synthetic Aperture Radar (SAR) systems (Stewart, 1985) represents a great potential in this direction since the Southern Ocean is characterized by almost continual cloud coverage. Such satellite-borne data could enhance the resolution of physical events around islands on space and time scales that have so far eluded conventional oceanographic investigations.

APPENDIX

Copyright acknowledgements

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20 June 1990

Mr Renzo Perissinotto,
Department of Oceanography,
Dalhousie University,
Halifax N.S.,
Canada.

Dear Renzo,

Thank you for your letter of June 4, 1990. It was great to hear from you. Thank you also for the copy of the paper on Vertical Stability.

I have, of course not the slightest objection to your using co-authored papers in which I am involved in your doctoral dissertation. This will also apply to the Oban symposium paper if you were to use this work in your dissertation.

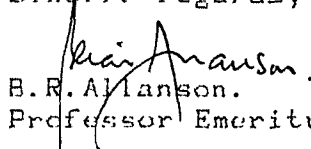
I am going to Oceans 90 at the end of the week. It looks a very useful meeting which the people in Durban have put together. I have been asked to chair the session of the Southern Ocean work. It will be interesting what comes out of this session, particularly as regards ideas on the new research programme.

Our poster has been vetted and edited by Christopher McQuaid and he has agreed that the person who has replaced Ismail will actually draw up the poster.

Dear old SA seems to be going ahead slowly and somewhat haltingly. With Mandela in Canada and the USA shouting the odds about sanctions it makes the reformists life very difficult. Add to this the drop in the gold price and life is very chill as midwinter approaches.

We are of course greatly looking forward to having you back with us as Dr Perissinotto!

Sincerely regards,


B.R. Allanson.
Professor Emeritus.



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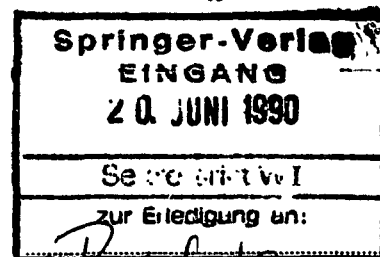
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9

1. The first step is to identify the problem. This involves understanding the current situation and what needs to be changed.



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For the above to amount to fraud, the victim must believe he is being deceived. The victim will understand the defendant's conduct as a deception if and only if the defendant can reasonably "expect the victim to understand and act on the deception at the point in time of the victim's belief." Federal Circuit, *supra* note 3, at 10. The Supreme Court has also held that a defendant's belief that a victim is deceived is not sufficient to establish fraud. Federal Circuit, *supra* note 3, at 10. The defendant must believe that the victim is deceived at the time of the deception.

It is noted that the γ (0.35) and β (0.20) needed to add a little more than one extra state must be used. This is especially true because the added states are on the left-hand pole and are not necessarily the lowest states. Hence, the β and γ

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