THE UNIVERSITY OF HULL

Environmental aspects of growth in the Antarctic molluscs *Nacella concinna* (Patellidae) and *Yoldia eightsi* (Nuculanidae) at Signy Island, South Orkney Islands.

being a Thesis submitted for the Degree of

Doctor of Philosophy

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by

Conor Paul Nolan

B.A.(Hons) Zool., MSc. Env. Sci. (Univ. of Dublin, Trinity College)

November 1991.

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BACK COVER POCKET

Nolan, C.P., 1991. Size, shape and shell morphology in the Antarctic Limpet *Nacella concinna* at Signy Island, South Orkney Islands.
J. Moll. Stud., 57, 225-238.

Study Aims

The rate of growth in many localised or sedentary marine species is governed by the effects and variation of environmental parameters.

At high latitudes few studies have investigated this relationship in marine invertebrates and a lack of information exists on growth studies combined with an ecological and physical assessment of the contemporary marine environment.

Antarctic growth studies have generally been limited to short term periods of summer research due to the logistic difficulties and commitment required for longer periods of work. These investigations, whilst contributing to the seasonal pool of Antarctic growth data, provide a basis for further work and generally speculate on the causes and effects of the limitations to the annual growth cycle in benthic marine species.

The present study aims to elucidate and interpret annual variations within the inshore marine environment and investigate the interactions of physical, chemical and ecological parameters on the growth rates and ecology of two Antarctic inshore marine molluscs; the limpet *Nacella concinna* and the bivalve *Yoldia eightsi*.

Acknowledgements

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I extend my thanks to Dr. Andrew Clarke (BAS) whose direction and detailed attention, from a personal and professional level, in the supervision of this study was fully appreciated. I am also indebted to Dr. Nev Jones (Hull University) for his assistance, supervision and advice throughout the course of this study.

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CHAPTER 1

Introduction

1.1 The Maritime Antarctic Environment

Surrounding the Antarctic continent, the Southern Ocean represents a marine environment of physical and ecological extremes which provides a predictable but demanding habitat for the diverse Antarctic benthic fauna.

The benthos of the continental shelf associated with the Antarctic continent and island groups has been subjected to an enormous amount of basic descriptive and taxonomic work (Dell, 1972 for a review, Dell, 1990; Hain, 1990; Sieg and Wägele, 1990). Specific attention has been paid to the littoral ecology and biogeography of the Southern Ocean (Knox, 1960), the major taxonomic affinities of the groups found therein (Knox and Lowry, 1977) and the origin of the marine fauna (Lipps and Hickman, 1982; Clarke and Crame, 1989). The common conclusion from these data is that the fauna represents a collection of a wide variety of taxa with differing biogeographic affinities and a very high degree of endemism in many of the taxonomic groups (Cailleux, 1961; White, 1984; Picken, 1985). This highly endemic characteristic suggests that the biota has been isolated for a long time and possibly since the inception of the Antarctic convergence which effectively created a oceanographic barrier

for gene exchange with lower latitudes (Ekman, 1953; Briggs, 1974; Clarke and Crame, 1989).

In association with this hypothesis Dell (1972) suggests that water temperature is the primary barrier to the dispersal of the Antarctic fauna concluding that the biota of the southern hemisphere have their dispersal effectively stopped by water temperatures below 0°C, and that organisms adapted to Antarctic water temperatures, on the whole, cannot efficiently migrate into warmer waters.

Low water temperatures have characterised the Antarctic marine environment since the late Miocene period 14 million years ago and have probably not changed greatly over this time (Savin *et al.*, 1975; Shackleton and Kennett, 1975). Seawater temperatures close to the continent are annually within the range of -2.0°C to -1.5°C (Littlepage, 1965; Hicks, 1974). At lower latitudes the annual range is wider increasing to -1.9°C to +1.0°C in the maritime Antarctic zone (Clarke *et al.*, 1988). A seasonal cycle within this range occurs annually (Clarke, 1988; Littlepage, 1965) and may have an important role in cuing physiological and ecological responses, as has been suggested for the reproductive activity observed in the Antarctic limpet *Nacella concinna* (Shabica, 1976; Picken, 1980b). Physiologically, however, the majority of the benthos examined show little or no evidence for temperature adaptation. Oogenesis proceeds extremely slowly, takes more than a year to complete with individuals typically containing more than one cohort of growing oocytes

(Pearse, 1963; 1965; Pearse and Giese, 1966; Picken 1979, 1980a; Richardson, 1979; Seager, 1979; McClintock and Pearse, 1987). The influence and consequences of low seawater temperatures on the physiological functioning and adaptation of the Antarctic fauna has consequently received much attention (Clarke, 1983 for a review). Many species and biological systems have been examined and this has resulted in the general synopsis that temperature is generally not rate limiting and it is the effects of ecological constraints such as food supply which shape the existence of the Antarctic biota.

An extremely seasonal period of high primary productivity punctuates the Antarctic summer months. Throughout this period there generally is no nutrient limitation to phytoplankton growth due to the eutrophic nature of Antarctic waters (Sverdrup *et al.*, 1942) but a depletion in associated nutrients has been shown to occur (Clarke *et al.*, 1988). In some areas, however, and particularly those associated with sea ice, nutrient depletion and limitation of the bloom does occur (Jennings *et al.*, 1984). Characteristically the duration of productivity is too short for a second peak (common in temperate latitudes) to develop and winter productivity falls essentially to zero (Cushing, 1959; Holm-Hanson, 1985; Perrin *et al.*, 1987; Vincent, 1988; Gilbert, (in press)). During this extremely brief period, however, primary production has been estimated by El-Sayed (1968) to be equivalent throughout the southern ocean to 20% of that produced by all the oceans

of the world. This view is consistent with a general body of belief that production is significantly greater in high latitudes (Sverdrup, 1955) but more recent observations however (Rodin *et al.*, 1975; El-Sayed and Turner, 1977; Vermeij, 1978) suggest that there may be little systematic difference with latitude.

Many shelf invertebrates feed on detritus or benthic autotrophs and are regulated in their activities by the supply of marine detritus and the seasonality of benthic production (Hart, 1942; Lightfoot *et al*, 1979). Quantitatively this food source, closely related to the peak and early decline of benthic and planktonic autotrophic populations, is vitally important to the benthos with seasonal lows having a much more devastating effect than sudden periods of low temperature (Vincent,1988). The seasonality of this food supply has been used to explain many physiological and ecological features of the benthos particularly in relation to reproductive strategies and growth rates (Thorson, 1950; White, 1977, 1984; Clarke, 1988)

In response to the highly seasonal and brief food supply, overall growth and reproductive rates for the majority of benthic species examined are extremely slow and in many species longevity and slow growth to maturity is commonly associated with this feature (Pearse, 1965; Shabica, 1971, Ralph and Maxwell, 1977; Picken, 1980b, Luxmoore, 1982). In the majority of instances, however, the slow yearly growth rates, when examined seasonally, are composed of a

relatively high rate of growth during the brief summer period with very slow or zero growth recorded during the winter months.

The selection and survival strategy for Antarctic shelf benthos is therefore attuned to the ecological efficiency of the animal in it's environment. This results in an unique, diverse and complex biota whose inter-relationships and ecological significance in the complexity of the Southern Ocean largely remain unknown.

1.2 The Inshore Marine Environment of Signy Island

The Scotia arc lies to the north of the Weddell sea and comprises the South Sandwich, South Orkney and South Georgia groups of islands. It is an important area in the northerly extension of the Antarctic shelf assemblages and at its most northerly limit is situated at the confluence of the Magellan and South Georgia provinces (Fig. 1)

The South Orkney islands (60°35'S, 45°38'W), first discovered by Powell in 1820, lie 600 km North West of the Antarctic peninsula and represent the intermittent continuation of the shelf zone in this area (Fig. 2). Powell returned in 1821 and was instrumental in charting the two main islands in the group: Coronation island to the west and Laurie island to the east.

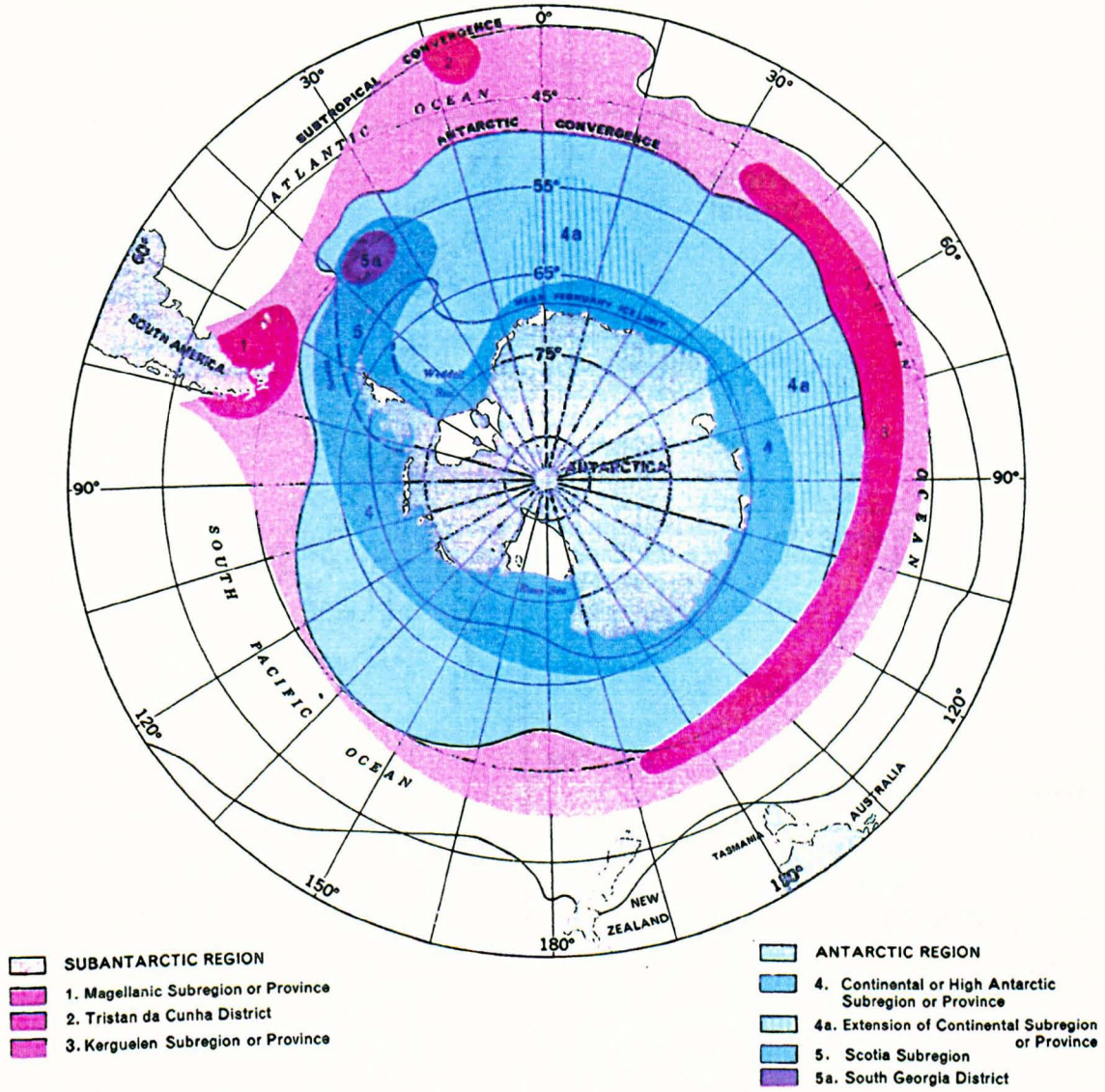


Figure 1. The biogeographic divisions of the Southern temperate and Antarctic regions (After Hedgepeth, 1969).

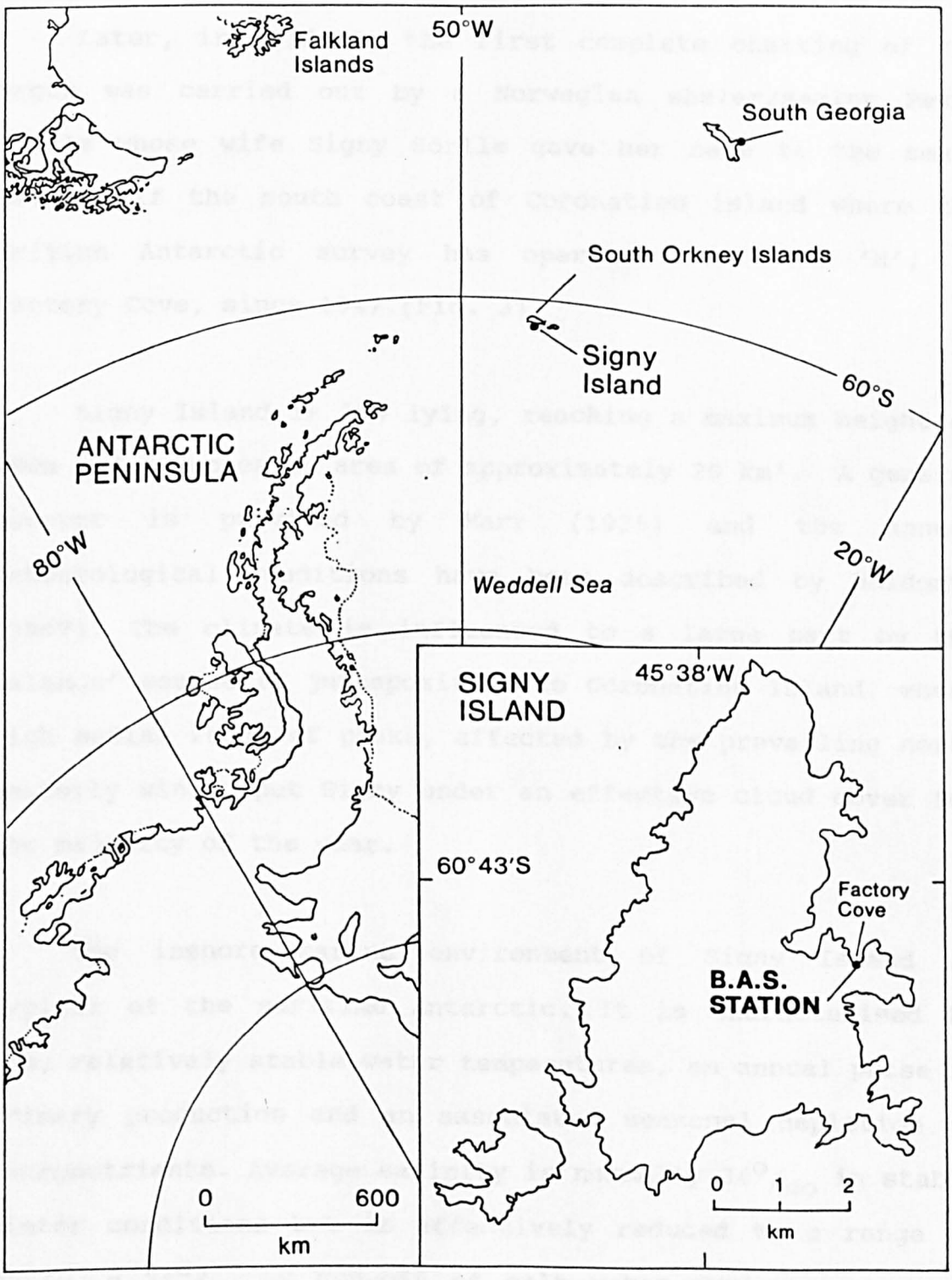


Figure 2. Map showing the location of the South Orkney Islands : Inset, an outline map of Signy Island showing the position of Factory Cove and The British Antarctic Survey (B.A.S.) station.

Later, in 1912-13, the first complete charting of the group was carried out by a Norwegian whaler/sealer Peter Sörlle whose wife Signy Sörlle gave her name to the small island off the south coast of Coronation island where the British Antarctic survey has operated its base 'H', in Factory Cove, since 1947 (Fig. 3).

Signy Island is low lying, reaching a maximum height of 280m and occupies an area of approximately 20 km^2. A general account is provided by Marr (1935) and the annual meteorological conditions have been described by Holdgate (1967). The climate is influenced to a large part by the islands' southerly juxtaposition to Coronation Island, whose high medial range of peaks, affected by the prevailing north westerly winds, put Signy under an effective cloud cover for the majority of the year.

The inshore marine environment of Signy Island is typical of the maritime Antarctic. It is characterised by low, relatively stable water temperatures, an annual pulse in primary production and an associated seasonal depletion of macronutrients. Average salinity is normally $34^{o}/_{oo}$ in stable winter conditions but is effectively reduced to a range of $33^{o}/_{oo}$ - $34^{o}/_{oo}$ as run-off of melt water during spring and summer dilute the inshore waters. A comprehensive record of sea-water data collected from Signy Island over a 13 year period from 1969 to 1982, including temperature, salinity and macronutrient profiles has been analysed and interpreted by Clarke *et al.* (1988).

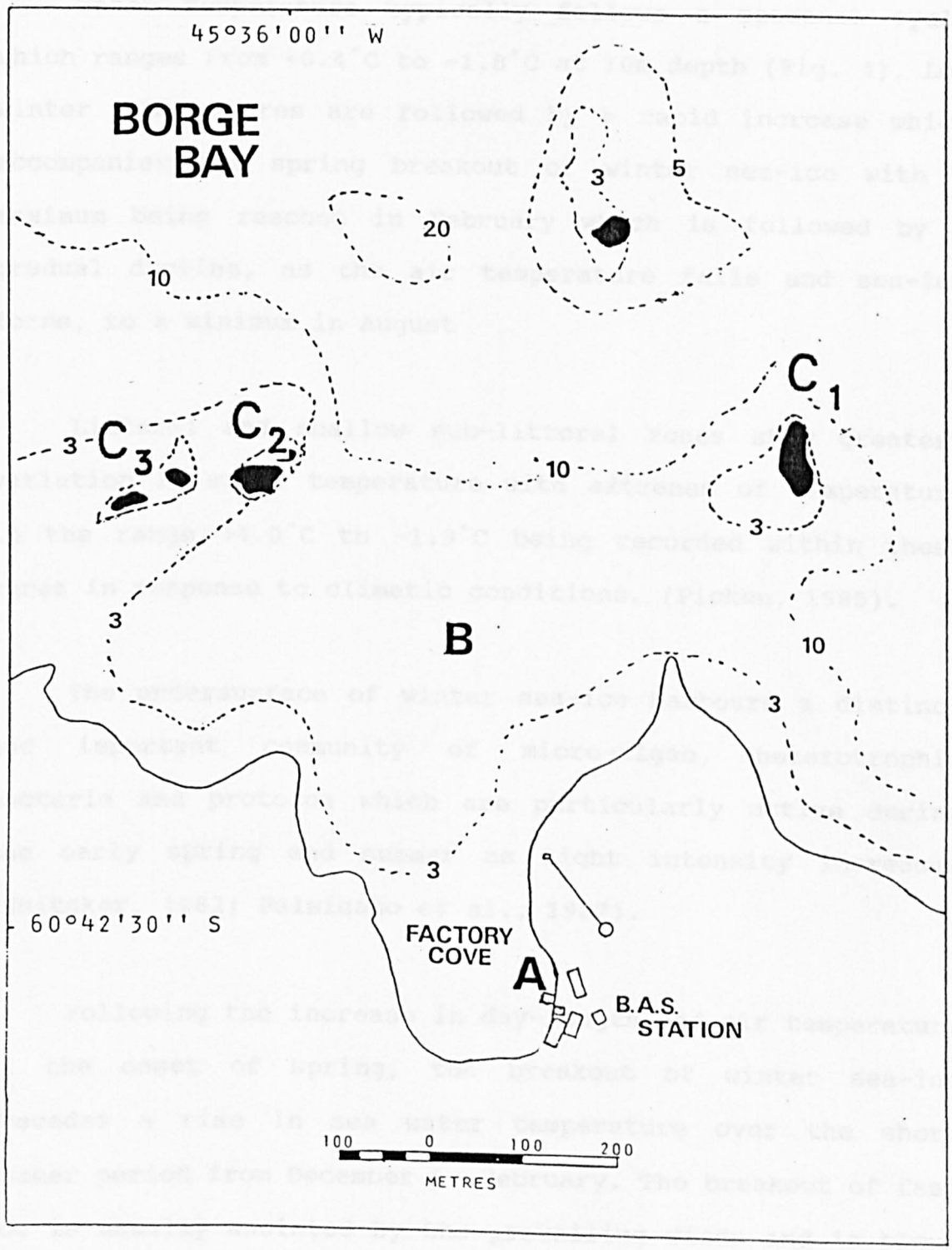


Figure 3. Map of Factory Cove showing the location of the British Antarctic Survey (B.A.S.) station and the sampling sites refered to in the course of the text. Depth contours in metres. A = *Nacella concinna* collection site, B = *Yoldia eightsi* collection site, C_1 - C_3 = Dominican Gull midden collection sites.

Water temperature typically follows a seasonal cycle which ranges from +0.4°C to -1.8°C at 10m depth (Fig. 4). Low winter temperatures are followed by a rapid increase which accompanies the spring breakout of winter sea-ice with a maximum being reached in February which is followed by a gradual decline, as the air temperature falls and sea-ice forms, to a minimum in August

Littoral and shallow sub-littoral zones show greatest variation in water temperature with extremes of temperature in the range +4.0°C to -1.9°C being recorded within these zones in response to climatic conditions. (Picken, 1985).

The undersurface of winter sea-ice harbours a distinct and important community of micro-algae, heterotrophic bacteria and protozoa which are particularly active during the early spring and summer as light intensity increases (Whitaker, 1982; Palmisano *et al.*, 1987).

Following the increase in day-length and air temperature at the onset of spring, the breakout of winter sea-ice precedes a rise in sea water temperature over the short summer period from December to February. The breakout of fast ice is usually assisted by the prevailing winds and is blown out into open water. Directly preceding the breakout of the annual sea-ice cover, the melting sea ice community releases both flocs of organic matter to the sediment and autotrophs to the water column, thus seeding the inshore algal bloom (Sakshaug and Holm-Hansen, 1984).

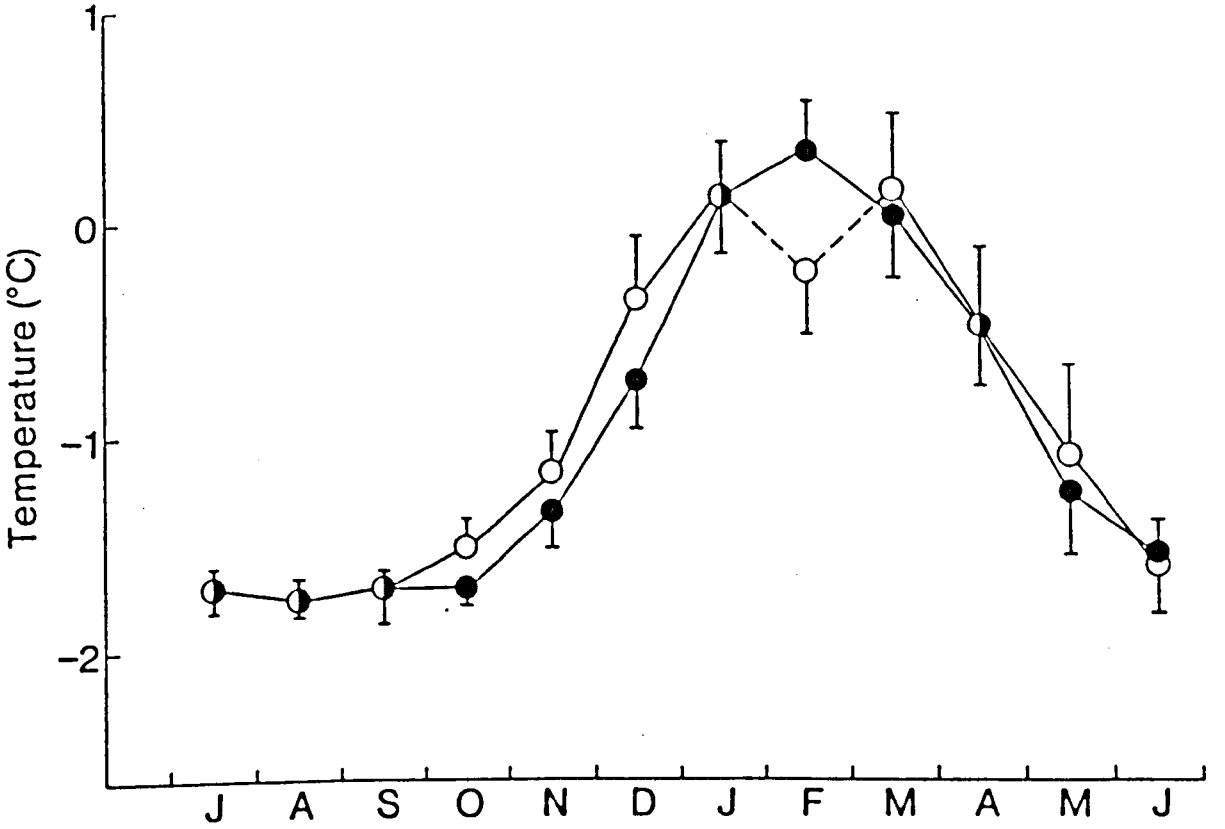


Figure 4. Seasonal variation in water temperature (°C) at 6m in Factory Cove (Open circles) and at 10m at a deep water site at the edge of Borge Bay (Closed circles) Signy Island over the period 1969 - 1982 (From Clarke et al, 1988). Data presented as mean ± 95% confidence intervals.

With high levels of macronutrients (Nitrate 28-30mg-atom/m^3; Phosphate, 2.0-2.2mg-atom/m^3; Silicate 85-90mg-atom/m^3) in the inshore waters, an input of terrigenously derived macronutrients through run-off and stability of the water column, the main period of primary production is induced, in both the planktonic and benthic phytoplankton communities (Clarke *et al.*, 1988) (Fig. 5).

Shortly after the peak of the spring bloom and prior to the formation of winter sea ice the vertical downward flux of organic material in the form of faecal pellets, flocs and bloom derived material, effectively couples benthic production with that of the overlying water column (Fig. 6) (Clarke & Price, unpubl. data), a feature commonly observed in deep-sea environments (Gilkinson *et al.*, 1986).

Yearly variation in the standing stock of phytoplankton and the abrupt tail-off of the phytoplankton bloom appears to be unrelated to the date of disappearance or duration of the winter fast ice cover or the length of time that the sea-water temperature is above -1°C. The bloom does not appear to be nutrient limited (Heywood and Whitaker, 1984; Priddle *et al.*, 1986) with the vertical stability of the water column and a low occurrence of wind induced turbulence suggested to be the most important factors influencing the size and intensity of the phytoplankton bloom in inshore waters (Kopczynska, 1981; Sakshaug and Holm-Hansen, 1984; Whitaker, 1982; Clarke 1988). Similarly the productivity of the benthic bloom is affected, in inshore conditions, by the increase in

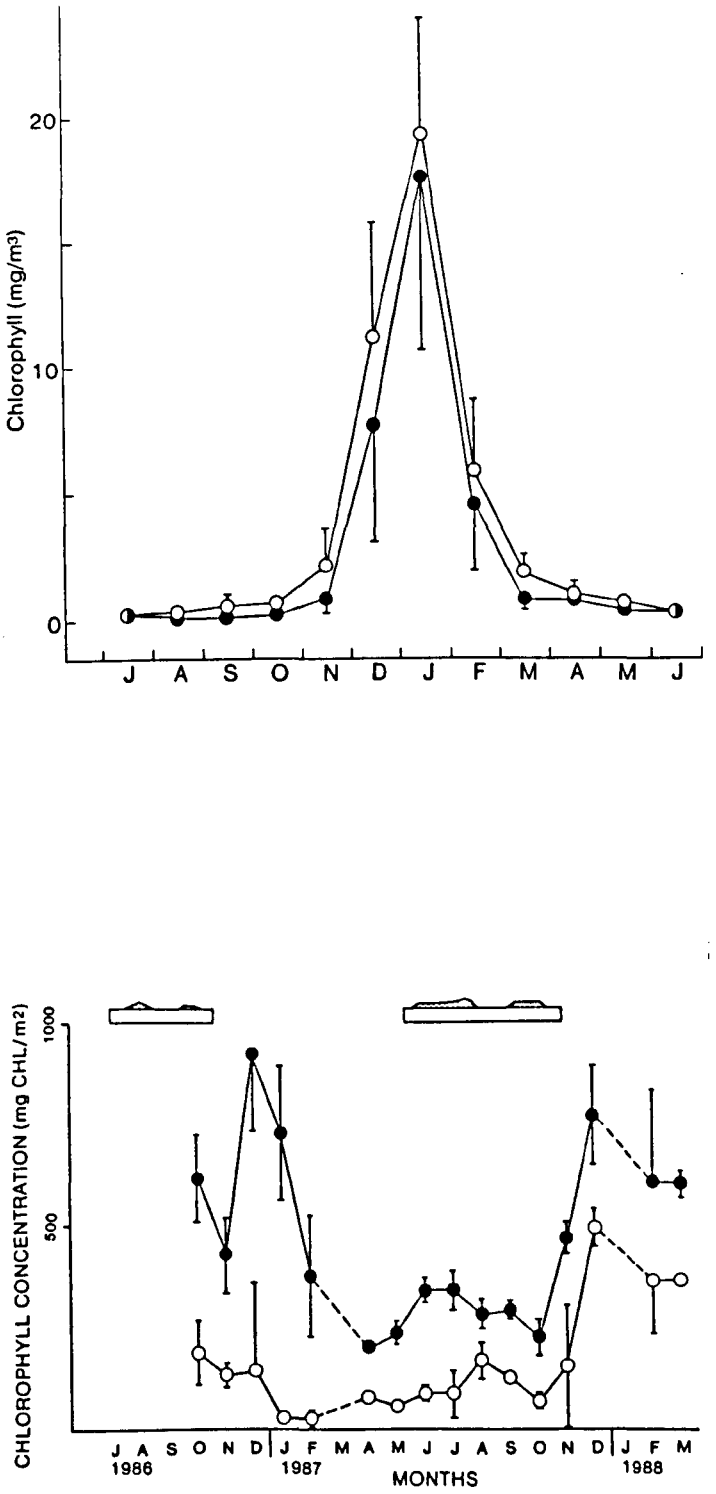


Figure 5. A) Seasonal variation in the standing crop of phytoplankton (Chl a) at 6m (Open circles) and 10m (Closed circles) from the inshore waters of Signy Island, taken over the period 1969 - 1982 (After Clarke *et al.*, 1988) and B) Seasonal variation in the Benthic algal biomass of Factory Cove. Open circles, chlorophyll a, closed circles, total chlorophyll (After Gilbert 1990). Both data sets presented as mean ±95% confidence limits.

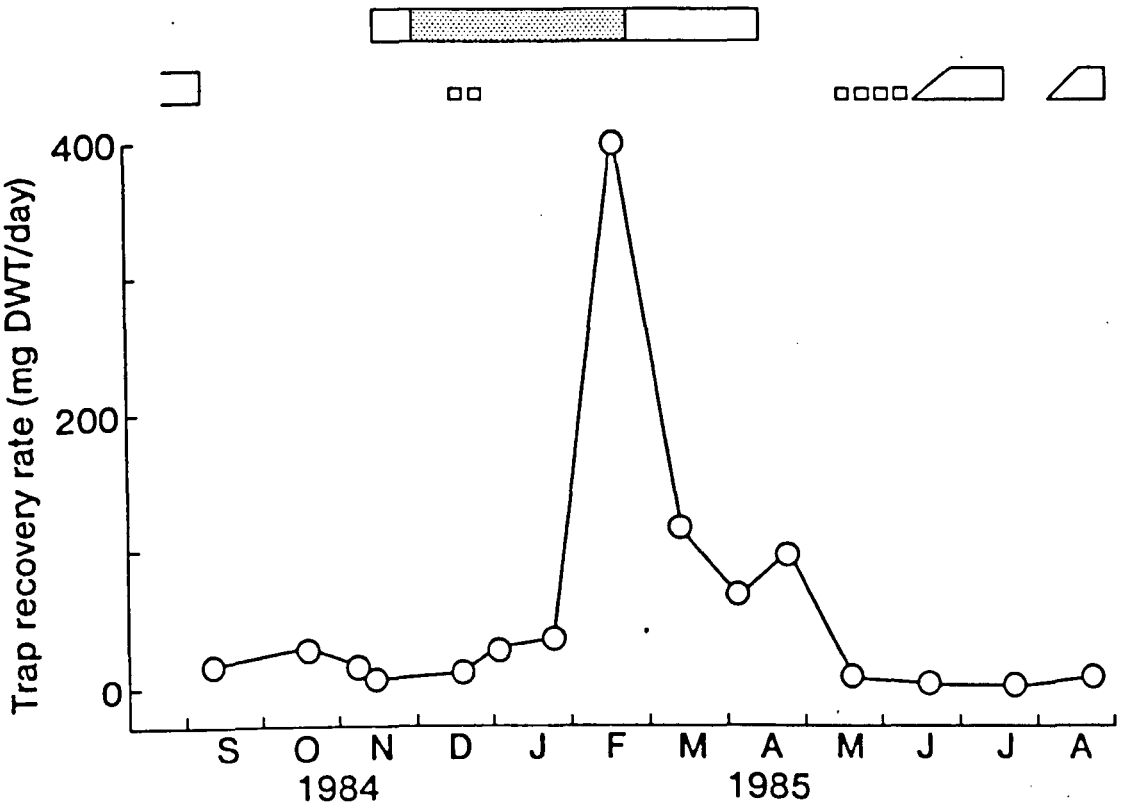


Figure 6. The seasonal pattern of sedimentation at a depth of 3m in Borge Bay, Signy Island. Data presented as Sediment trap recovery rate (mg Dry weight (DWT) per day) over the period September 1984 to August 1985. Upper bar represents duration of inshore phytoplankton bloom with hashed area denoting the peak period of the bloom. Square symbols = brash ice, Wedge shape symbols = periods of fast ice (After Clarke and Price, unpublished data).

intensity of solar radiation and penetration following the disappearance of the sea-ice (White, 1973).

The population dynamics of both pelagic and benthic herbivores and their survivorship and input to higher trophic levels are therefore inexorably linked to the pattern of variation in the intensity of the annual planktonic and benthic blooms.

CHAPTER 2

The chemical and physical characteristics of the inshore waters of Signy Island.

2.1 Introduction

The physiology of formation of molluscan shell has been the subject of frequent reviews (Wilbur, 1964, 1972; Wilbur and Simkiss, 1968; Grégoire, 1972, Crenshaw, 1980). Shell material is deposited during periods of aerobic respiration with calcium and bicarbonate ions entering through the outer mantle epithelium to sites where crystals of calcium carbonate are formed (Wilbur, 1984). The blood of many bivalves has an ionic strength and calcium content close to that of ambient sea water but generally has a significantly higher carbon dioxide content. This results in a relatively high blood pH (7.70-7.52) with the majority of carbon dioxide being present as carbonate or bicarbonate ions and a significantly greater carbonate alkalinity than surrounding sea-water. The accumulation of calcium or other cations involved in the formation of shell carbonate is accomplished through a combination of dietary intake, differential absorption from ambient seawater or by the solution of previously deposited shell material.

The carbon dioxide/carbonate/bicarbonate system in the sea is complex and provides the ions required for molluscan shell formation. This system is regulated by pH and

temperature. At low water temperatures seawater has a higher alkalinity than warmer waters, is saturated with bicarbonate ions and show a greater solubility for oxygen and carbon dioxide.

Temperature and salinity fluctuations and their effects on skeletal carbonate mineralogy have received much attention (Lowenstam, 1954a, 1954b, 1964; Kennedy *et al*, 1969). In the majority of bivalves an inverse relationship exists between the percentage of calcite in the shell and the mean temperature of the environment inhabited by the bivalve. The precipitation of calcite and aragonite, the main biogenically deposited carbonate forms, is adversely affected by low temperatures. These have the effect of increasing the solubility products of the carbonates and as a consequence increase the energy required by the animal to precipitate shell carbonate under these conditions. This feature is concomitant with the general observations of decreased calcification at low water temperatures (Ansell, 1968; Graus, 1974) and a tendency towards thin, fragile and chalky shells in polar molluscs (Nicol, 1967b).

Theoretically there should be no limitations to the availability of either calcium or carbonate ions within polar waters. The chemical oceanography of Antarctic inshore waters has, however, received little attention with a lack of available information on the seasonal pattern of the parameters affecting the carbon dioxide system and cations involved in the formation of molluscan shell. The measurement

and interpretation of these parameters is therefore of importance in understanding the physico-chemical factors which may limit or control shell formation in Antarctic molluscs.

2.2 Materials and Methods

During the austral spring and summer of 1985/86 and throughout 1987/88, daily and bimonthly water samples, respectively, were taken from Factory cove at a depth of 10m. Temperature *in situ* was recorded using 3 standard oceanographic reversing thermometers and the samples sealed and transferred to the laboratory on Signy Island for analysis. Sub-samples of the samples taken during 1985/86 were removed for calcium, magnesium and strontium determination and stored at -20°C in acid washed polypropylene bottles prior to analysis in the U.K.. The remainder of the sample was used in the pH method of determination of carbonate species in sea-water (Strickland and Parsons, 1972).

50ml of the sample was warmed to 20° - 25°C and the pH measured subsequent to and after the addition of 12.5mls of 0.01N HCl. The quantification of carbonate species was determined for each sample by the application of the algorithms presented by Strickland and Parsons (1972).

Samples taken during 1985/86 were analysed after dilution for calcium, strontium and magnesium on an *Instrumentation Laboratory Video 11* atomic absorption spectrophotometer using standard air/acetylene flame techniques.

Salinity of collected water samples (1985/86) was measured within 30mins of collection using a *Plessey Environmental Systems* salinometer calibrated daily with Standard sea-water.

2.3 Results

Samples taken over the period from February 1987 to December 1988 covered one summer and two winter seasons. The maximum temperature recorded during this period was -0.84°C in February 1987 with a minimum of -1.86°C occurring in July of the same year. During 1988 the temperature regime was slightly shifted with the highest water temperature recorded in March and the lowest in August. The general yearly pattern evident over 1987 and 1988 (Fig. 7) starts in early November with a significant rise in water temperature from the stable winter low, reaching a maximum towards the end of the summer in February to March. An abrupt decline follows this period with water temperatures steadily declining over a period of two months to a winter low in May/June which remains relatively stable over the July to November winter period.

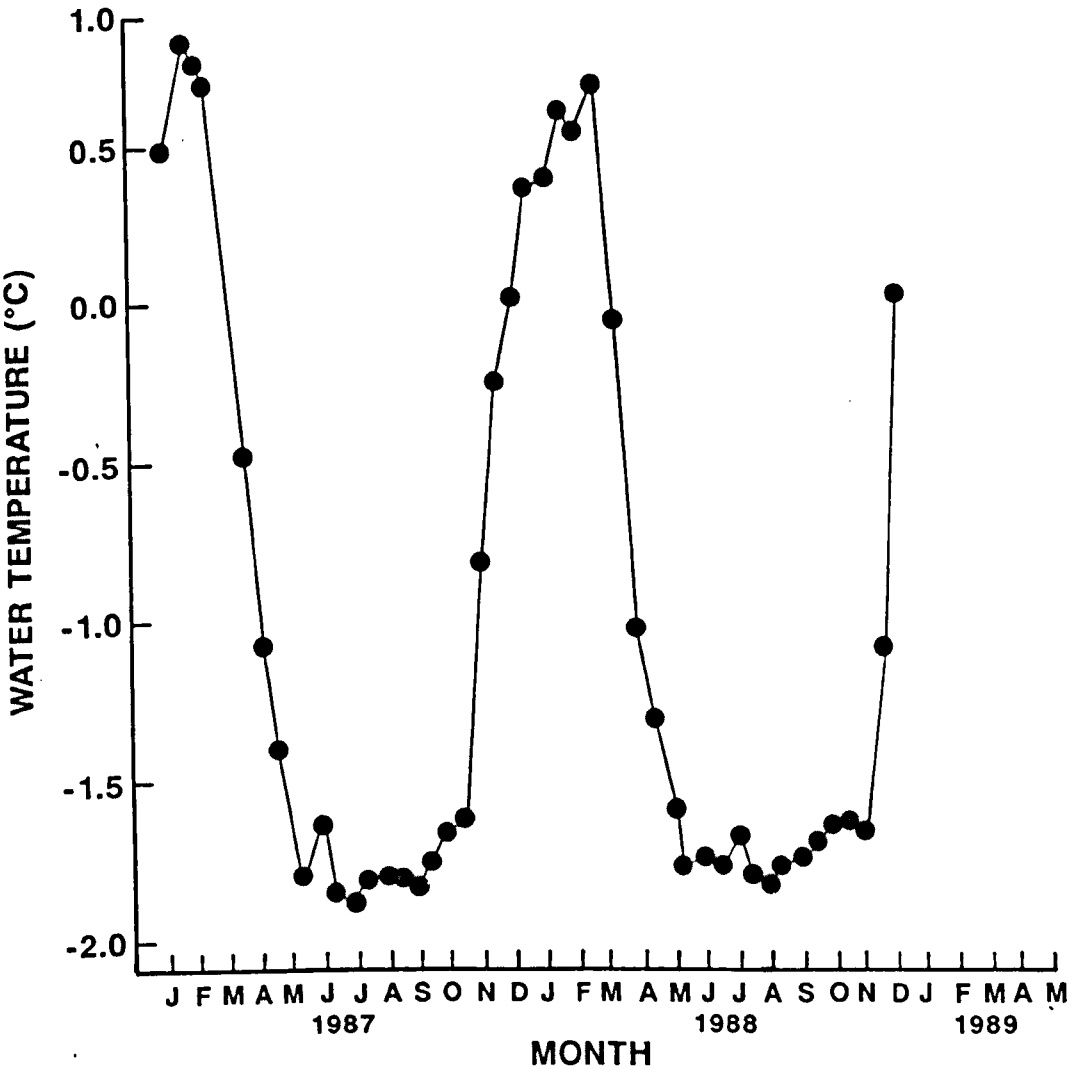


Figure 7. The seasonal cycle of seawater temperature in Factory Cove, Signy Island. Bimonthly measurements taken over the period February 1987 to December 1988, 95% confidence levels obscured by data points.

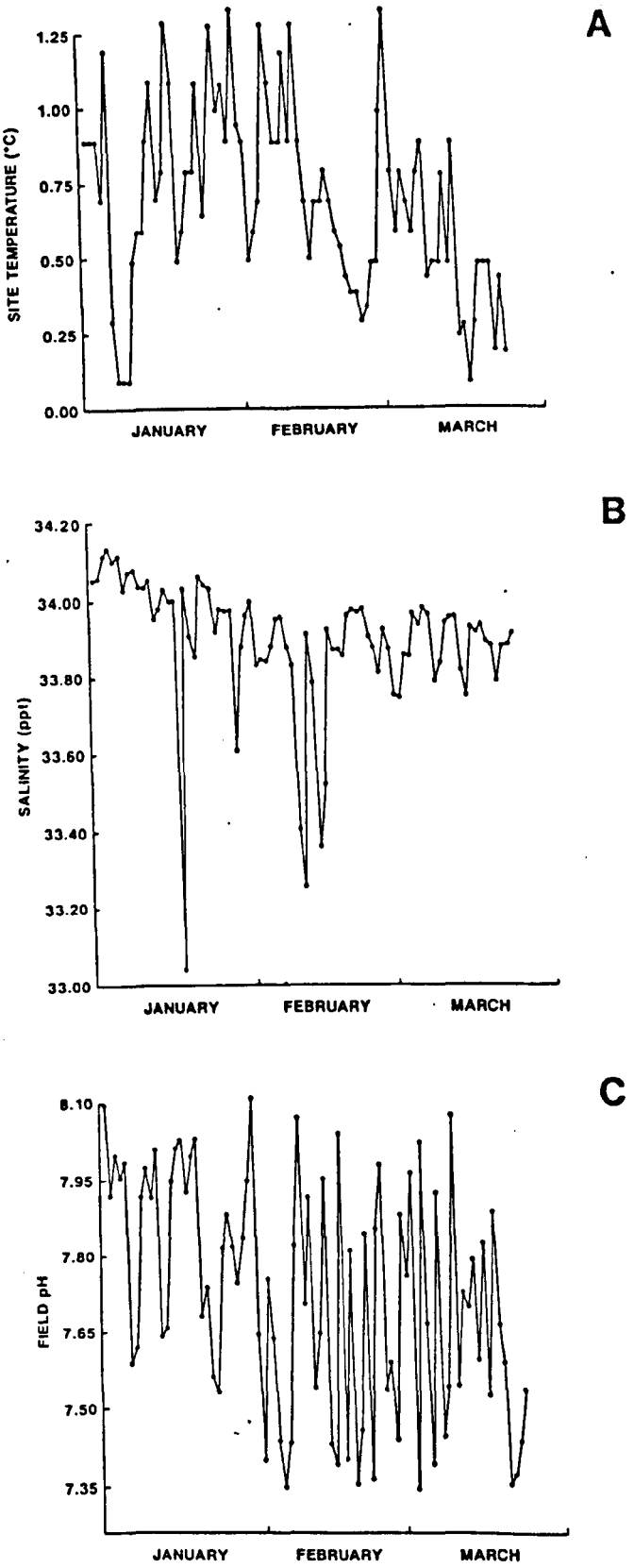


Figure 8. The seasonal pattern of variation in A ; Site temperature, B ; Salinity and C ; Field pH in the inshore waters of Factory Cove, Signy Island from January 1986 - March 1986.

Water temperature during the summer period of January to March 1986 ranged from +0.1°C to +1.35°C with an average over the three months of +0.71°C (Fig. 8a). Daily temperatures were highly erratic and apart for a period of 14 days during the end of February, showed no obvious trend or pattern to their variations. During this period, however, water temperature dropped from +1.26°C to +0.26°C

Salinity measurements taken during the period of February to December varied from 33.045$^{o}/_{oo}$ to 34.148$^{o}/_{oo}$ and were highly erratic responding to brief periods of terrigenously derived melt water during the summer (Fig. 8b).

Using the equation :

$$FP = - 0.0966\ Cl - 0.0000052\ Cl^{3} \quad \text{(Thompson, 1932)}$$

(where FP = Freezing point and Cl = Chlorinity), a theoretical freezing point of -1.85°C is obtained for the average salinity over the study period of 33.91$^{o}/_{oo}$. This is slightly higher than the observed coldest water temperature but is representative of the "initial" freezing point of the sea water, namely the temperature at which an infinitely small amount of ice is in equilibrium with the solution. Further to this point and as soon as any ice has formed the concentration of the dissolved solids, or brine, increases and hence the formation of additional ice can take place only at a lower temperature. Observations confirming a lower than expected sea water temperature have been reported for the

inshore waters of Signy Island suggesting that the phenomenon may be associated with very low air temperatures in combination with the formation of sea ice (Clarke *et al.*, 1988).

The measurements of total alkalinity over the two periods are presented in Figure 9. Throughout the two year period values varied erratically around a mean of 2.325 millieq/l and ranged from 1.778 to 2.784 millieq/l with no obvious seasonal trend. The daily analysis of samples taken throughout the summer period of January to March 1986, however, shows a definite trend with total alkalinity dropping steadily from late January to the beginning of March and then returning to its January level by the end of March. Values ranged from 0.275 millieq/l to 2.877 millieq/l with an average value of 2.158 millieq/l over this period.

Carbonate alkalinity (0.225 - 2.827 millieq/l), total carbon dioxide (22.02 - 286.79 mols/l x 10^{-5}) and bicarbonate ion concentration (20.83 - 271.72 mols/l x 10^{-5}) (Fig. 10a) show a similar trend but apart for a weak tendency towards a low at the end of February no corresponding pattern is evident in either partial pressure of carbon dioxide (1071 - 9214 kPa), dissolved carbon dioxide (0.334 - 14.699 mols x 10^{-5})(Fig. 10b) or carbonate ion concentration (0.239 - 14.71 mols x 10^{-5}) over this period.

No obvious pattern was evident in these parameters over the period sampled from February 1987 to December 1988 though

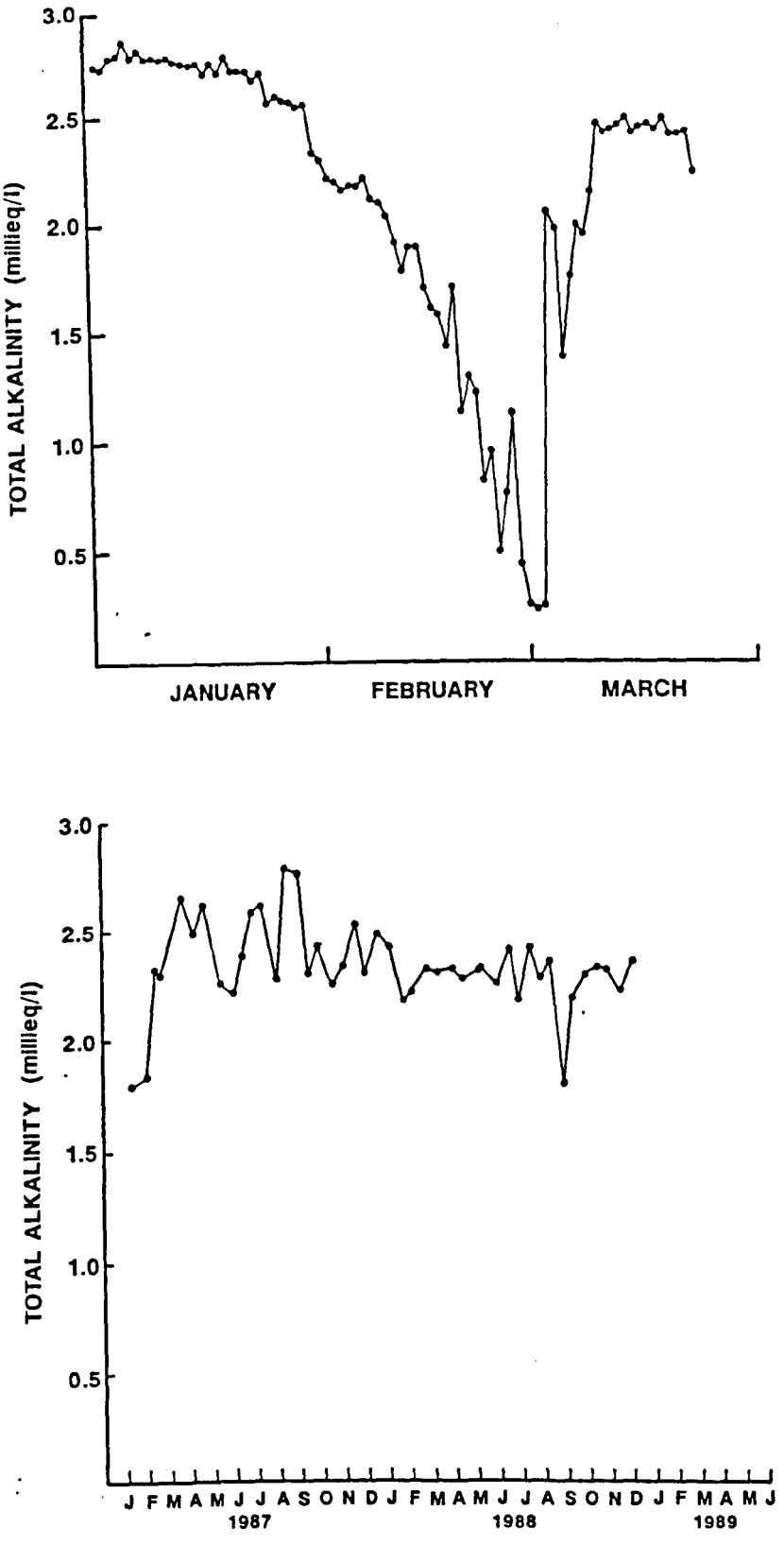


Figure 9. The seasonal and yearly pattern of flux in total Alkalinity (milleq/l) of the inshore waters of Factory Cove, Signy Island. a) Daily measurements from January 1986 - March 1986 and b) Bimonthly measurements from January 1987 - December 1988.

less variation was evident over this interval. pH Values over the two periods ranged from 7.35 to 8.12 (Fig. 8c) and 7.73 - 8.62 respectively corresponding to mean values of 7.74 and 8.14. These results are summarised in Tables 1 & 2.

Calcium, strontium and magnesium concentrations showed little variation throughout the range of measurements (Fig. 11) with mean values of 395 ± 4.92 mg/l, 7.41 ± 0.13 mg/l and 1315.5 ± 24.3 mg/l respectively. No significant trends were evident when analysed statistically with correlation coefficients (R^2) of 8.6%, 50.2% and 22.6% recorded respectively for the relationship of calcium, strontium and magnesium levels with time.

Strontium levels show a peak towards the end of January which corresponds to the period during which the minimum salinity was recorded (Fig. 11c). This feature is not evident in calcium or magnesium levels and is suggested to be in response to a period of melt and associated runoff of terrigenously derived strontium rich water.

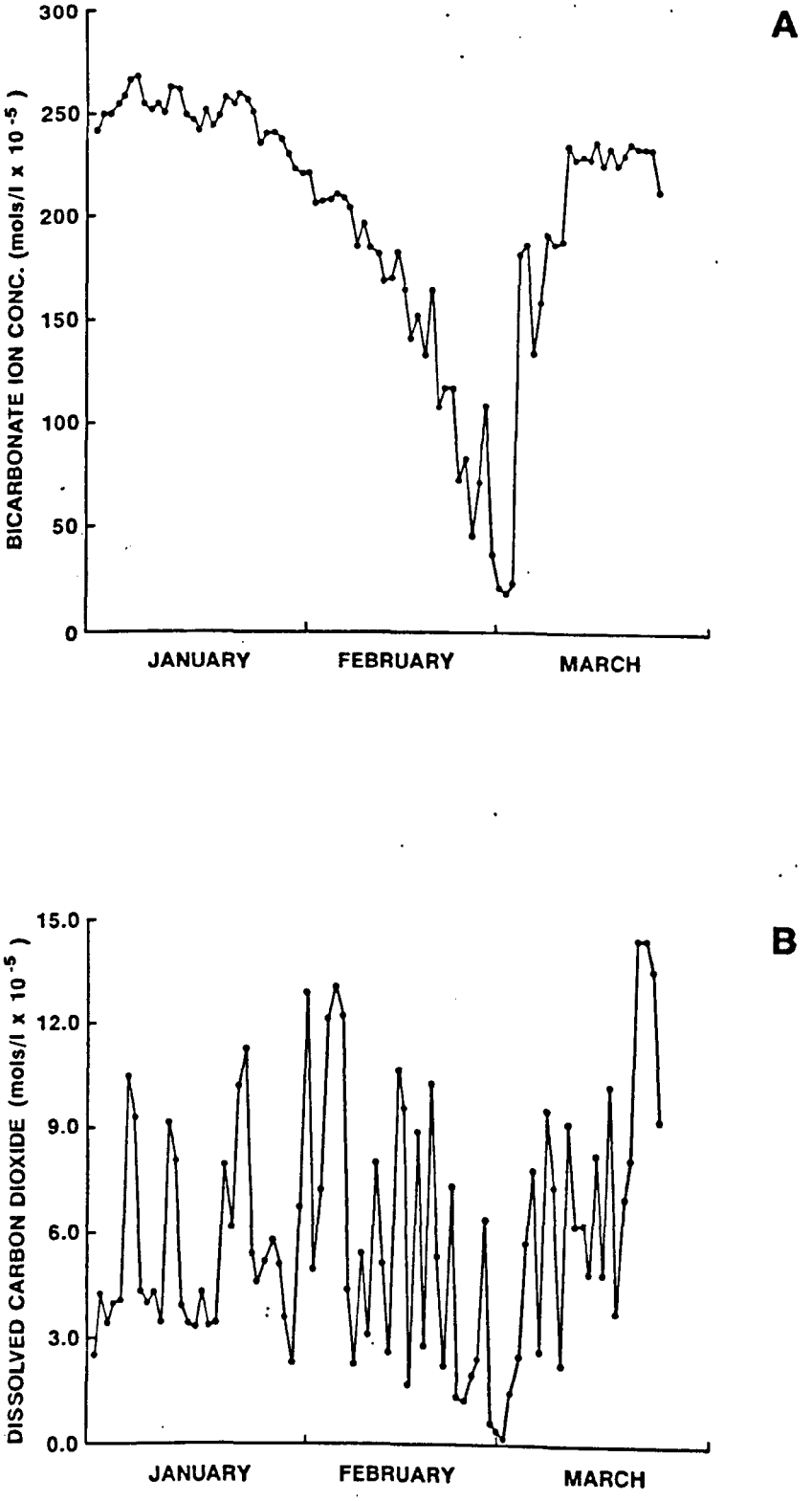


Figure 10. The seasonal pattern of; A, Bicarbonate ion concentration and B, Dissolved Carbon dioxide in the inshore waters of Factory Cove, Signy Island from January 1986 - March 1986.

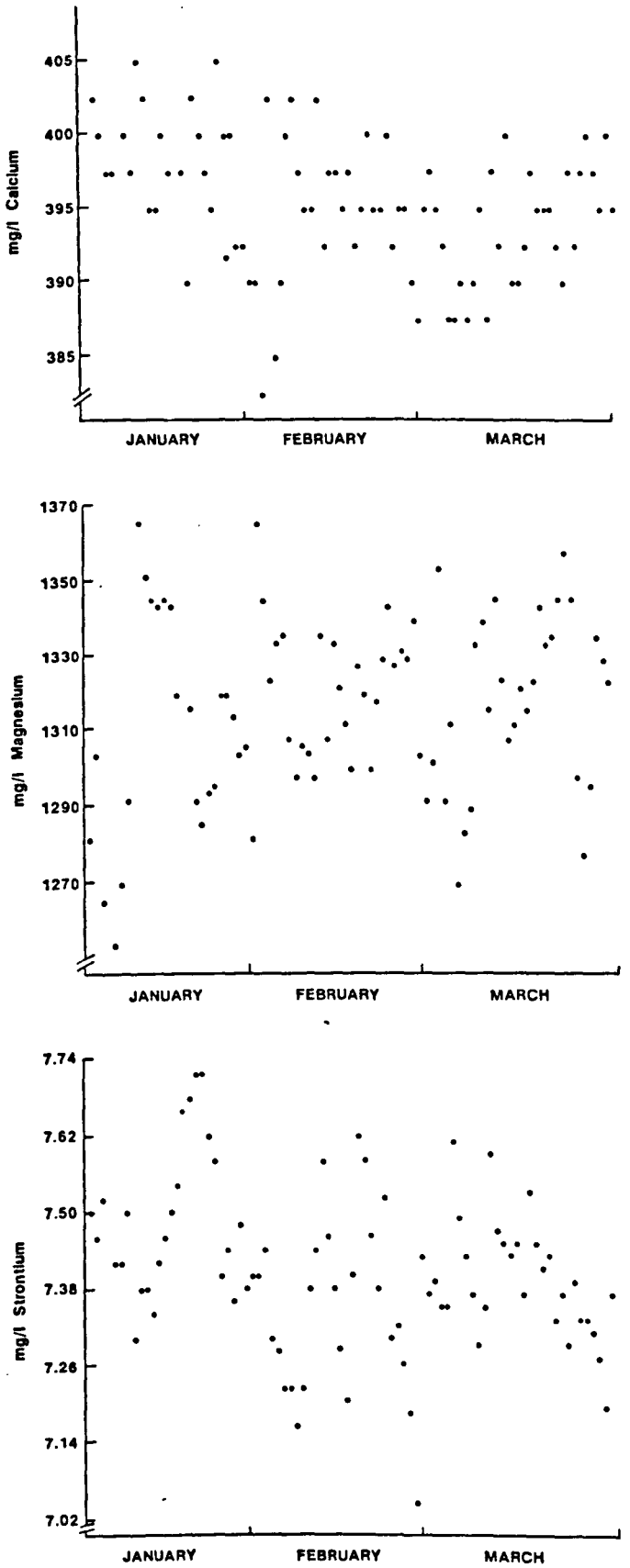


Figure 11. The concentration (mg/l) of a) Calcium, b) Magnesium and c) Strontium in the inshore waters of Factory Cove, Signy Island during the period January 1986 to March 1986.

Table 1. Summary statistics of seawater analyses of daily samples (N = 83) taken between 08, January 1986 and 31, March 1986. Alk. = Alkalinity, millieq = milliequivalents, kPa = kilo Pascals, pCO_2 = Partial pressure of CO_2, $^{o}/_{oo}$ = parts per thousand.

	MEAN	MEDIAN	STDEV	MIN	MAX
Total Alk. (millieq/l)	2.158	2.431	0.69	0.275	2.877
Carbonate Alk. (millieq/l)	2.128	2.421	0.69	0.225	2.827
Total CO_2 (mols/l x 10^{-5})	213.75	241.63	68.28	22.02	286.79
pCO_2 (kPa)	9584	8345	5571	524	23055
Dissolved CO_2 (mols/l x 10^{-5})	6.11	5.32	3.55	0.33	14.70
$[HCO_3^-]$ (mols/l x 10^{-5})	202.29	228.48	64.61	20.83	271.72
$[CO_3^{2-}]$ (mols/l x 10^{-5})	5.31	4.59	3.41	0.24	14.71
Site Temperature (°C)	0.71	0.70	0.32	0.10	1.35
Field pH	7.74	7.75	0.23	7.35	8.12
Salinity ($^{o}/_{oo}$)	33.907	33.939	0.18	33.045	34.148
Calcium (mg/l)	395.60	395.00	4.92	382.50	410.00
Strontium (mg/l)	7.41	7.40	0.13	7.04	7.72
Magnesium (mg/l)	1315.5	1318.0	24.3	1252.0	1364.0
Ca/Sr	53.41	53.46	1.05	51.17	56.11
Mg/Ca	3.28	3.28	0.09	3.08	3.49

Table 2. Summary statistics of seawater analyses of bi-monthly samples (N = 45) taken between 02, February 1987 and 31, December 1988. Alk. = Alkalinity, millieq = milliequivalents, kPa = kilo Pascals, pCO_2 = Partial pressure of CO_2, ppt = Parts per thousand.

	MEAN	MEDIAN	STDEV	MIN	MAX
Total Alk. (millieq/l)	2.325	2.315	0.21	1.778	2.784
Carbonate Alk. (millieq/l)	2.259	2.256	0.20	1.708	2.644
Total CO_2 (mols/l x 10^{-5})	215.98	218.02	17.12	162.28	242.23
pCO_2 (kPa)	3681	3452	1504	1071	9214
Dissolved CO_{2_5} (mols/l x 10^{5})	2.35	2.20	0.96	0.68	5.87
$[HCO_3^-]$ (mols/l x 10^{-5})	201.35	205.00	15.51	151.40	224.54
$[CO_3^{2-}]$ (mols/l x 10^{-5})	13.30	10.89	6.49	4.72	35.85
Site Temperature (°C)	-0.98	-1.60	0.96	-1.86	0.84
Field pH	8.14	8.10	0.17	7.73	8.62

2.4 Discussion

Levels of the major constituents calcium, magnesium and strontium in the inshore waters of Factory Cove lie close to, or within the ranges of 1256-1272 mg/l Magnesium, 396-400 mg/l Calcium and 7.7-13.0 mg/l Strontium, reported by other workers for ocean waters of similar salinity (Sverdrup *et al*, 1942; Nicol, 1967b; Kalle, 1971; Millero, 1974; Riley and Skirrow, 1975).

The essential steps in the seawater carbonate equilibria are ;

$$CO_2(\text{gaseous}) \rightleftharpoons CO_2(\text{Aqueous})$$

$$H_2O + CO_2(\text{Aq.}) \rightleftharpoons H_2CO_3$$

$$H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$$

$$HCO_3^- \rightleftharpoons H^+ + CO_3^{2-}$$

with the relative proportions of these four major forms of inorganic carbon depending on the temperature, pressure, pH and salinity. The interconversion routes between dissolved CO_2, H_2CO_3 and HCO_3^- are probably best depicted by ;

$$\begin{array}{ccc} H^+ + HCO_3^- & \rightleftharpoons & H_2CO_3 \\ \searrow\!\!\!\searrow & & \swarrow\!\!\!\swarrow \\ & CO_2 + H_2O & \end{array}$$

As carbon dioxide is removed from seawater, bicarbonate dissociates to rebalance the system. This results in a

relatively stable dissolved concentration and partial pressure of carbon dioxide and a decline of bicarbonate species as the carbon dioxide is used, until the excesses of the demand can be compensated for by the solution of atmospheric carbon dioxide into the water mass.

Clarke *et al*, (1988) have collated and reviewed seawater nutrient and chlorophyll data for Factory Cove over a 13 year period from 1969 - 1982. The development and variation in the standing stock of the annual phytoplankton bloom and the level of macronutrients is analysed over this period and reveals a typical annual trend in bloom occurrence and duration. Negligible winter chlorophyll levels (0.23mg/m^3; minimum monthly mean) begin to increase as the bloom begins in November reaching peak chlorophyll biomass (22.4 - 50.9mg/m^3) in mid-January. The bloom then declined rapidly reaching winter levels by March. Associated with the increase in phytoplankton biomass was an extensive depletion in the levels of nitrate (28-30mg-atom/m^3 to 13-16mg-atom/m^3) , phosphate (2mg-atom/m^3 to 1.2mg-atom/m^3) and silicate (85mg-atom/m^3 to 65mg-atom/m^3) . Minima for these nutrients typically occurred in January and February with a gradual recovery to pre-bloom levels over winter.

In 1986 the decrease in total alkalinity, carbonate alkalinity, total carbon dioxide and bicarbonate ion concentration during the summer period began to occur during mid to late-January and recovered in early March. This is concurrent with the timing of nutrient depletion and the

decline of the bloom described by Clarke *et al* (1988) and represents the removal of carbon by phytoplankton during this period. The depletion of dissolved carbon dioxide alters the equilibrium states of the other elements in the carbonate system decreasing the bicarbonate concentration and by so doing reduces the total alkalinity. The standing stock at the peak of the bloom depletes nutrient and bicarbonate levels significantly, with the nutrient and total alkalinity minima, occurring after this event, representing the continual reduction of these parameters as the season progresses. Pre-bloom bicarbonate and nutrient levels are restored following the decline of the phytoplankton community and the reduction of phytological demands.

The carbonate system is relatively stable during the winter period, with most anomalies occurring in response to physical or biological events during the spring and summer.

Despite the seasonal decrease in total alkalinity and related carbonate species in the waters of Factory Cove, levels of these ions and those of calcium, strontium and magnesium, necessary for the biogenic production of skeletal carbonate, are sufficient to suggest that the chemical environment of Factory Cove does not appear to limit the growth of shell forming organisms.

CHAPTER 3

Ecological aspects of growth in the Antarctic limpet *Nacella concinna*.

3.1 Introduction

The patellid limpet *Nacella (Patinigera) concinna* (Strebel, 1908), is the dominant and most conspicuous shallow water macro-invertebrate of the maritime Antarctic region. The type locality is South Georgia (54° 16′ S, 26° 30′ W), and it has been recorded from the South Orkney Islands, Bouvetϕya and Seymour, Paulet, Wandel, Anvers and Petermann Islands and the Antarctic peninsula (Powell, 1951, 1960, 1965; Dell, 1964, 1990). *N. concinna* occurs from the intertidal to 110 m depth (Powell, 1973), and at Signy Island, South Orkneys (60° 43′S, 45° 38′W), it accounts for approximately 83% of the prosobranch biomass and 3% of prosobranch numbers on rocky substrates in the depth range 0 - 12m (Picken, 1980b).

Powell (1973) recognised two distinct forms of *Nacella concinna* from specimens collected at South Georgia. These were a shallow water "polaris" form and a deeper water, more typical, "concinna" form, separated on the basis of shell profile and morphology. Typical shells of the "polaris" form possess a central to anterior third apex and have a moderately thin but robust shell, while those of the "concinna" form have the apex in the anterior third and possess a thin and fragile shell (Fig. 12)

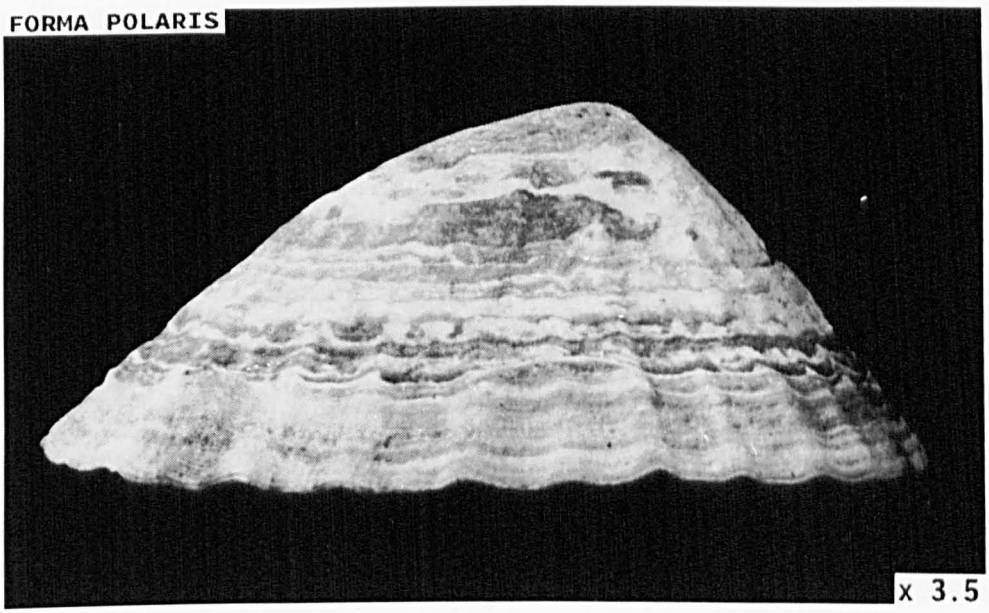
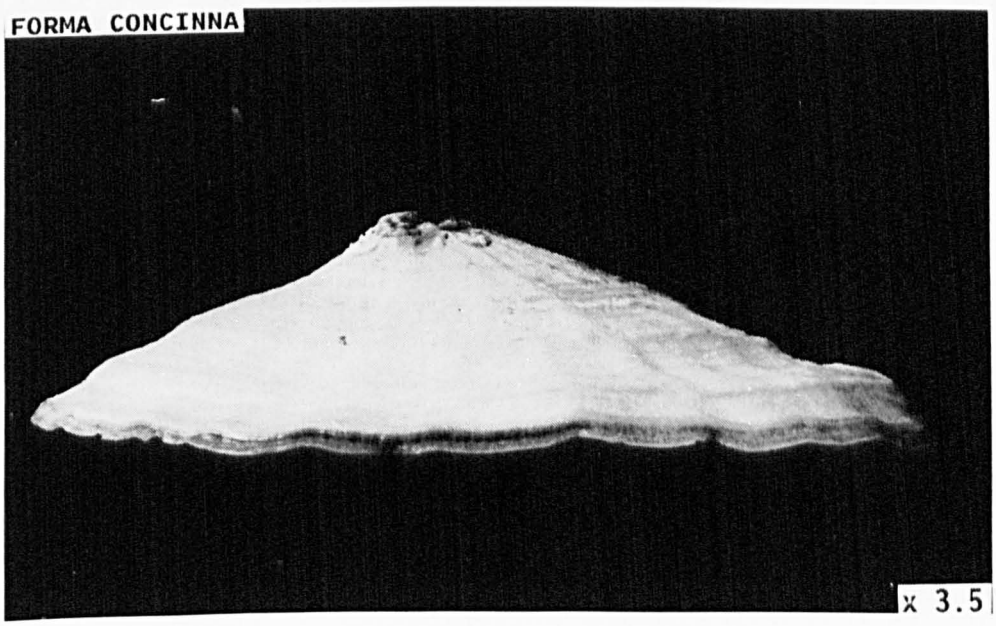


Fig. 12. Examples of the shallow water *polaris* and the deeper water *concinna*, forms of the Antarctic limpet *Nacella concinna* as recognised by Powell (1973).



Walker (1972) recognised the "polaris" form of *Nacella* as the only form present in the nearshore and littoral environment of Signy. Walker separated this population into two distinct sub-groups, one in the littoral zone, the other in the deep sub-littoral zone, below 4m. These exist as discrete morphological groups overlapping only at zone edges during summer. Differences in the shell height to shell length ratio characterise these groups with typical littoral shells having a greater shell height for a given length than those of the deep sub-littoral group (Fig. 13). At the onset of winter there is an migration of littoral animals into the shallow sub-littoral, producing a mixed winter population in this zone. This is associated with falling air temperatures, increasing wave action, an increase in bird predation and the formation of a detrimental ice film in the littoral zone (Walker, 1972). At Palmer Station, Anvers Island (64° 46'S, 64° 05'N), *N. concinna* has been reported to respond to low temperatures and exposure to anchor ice by secreting a highly viscous mucus sheath which prevents extracellular ice formation down to -10°C and inhibits the external growth of ice crystals (Hargens & Shabica, 1973).

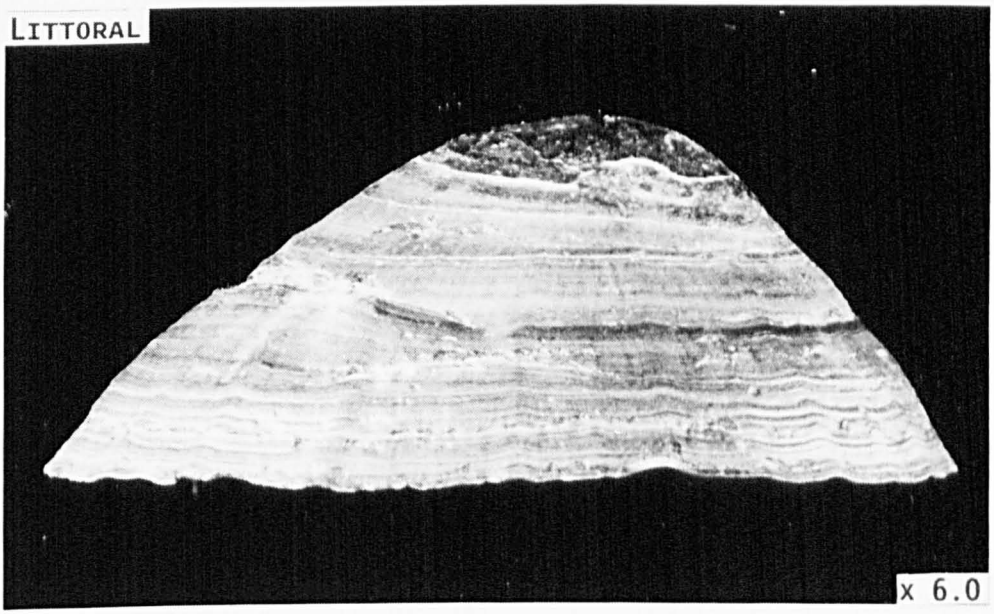
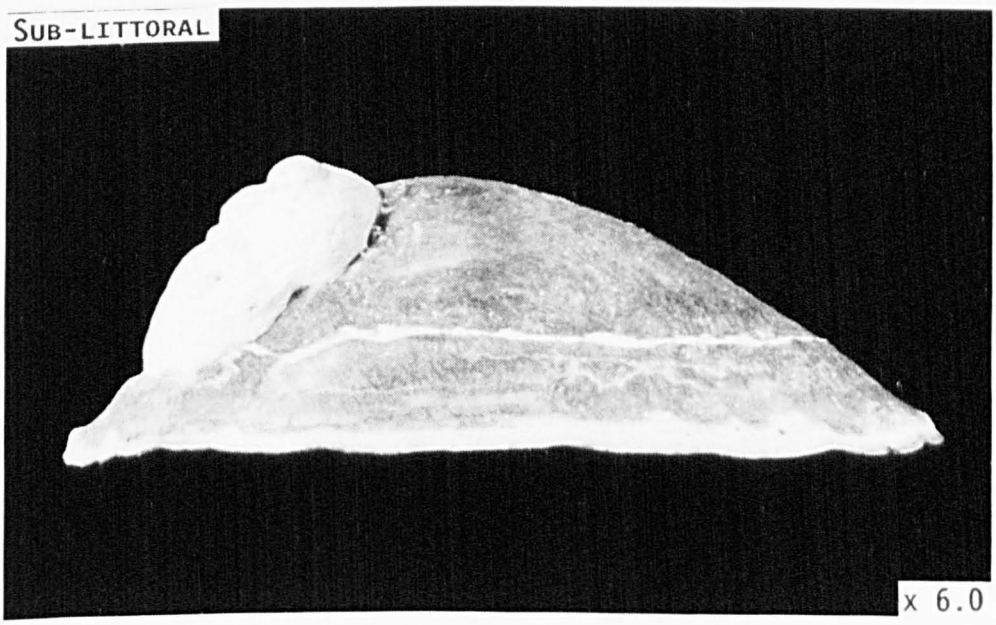


Fig. 13. Typical shell types of littoral and sub-littoral *Nacella concinna* from the inshore population of Signy Island, South Orkney Islands.



3.2 Materials and Methods

Nacella concinna were collected from littoral and sub-littoral areas of Factory Cove, Signy Island, South Orkney Islands (Fig. 3), during the austral summer from November 1985 to April 1986. Sub-littoral animals were collected from depths of between 3m and 5m , by SCUBA diving, and littoral animals were collected from the area around the station jetty and at Knife Point in Factory Cove (Fig. 3). In each case all animals over 10mm shell length occurring within two 10m x 2m transects were collected. This lower shell length limit was chosen following the observations of Walker (1972) of a change in the shell length/height relationship being evident only in those animals over 20mm in length.

Shell length, height and width were measured to ± 0.01 mm with Vernier calipers. The tissues were then excised, blotted gently and the wet mass determined. Dry mass was measured after drying at 60°C for 24 hrs, and ash content calculated following ignition at 550°C in a muffle furnace for 12 hrs. Shell mass was measured to ± 1mg in air and in distiled water at 20°C, and the density of the shell calculated. Internal shell volume was determined from the weight of distiled water which would fill a level upturned shell. The presence of epibiota and the sex of mature individuals were recorded.

Shell chlorophyll content (that is the chlorophyll within the shell matrix) was determined in 5 freshly shucked

Shell chlorophyll content (that is the chlorophyll within the shell matrix) was determined in 5 freshly shucked individuals from each of the two populations. Individual shells were firstly scrubbed externally to remove epiphytic material and then finely powdered with a pestle and mortar. Chlorophyll was extracted individually from each shell by shaking the powder with 5mls of 90% acetone in a test tube and placing it in darkness at 4°C for 24 hours. The mixture was then centrifuged for 20 mins at 1000 g_{av}, the supernatant removed and made up to 5 mls. Absorbence was measured at 665nm and 750nm in a Pye SP6 spectrophotometer and total chlorophyll content determined from standard algorithms.

A sample of limpets was sacrificed for detailed internal and surface analysis of the shell and radula. Shells were brought through a five fold series of resin concentrations in acetone (Metset SW resin, Buhler UK) from 40% to 100%. The material was embedded, sectioned and the shell material dissolved in 0.5N HCl. Radulae were isolated by dissection, incubated in 0.1N KOH for 5 hours, and were prepared using standard electron microscopical techniques. Both preparations were examined with a Cambridge Stereoscan Mk III scanning electron microscope.

In preparation for optical microscopy a sample of shells was ground to a medial plane on a diamond embedded wheel, presoaked for 24 hours in a 60% acetone/resin solution and embedded in a 5% dental plaster/resin mixture. This mixture helped to disperse contractive forces induced on the

material as the resin hardened, and was of a final hardness comparable with the shell material. Thin sections were made from the resultant blocks using standard geological techniques.

Nacella middens of the Dominican Gull *Larus dominicanus* (Lichtenstein) were randomly sampled using a 25cm x 25cm quadrat at three sites close to the *Nacella* collection sites in Factory Cove (Fig. 3.). Length, width and height of the shells were measured to ± 0.01mm using a Vernier callipers and shells were assigned visually to either littoral or sub-littoral population groupings on the basis of shell shape.

Sub-samples of thirty individuals from the living littoral and sub-littoral populations and from Dominican gull middens of littoral origin were used in the determination of shell shape.

For each shell a shell uniformity index (S.U.I.) was calculated. Width measurements of the shell base were taken one third of the way from the anterior edge (W_1) and one third of the way from the posterior edge of the shell (W_2) (Hockey & Branch, 1983). S.U.I. values were calculated as the ratio of anterior to posterior measurements (S.U.I. = W_1/W_2) with values close to unity indicative of a more elliptical base shape than those with lower S.U.I. values.

Shell widths were measured to ± 0.01mm with a vernier calipers. Mean S.U.I.s were calculated for each shell

collection and compared using T-tests, following arcsin transformation of the data. Statistical analysis of all data was performed using the computer statistical software package MINITAB *v6.1.1* (Minitab Inc., 1987).

3.3 Results

3.3.1 Shell morphology

The relationships between shell length and shell height for the two populations of *Nacella concinna* at Signy are shown in Figure 14, and the regression parameters are given in Table 3. In neither the littoral nor the sub-littoral populations were the relationships for males and females significantly different ($P > 0.05$ for both slope and intercept). In each case therefore, relationships have been calculated for both sexes combined. The slopes and intercepts of these two relationships differ significantly ($P < 0.001$). The height to length relationship of animals from the sub-littoral shows a large amount of variability unexplained by the regression, in contrast to the tight relationship in the littoral animals. Thus for an animal 25mm in length a littoral individual will have an average height of 8.07mm, in contrast to 6.62mm in a sub-littoral individual (95% C.L., ± 0.016 and 0.030 respectively).

With a clear distinction between populations in terms of their height to length relationship, measurements of breadth and shell dry mass were included in the data set with the intention of using a discriminant function analysis to separate the populations using all four parameters. With individual shells already assigned to a particular population on the basis of their shell length/height relationship, a discriminant analysis was performed on the data.

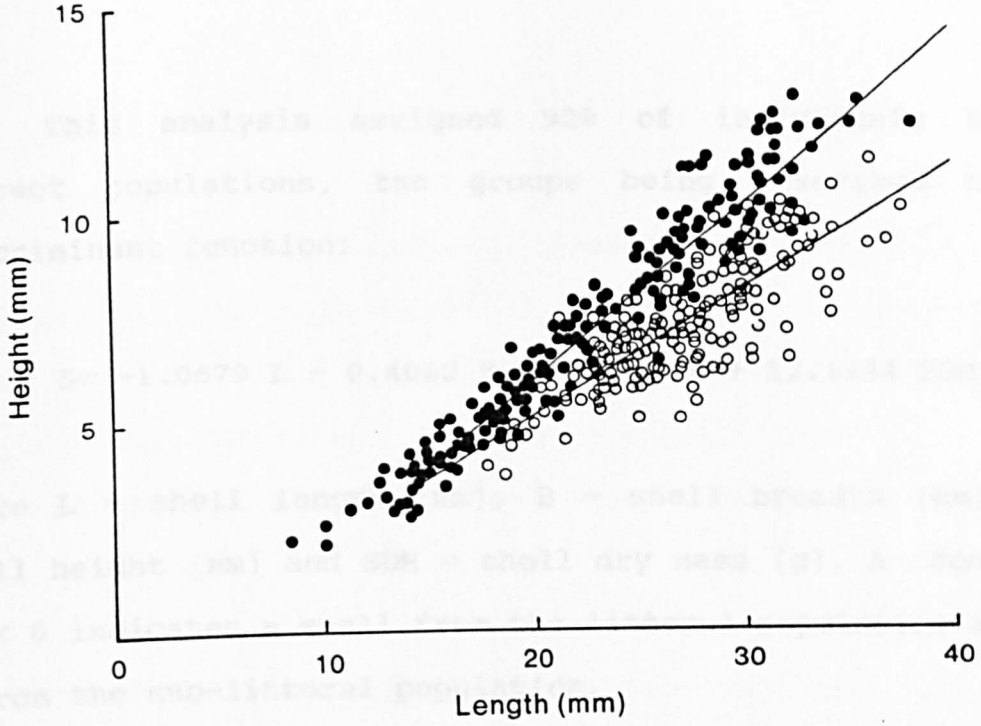


Figure. 14. The relationship between shell length (mm) and shell height (mm) in the littoral, ●, and sub-littoral, o, populations of ***Nacella concinna*** in Factory Cove, Signy Island. The fitted regression lines for the total populations are given in Table 3. 95 points (43 ●, 52 o) have been omitted to prevent obscuring the diagram. All data points are included in the analysis.

Table 3. *Nacella concinna*. Least squares regressions of shell length (mm) on shell height (mm). Separate relationships are given for males and females, and for the littoral and sub-littoral populations. Factory Cove, Borge Bay, Signy Island, 1985/86. b = regression co-efficient, SE = Standard error, int = intercept (regression constant), n = number of individuals, %var = percentage variance explained by the fitted line, F = variance ratio (all $p < 0.001$, two tailed). Range of shell lengths examined, 8mm to 40mm.

	b	SEb	int	n	%var	F
Littoral						
Males	0.453	0.045	-3.22	45	91.1	450.38
Females	0.390	0.046	-1.78	61	87.1	407.74
Total	0.416	0.018	-2.33	218	92.9	2786.51
Sub-littoral						
Males	0.287	0.068	-0.587	86	60.4	130.71
Females	0.293	0.070	-0.709	73	65.0	134.47
Total	0.299	0.040	-0.860	217	65.1	403.47

This analysis assigned 92% of individuals to the correct populations, the groups being described by the discriminant function;

$$S = -1.0679\ L - 0.4022\ B + 0.9733\ H + 12.1184\ SDM$$

where L = shell length (mm), B = shell breadth (mm), H = shell height (mm) and SDM = shell dry mass (g). A Score (S) of < 0 indicates a shell from the littoral population and $S > 0$ from the sub-littoral population.

3.3.2 Shell shape

Mean S.U.I. values for the living littoral collection (mean = 0.95, s; ± 0.03, n=30) were significantly greater than those of either the sub-littoral (mean = 0.94, s; ± 0.03, n=30, $t = 1.72$, $0.05 < P < 0.1$) or midden (mean = 0.93, s; ± 0.04, n=30, $t = 1.82$, $0.05 < P < 0.1$), collections. Comparison of sub-littoral and midden collections were not significantly different ($t = 0.37$, $P > 0.5$, n=30).

There was no correlation between shell length and S.U.I. values in any of the collections ($r < 0.1$, $P > 0.5$) eliminating variation in limpet size as a factor influencing the S.U.I.

3.3.3 Shell volume and tissue mass

Internal shell volume was measured in a small number of individuals from both populations (n=9). The relationships between volume and length in the two populations were significantly different, having similar slopes ($0.1 < P < 0.2$) but significantly different intercepts ($P < 0.001$) (Fig. 15).

The relationship between ash free dry mass and length for the two populations showed a significant difference ($P < 0.001$) in the biomass for animals of given length (Fig. 16; Table 4). They indicate that for an individual 25mm in length the mean tissue dry masses of littoral and sub-littoral animals will be 218mg and 233mg respectively. These figures are slightly higher than those data of Picken (1980b) (25mm : 204mg) for a sub-littoral population collected over a similar sampling period at a nearby locality in Factory cove (Table 5).

The differences in shell morphology between littoral and sub-littoral *Nacella* are matched by changes in shell density and organic content (Table 6). Littoral shells are denser and have a lower organic content than those of the sub-littoral, and these differences are highly significant (Organic content: $t = 6.08$, $df=7$, $P < 0.001$; Density: $t = 12.55$, $df=432$, $P < 0.001$).

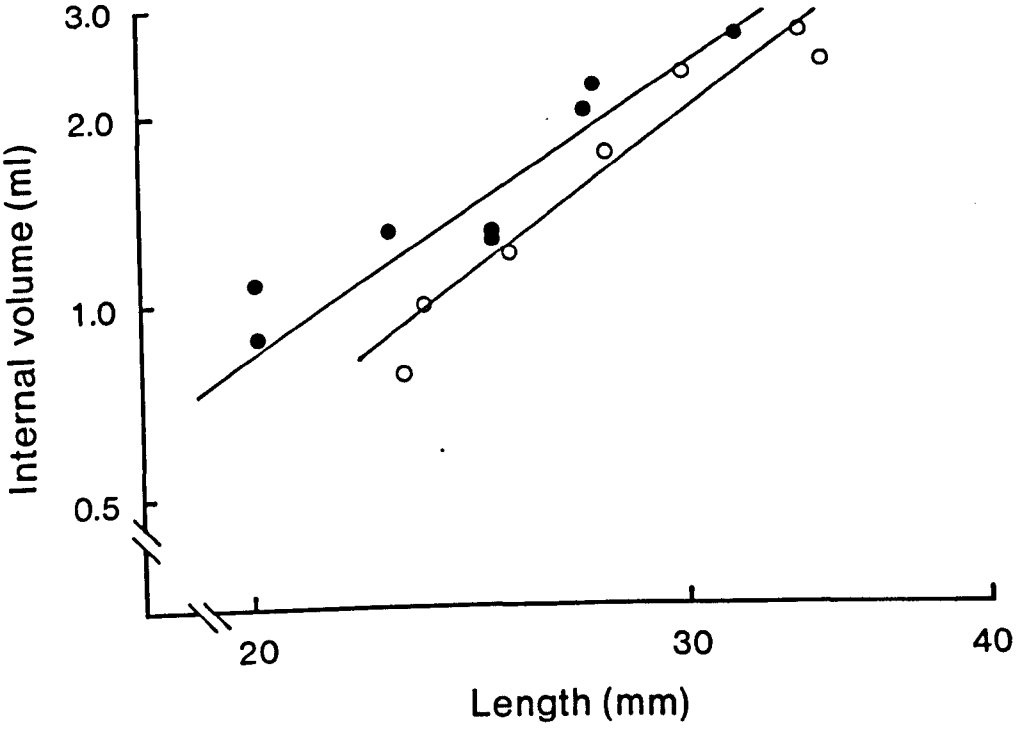


Figure 15. The relationship between internal shell volume (mls) and shell length (mm) in the littoral, ●, and sub-littoral, o, populations of ***Nacella concinna*** in Factory Cove, Signy Island. Note that both axes are logarithmic. The fitted individual regression lines are;

Littoral : Ln (Volume) = 2.53 Ln (Length) - 7.77
Sub-littoral : Ln (Volume) = 3.00 Ln (Length) - 9.51

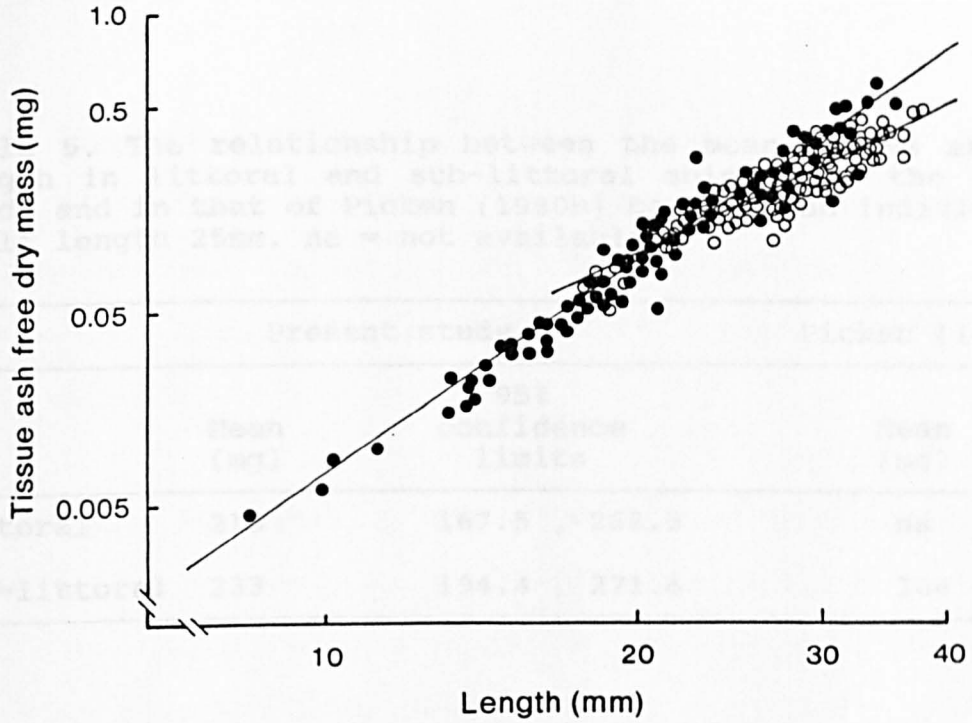


Figure 16. The relationship between shell length (mm) and tissue ash free dry mass (mg) in the littoral, ●, and sub-littoral, o, populations of ***Nacella concinna*** in Factory Cove, Signy Island. The fitted regression lines are given in Table 4. 142 points (33 ●, 109 o) have been omitted to prevent obscuring the diagram. All data points are included in the computation of the regression lines. Note that both axes are logarithmic.

Table 4. ***Nacella concinna***. Least squares linear regressions of Ln shell length (mm) on Ln Tissue dry mass (g) and Ln Tissue ash free dry mass (g). Separate regressions have been computed for littoral and sub-littoral populations. Factory Cove, Borge Bay, Signy Island, 1985/86.
DRY = Tissue dry mass, AFDM = Tissue ash free dry mass. Other abbreviations as for Table 1.

	b	SEb	int	n	%var	F
Littoral						
DRY	3.41	0.041	-12.50	117	96.3	3001.48
AFDM	3.45	0.042	-12.80	117	95.9	2707.75
Sub-littoral						
DRY	2.44	0.078	-9.31	217	72.7	576.16
AFDM	2.41	0.075	-9.57	217	79.6	845.53

Table 5. The relationship between the mean tissue mass and length in littoral and sub-littoral animals in the present study and in that of Picken (1980b) based on an individual of shell length 25mm. na = not available.

	Present study		Picken (1980)
	Mean (mg)	95% confidence limits	Mean (mg)
Littoral	218	167.5 , 268.5	na
Sub-littoral	233	194.4 , 271.6	204

Table 6. Shell density and organic content in *Nacella concinna*, Factory Cove, Borge Bay, Signy Island. Organic content determined as loss on ignition (% dry mass of shell). SD = Standard deviation, n = number of individuals analysed.

	Mean	SD	n
Organic content (% dry mass of shell)			
Littoral	2.89	0.268	5
Sub-littoral	4.02	0.316	5
Density (g/ml)			
Littoral	2.62	0.032	218
Sub-littoral	2.58	0.031	217
Chlorophyll (mg/g dry mass shell)			
Littoral	2.13	2.02	4
Sub-littoral	65.00	23.48	5

Associated with the higher organic content of sublittoral shells is a significant difference in chlorophyll content between the two morphs (Mann-Whitney U test, $U = 10$, $P < 0.02$), suggesting an endolithic algal infection of the shell material.

Resin impregnation and subsequent etching of the shell shows a highly developed matrix of resin filled burrows.(Fig. 17). The shell material exhibits high levels of chlorophyll (35 - 95 mg/g wet mass shell) and the endolithic *Conchocelis* phase of a red alga, typical of *Bangia sp.* and *Porphyra sp.* which occur locally, has been isolated as the causative agent in this instance (Porter & Peck, pers. comm.). The intensity of infection and the penetration of the algal hyphae through the shell layers declines with depth into the shell. The outer layers show most perforation and severe alteration of these layers by the algae is evident (Fig. 19).

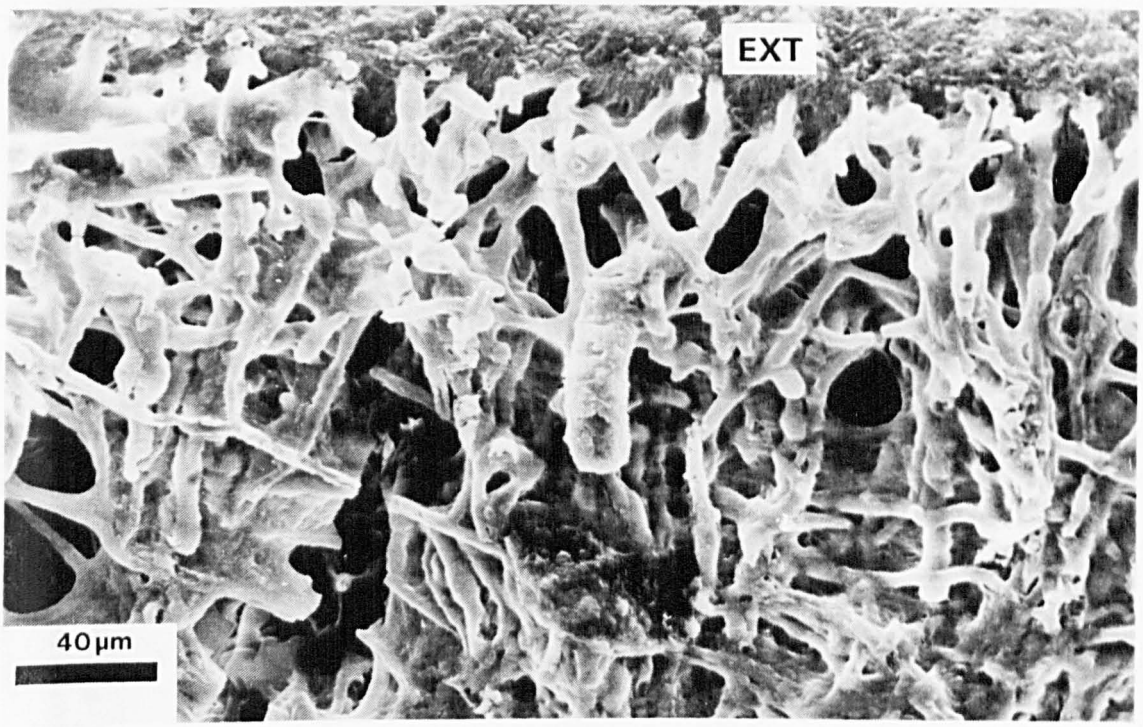


Fig. 17. Electron micrograph of a sub-littoral *Nacella concinna* shell ; a, Resin impregnation showing resin filled algal borings, revealed on dissolution of the shell material, bar = 40µm, EXT = External surface.

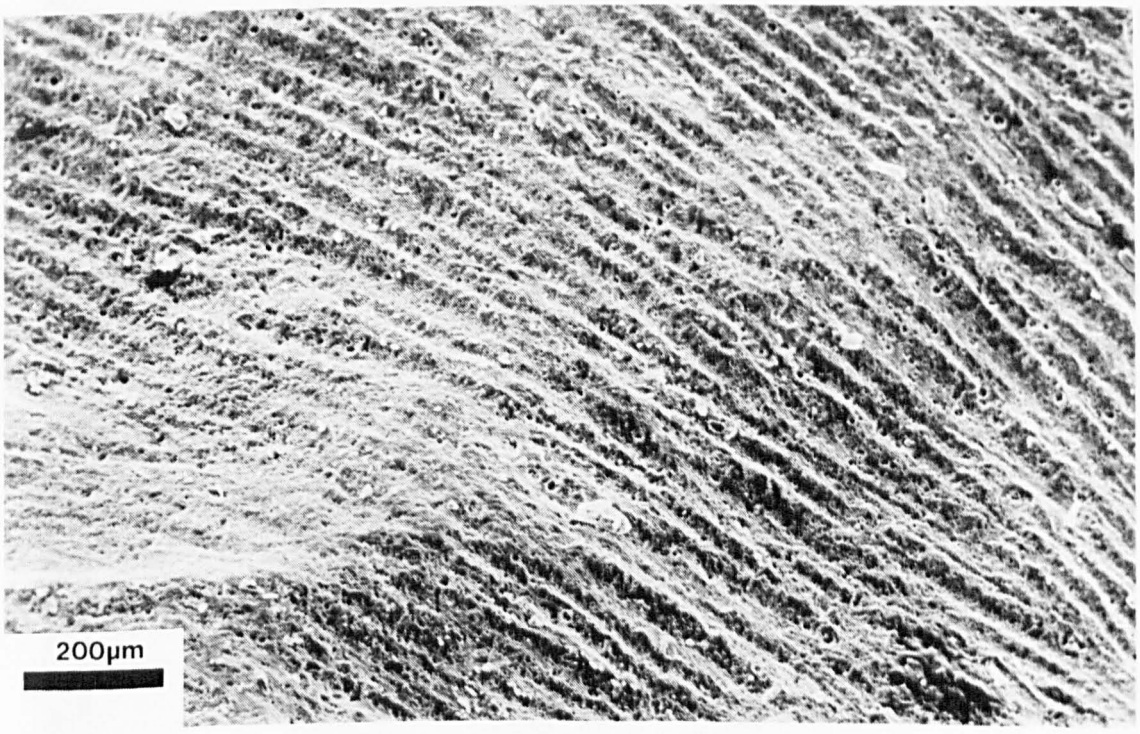


Fig. 18. Electron micrograph of a sub-littoral *Nacella concinna* shell showing shell surface abrasion and grooving, bar = 200µm.

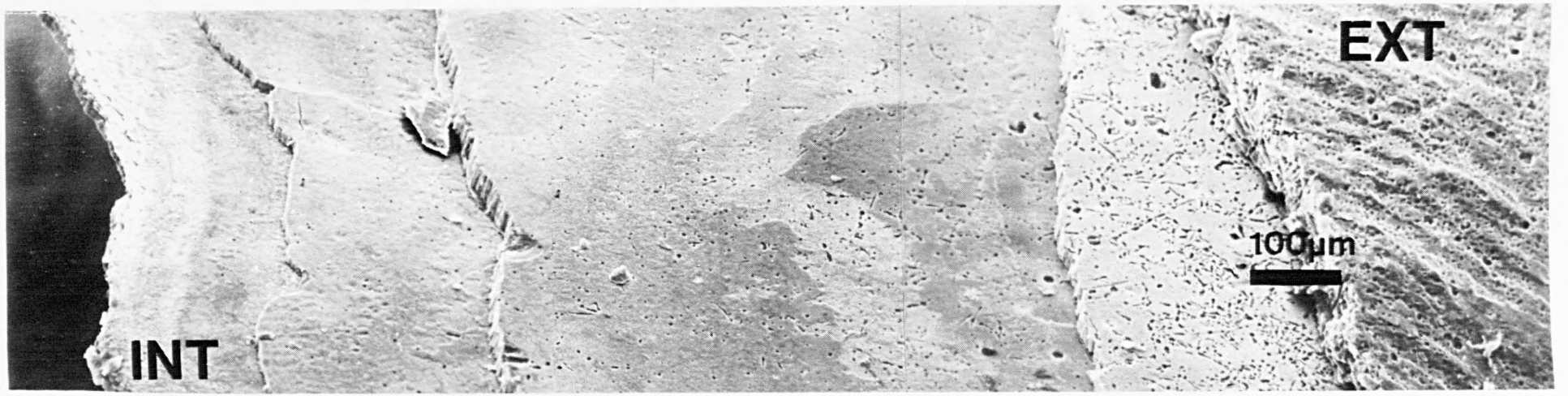


Fig. 19. Composite electron micrograph of a transect across and through a sub-littoral *Nacella concinna* shell showing varying intensity of algal penetration from external (EXT) to internal (INT) shell layers, bar = 100µm.

3.3.4 External shell morphology

Examination of the external surface of all sub-littoral shells revealed an extensive pattern of fine grooves (Fig. 18). When present in littoral animals these grooves were restricted to the apical region of the shell. Usually a standard arrangement of 4 grooves, two narrow inner and two broader outer grooves, could be seen. This characteristic surface sculpture can be matched by the configuration and alignment of the radular teeth of *Nacella concinna* (Figs. 20 & 21 ; Table 7). In particular the ratio between the large and small grooves matches that of the large and small teeth on the radula of *Nacella*. Although the actual size of radular teeth (and hence any grazing marks) will vary with limpet size, the similarity of the ratios suggests strongly that the grooves on the shells of *Nacella* are made by the radulae of other *Nacella*.

Table 7. *Nacella concinna*. Comparison of the distance ratios; small to large shell surface grooves and small to large radular teeth. Data analysed after arcsin transformation. SD = Standard deviation, n = Number of individuals examined.

	Mean	SD	n
Grooves	49.07	1.28	5
Teeth	48.89	1.64	5

Student's t, $t = 0.20$, $df = 7$, $p > 0.5$, two-tailed.

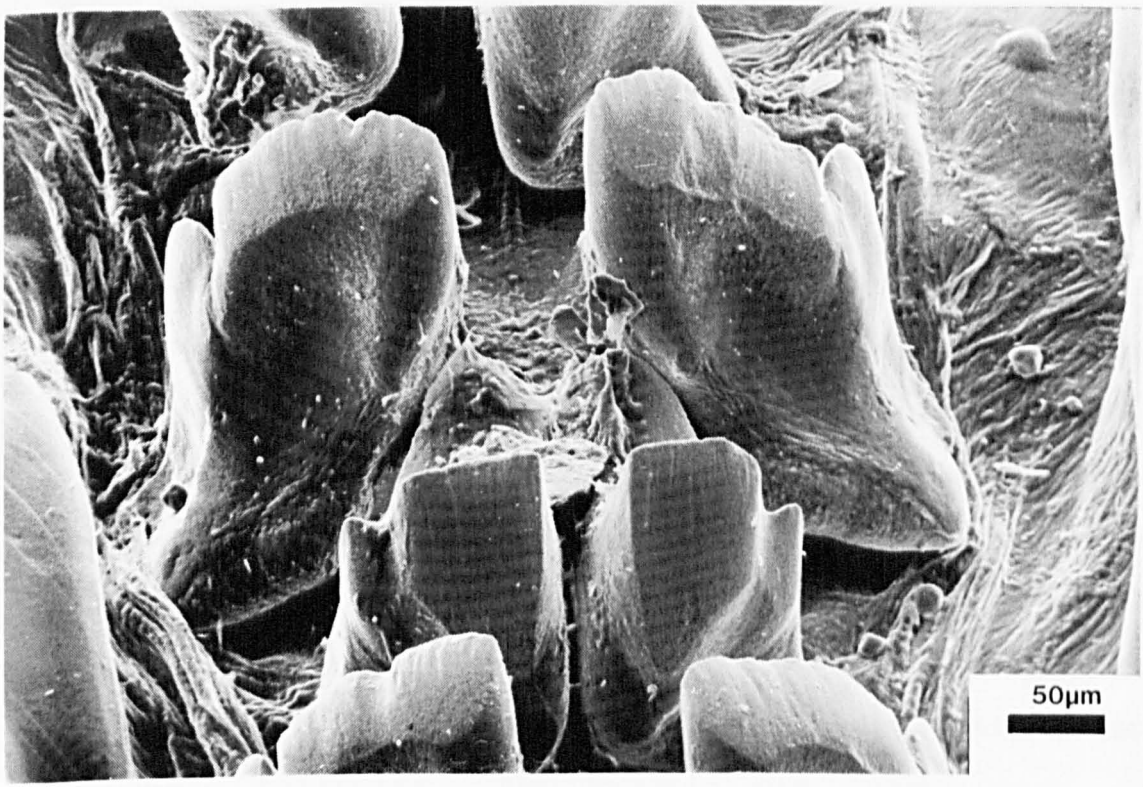


Fig. 20. Dorsal view of the radula of *Nacella concinna*, bar = 50µm.

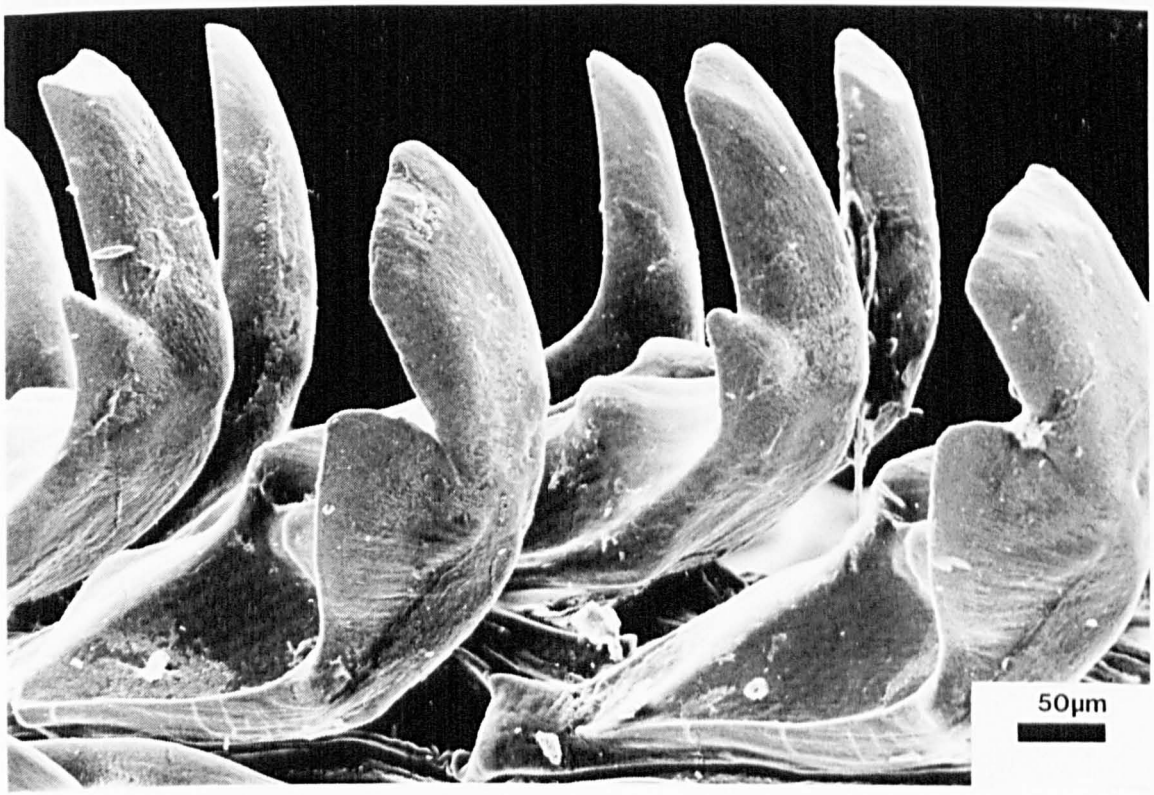


Fig. 21. Lateral view of the radula of *Nacella concinna*, bar = 50µm.

Where epibiotic organisms are present on the shell, the underlying shell material is usually preserved in its original state (Fig. 22). Using these epibiotic organisms as a plane of reference, it can be seen how greatly the unprotected shell has become eroded. The robust, layered structure of the shell, deposited under conditions of undisturbed accretion and growth, is evident below the protective epibiotic crust. The unprotected shell material surrounding this area has been reduced, from this original state, to one or two layers in thickness, the process occurring gradually from the time of epibiotic settlement to that of collection. In sub-littoral animals, this reduction in shell thickness often reveals the 'horse-shoe' shaped myostracal layer which shows externally in severely eroded animals and provides a translucent, thin site for shell fracture. In extreme cases where the shell has been reduced to a critical thickness, fracture has occurred and the apex has become detached, exposing the soft tissues of the animal.

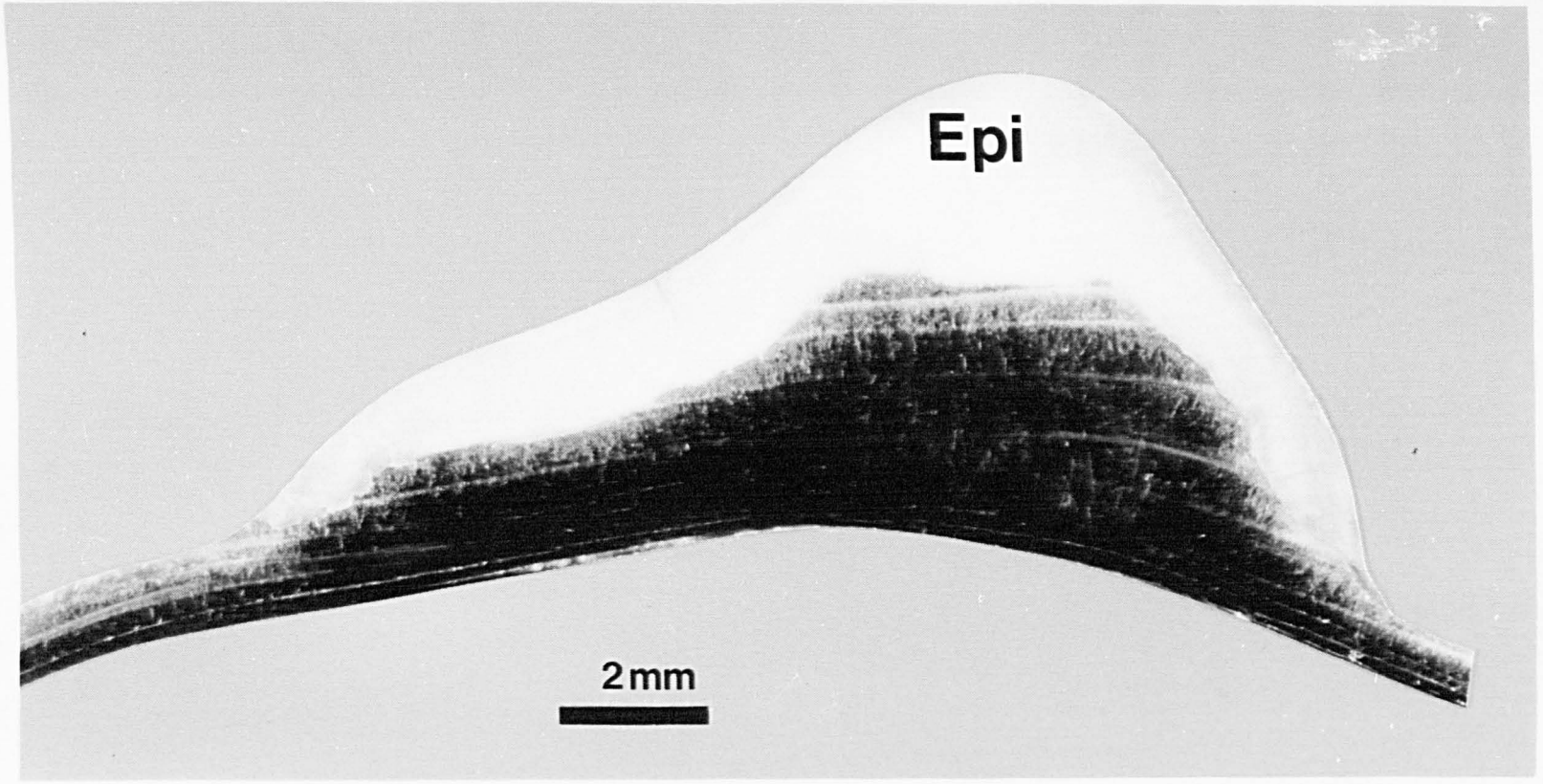


Fig. 22. Cross section of a sub-littoral *Nacella concinna* shell showing the protection afforded by an epibiotic encrusting organism (Epi) against shell erosion. Scale bar = 2mm.

3.3.5 Avian predation

The Dominican Gull *Larus dominicanus* and the Sheathbill *Chionis alba* (Gmelin) are the two major predators of *N. concinna* from the littoral and very shallow sub-littoral zones, particularly during the late autumn and winter months (Jones, 1963; Voous, 1965; Hedgpeth, 1969; Shabica, 1971, 1976; Walker, 1972). Both species remove attached limpets from the substrate, with a combination of pecking, prying and twisting.

Sheathbills, when successful, remove the limpet from its shell which is then simply discarded in the littoral zone. Those animals which survive the predatory attentions of sheathbills show external peck marks which can pierce and break the shell. This is particularly evident in the thin shelled sub-littoral animals. Shabica (1976) attributes these marks to the erratic woodpecker type pecking behaviour of sheathbills, although animals surviving Dominican gull attacks also possess similar shell damage.

Limpets from the living population bearing peck marks formed 15.2% of the 218 littoral and 2.3% of the 217 sub-littoral shells examined. This difference reflects the differing availability of the animals to avian predation, and agrees with previous observations of maximum foraging on populations of *Nacella concinna* (Shabica, 1976) and the related *Nacella delesserti* (Branch, 1985) during periods of low water, especially spring tides.

Dominican Gulls ingest 2-5 limpets during a feeding cycle, and regurgitate the empty shells after digestion at regularly used sites. Limpets which are larger than 40mm in length and too big to swallow, are taken to a similar area and the flesh removed and eaten (Shabica, 1976). This systematic and localised deposition of shells in safe roosting areas results in the accumulation of extensive shell middens contributed to by gulls of all age classes.

All middens sampled contained both littoral and sub-littoral shells. Within the combined midden collections the size distribution of sub-littoral shells (18.00mm-32.00mm) fell within the range of the littoral shells (8.00mm-46.00mm). Littoral shells dominated each midden sample, indicating selective predation of the more easily accessible animals of the littoral zone (Fig. 23). Although the size ranges of shells from individual midden sites were similar, there were significant differences between the distributions of animals taken from each zone ($P < 0.01$) and between different middens ($P < 0.01$) (Table 8).

Table 8. *Nacella concinna*. Two-way analysis of variance of midden shell length on the interaction between midden site and shell type. df = Degrees of freedom, SS = Sum of Squares, MS = Mean Square.

Source	df	SS	MS	F	P
Site	2	1099.28	549.64	31.79	< 0.01
Shell type	1	186.92	186.92	10.81	< 0.01
Interaction	2	41.46	20.73	1.20	> 0.05
Error	1186	20501.30	17.29		
Total	1191	21828.97			

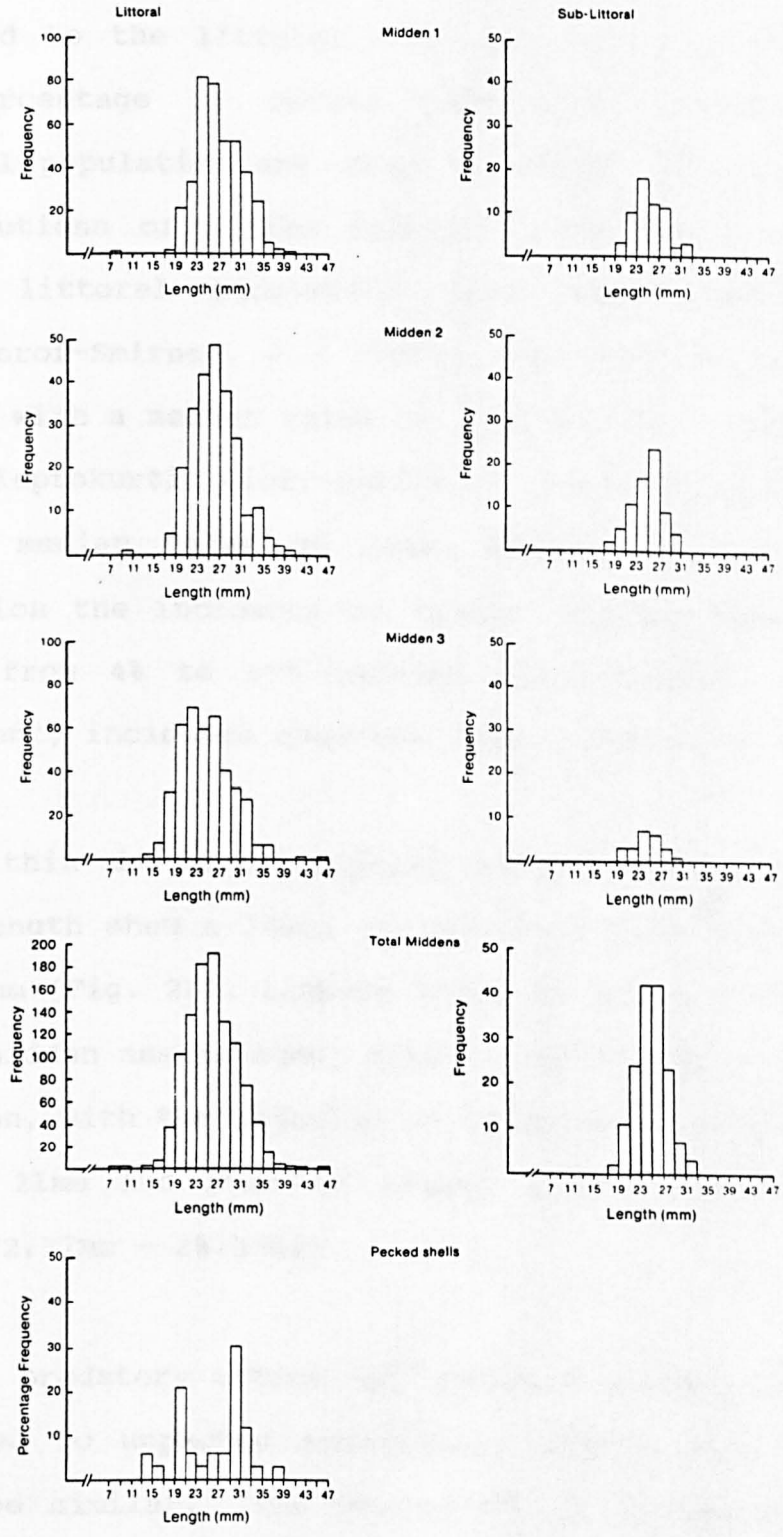


Figure 23. Length frequency distributions of littoral and sub-littoral assigned shells of individual and combined middens and the percentage length frequency distribution of pecked shells within the living littoral population of *Nacella concinna* at Signy Island, South Orkney Islands.

The length/frequency distributions of midden shells assigned to the littoral and sub-littoral populations, and the percentage of pecked individuals within the living littoral population are shown in Figure 23. Population size distributions of midden shells of littoral origin and the living littoral population were significantly different (Kolmogorof-Smirnov, $P < 0.001$). The littoral population is bimodal with a median value of 22mm and is in direct contrast to the leptokurtic distribution of the littoral midden shells with a median value of 26mm. Within the living littoral population the incidence of shells showing predatory attack varies from 4% to 55% between size classes, with a low, consistent, incidence over the 22mm - 28mm size intervals.

Within the living populations individuals below 29mm in shell length show a lower incidence of peck marks than those over 29mm (Fig. 23). Limpets taken by gulls, and represented in the midden assemblages, show a similar upper limit to size selection, with the majority of individuals preyed upon being between 21mm and 29mm in length (25% - 75% interquartile range; 22.77mm - 28.35mm).

If predatory attack was entirely random the proportion of pecked to unpecked individuals within each size class should be similar. The proportion of pecked shells within the various size classes is, however, significantly non-random ($X^2=20.66$, DF=4, $P < 0.001$), indicating a size selective preference in the foraging behaviour of feeding gulls.

3.4 Discussion

The Signy Island population of *Nacella concinna* exhibits unusual shell morphologies which may be attributed to a combination of behavioural and stress-induced effects.

Walker (1972) noted a considerable variation in shell structure both between the summer littoral, and sub-littoral limpets and also within the sub-littoral population. Animals up to 20mm in length did not appear to vary consistently with the environment. Above this length morphometric relationships showed significantly different slopes ($P < 0.001$) giving shell heights for animals of standard length consistent with the predictions of the present study. He suggested that differences in morphology and epibiotic encrustation between the two groups were phenotypic and related to exposure, breaking waves or possibly, both of these factors. These views are supported by the observations of Berry and Rudge (1973) from sites of varying wave exposure throughout the latitudinal range of *Nacella concinna*.

Shabica (1976) recorded both of Powell's forms, as well as hybrid shell types from the *N.concinna* population of Arthur harbour, Anvers Island (64°46'S, 64°05'W), suggesting that for this population the size differential and variation in shell morphology between the observed shell types may be induced environmentally and is only evident in sub-littoral animals.

In contrast to Walker (1972), Shabica (1976) suggested that wave action had little effect on the shell morphology of *N. concinna* because he could detect no significant difference between the littoral animals of exposed and sheltered shores. Shabica (1976) also observed a decrease in shell thickness with depth, and stated that the robust nature of the littoral shell was an environmentally induced adaptation to the crushing effects of ice. This adaptation, eventually leading to the "polaris" form, was suggested to arise from the migration of the deeper water, ribbed, "concinna" form towards the surface as they get older, where an irreversible environmental alteration to the shell morphology takes place.

It seems likely that the population of *N. concinna* described from Anvers Island consisted of Powell's "polaris" form showing the same morphological variation described by Walker from Signy. The assumption of "polaris", "concinna" and hybrid forms suggested by Shabica (1976) was based on the profile descriptions of Powell on intact and structurally undamaged shells and does not take into account shell erosion.

The "concinna" form, described from South Georgia, has a distinctive bathymetric distribution which makes it unlikely to be present in the Anvers Island population. It seems more plausible therefore that the shell differences observed by both Walker (1972) and Shabica (1976) within inshore populations of *Nacella concinna* forma *polaris* are

phenotypic effects, environmentally controlled and spatially significant.

Variation in limpet shell shape, expressed as a function of length and height has been well documented and attributed to a variety of environmental influences. Water turbulence and wave action (Russell, 1907; Ebling *et al.*, 1962; Walker, 1972; Berry & Rudge, 1973; Simpson, 1985), desiccation (Orton *et al.*, 1956; Lowell, 1984) and shore zonation (Moore, 1934; Ebling *et al.*, 1962, Branch, 1981), have all been shown to effect spire height and position, with individuals under the most environmental stress generally having higher profiles.

At Signy, the difference in the length to height ratios between the different shell morphs is coupled with a significant difference in the relationship between biomass and shell volume. A littoral limpet has on average about 20% less biomass (ash-free dry mass) compared with a sub-littoral animal of similar volume. A large proportion of the available shell volume is therefore void of tissue. This phenomenon is common in littoral limpets which require to clamp down and retract their tissues during periods of environmental stress (Thomas, 1948). The muscular effort involved is thought to induce mantle distortion resulting in the formation of a high spired shell (Russell, 1907; Orton, 1932; Moore, 1934; Ebling *et al*, 1962; Fretter & Graham, 1962; Branch & Marsh, 1978).

Comparison of the tenacity between the two morphs at Signy showed no significant differences (Davenport, 1988c). Results indicated a higher level of adhesion in sessile animals over mobile individuals, but lower overall tenacities than previously recorded for limpets in general. Mobility and shell deportment also differed between littoral and sub-littoral morphs and were generally shown to be attributed to differences in shell density and exposure to air experienced by the different forms.

A recent study of allelic variation, based on the examination of 5 enzyme loci in 600 individuals revealed no discernible difference between the two forms at Signy (Wei, 1988). Littoral and sub-littoral animals thus appear to be genetically identical, which suggests environmentally induced, phenotypic changes as being responsible for the observed differences between the two forms.

3.4.1 Endolithic infestation.

Endolithic algae have been frequently reported attacking the shells of gastropods and bivalves (Johnson & Anderson, 1962; Bathurst, 1966; Alderman & Jones, 1967; Golubic, 1969; Golubic *et al*, 1970; Kohlmeyer, 1969, 1972; Cavaliere & Alberte, 1970; Bergman *et al*, 1982). Infestation is usually localised to areas of erosion or shell damage (which are sites of easy access to the organic matrix of the shell) and proceed along axes of crystal growth penetrating successive shell layers. In the majority of cases this does

not affect the animal's well being, but does increase the organic content of the shell. Sub-littoral shells are prone to harbour invading alga due to the relative stability of their environment, their lack of exposure to surface conditions and their greater proximity to the algae, *Bangia sp., Porphyra sp.* which are likely to provide source organisms for infection (Peck & Porter, pers comm). A similar *conchocelis* phase infection to that found in *Nacella* has been reported in the brachiopod *Liothyrella uva* also at Signy Island with heavily infected animals showing a 15% increase in shell organic content over uninfected, or poorly infected individuals (Peck *et al*, 1987).

The presence of endolithic borers adversely affects the strength of the material invaded (Kohlmeyer, 1969, 1972; Golubic, 1969; Bergman *et al*, 1982). Sub-littoral *Nacella* are highly infected with algal borers particularly in the external shell layers. Ramification of the algae within these layers produces an intricate, perforate structure which decreases with depth into the shell and provides an easily accessible algal biomass within the soft and exposed shell substrate to grazers capable of its excavation. The significant morphological differences between shells of littoral and sub-littoral forms are a consequence of algal boring, with the presence of such an algal food source within the shells of sub-littoral animals indirectly having a detrimental effect by encouraging grazing which weakens the shell and leads to shell damage.

3.4.2 Intraspecific shell grazing

The composition, morphology, operation, excavation efficiency and effect of the docoglossan radula found in the Patellacea has received much attention (Jones, 1946; Brian & Owen, 1952; Lowenstam, 1962; Powell, 1973; Branch & Branch, 1980; Steneck & Watling, 1982; Black *et al*, 1988; Clarke, 1989; Hawkins *et al*, 1989; Van der Wal, 1989).

The shells of *N.concinna*, particularly those of the sub-littoral form, show excavation marks which correspond precisely with this limpet's radular dentition (Table 7). The matching of the external shell sculpture with radular configuration indicates that the embedded algal food source within the shell is being exploited by other individuals of the sub-littoral limpet population. It is during November and December, the period directly preceding and including the reproductive phase of the year that intraspecific shell grazing is most likely to occur. During this period the animals aggregate, form stacks and generally come into physical contact more often than would usually occur (Picken & Allan, 1983). Throughout the rest of the year however, feeding habits and diet will bring sub-littoral animals into contact with many varied substrates. During this period individuals will frequently clamber over one another in the process of feeding and abrasion of the shell surface is likely to occur (Nolan, unpubl. obs.). The excavation of the underlying shell material may be random and follow a general pattern of opportunistic substrate testing. Conversely, if

animals are feeding on crustose coralline algae it may present a substrate of similar algal content and hardness to the foraging animal, and be grazed accordingly.

The characteristic grazed sub-littoral shell is also evident in midden collections from South Georgia and the Antarctic peninsula (Nolan, unpubl. obs.), indicating that this behaviour occurs widely within the geographical range of *Nacella concinna*.

3.4.3 Predation

Below the low water mark asteroids, echinoids, prosobranch gastropods, pycnogonids, nemertine worms and two Antarctic cod species have all been reported to prey on *N. concinna* (Walker, 1972; Shabica, 1976; Blankley, 1982).

Within the littoral zone the Dominican gull, *Larus dominicanus* and the Sheathbill, *Chionis alba* are the major predators of *N.concinna* (Jones, 1963; Hedgpeth, 1969a; Shabica, 1971; Walker, 1972; Blankley, 1981).

Predation strategies of *L. dominicanus* are dependent on the size range of available individuals. Shells between 5mm and 40mm long are generally eaten whole and the shells later regurgitated, whilst those from 40mm to 60mm in length are removed from the substrate, the tissue removed from the shell, and eaten *in situ*, or in the supra-littoral zone. On Marion Island the limpet *N. delesserti* forms a large part of

the diet of *L. dominicanus* (Blankley, 1981; Blankley & Branch, 1985). Regurgitated shells are comparatively rare, and limpets of shell lengths ranging from 40mm to 55 mm are most heavily preyed on. Similarly on Macquarie Island *N. maquariensis* accounts for 15% of the diet of *L.dominicanus* with larger individuals consumed *in situ* (Simpson, 1976). Where individuals over 40mm are rare the majority of shells are regurgitated in communal middens. At Anvers Island Shabica (1976) calculates a midden accumulation rate of 1.3 x 10^4 limpets/year/hectare under these circumstances.

There is a general decrease in bathymetric range (Shabica, 1971) and a suggestion towards smaller size (Berry & Rudge, 1973) within Antarctic limpet populations as latitude increases. In consequence the predation strategy and post foraging behaviour of the Dominican gull at Signy is dictated by the general absence of individuals above 45mm in length within the exposed *Nacella concinna* population. In the absence of individuals too large to swallow, the regurgitated shells of digested limpets, contained in gull middens, are therefore an accurate measure of the predation pressure on different size classes of the limpet population.

Peck marks indicate the survival of an individual to an attack. Although Shabica (1976) could find no evidence of size selective predation in the similarly distributed Arthur harbour population of *Nacella*, the distribution of peck marks in *Nacella* at Signy suggests strongly that prey selection

does occur, and is particularly important within the littoral community.

Individuals below 21mm in length would appear to be generally avoided whereas the majority of those over 29mm in length, although attractive to the foraging gull (evident in the relatively large number within the living population showing peck marks), survive through greater tenacity with increasing shell size. The selection of prey is therefore restricted to a size range of limpets which maximises the foraging efficiency of the gull.

Observations by Hockey and Branch (1983) on the predation of *Patella granularis* by the Black African Oystercatcher *Haematopus moquini* have shown that limpets in predator-free populations are more pear-shaped than those in depredated populations. They suggest that limpets with a recognisable anterior and posterior end are more susceptable to attack as they are less likely to clamp down prior to attack if approached from behind.

Midden shells represent foraging success of the Dominican gull in the littoral zone and have a shape which is significantly more pear-shaped than those animals remaining within the littoral population. Sub-littoral animals generally possess a pear-shaped shell which is evidence of the lack of avain attention caused through inaccessibility in this population.

Hockey and Branch (1983) suggested that the selective influence by Oystercatchers on the genotypes of *Patella granularis* was sufficient to be detectable in the phenotypes. Littoral and sub-littoral populations of *N. conncina* at Signy Island appear to be genetically identical (Wei, 1988). Predation by Dominican gulls predominantly occurs upon the littoral population and has a selective influence on the phenotypes of the littoral population. This, however, does not appear to effect a genotypic difference between the limpet populations.

3.4.4 Conclusions

Wave action, ice-film formation and exposure to air are likely to be of major consequence in determining shell formation and shape of the Antarctic limpet. Dominican gull predation also represents a contributing force influencing the differences in shell morphology between the littoral and sub-littoral forms of *N. concinna*. The significant morphological discreteness of the littoral and sub-littoral forms is further compounded by the presence of endolithic algae within the shells of sub-littoral animals and the intraspecific shell grazing activities of the animals themselves. Within the sub-littoral zone intraspecific shell grazing induces shell fragility and affects an individual's longevity and resistance to predation. Conversely, littoral animals have a low incidence of intraspecific shell grazing but experience a level of Dominican gull predation which selectively influences the phenotype of the littoral

population. The apparent differences in shell form between littoral and sub-littoral animals are therefore induced by a combination of physical, biological and behavioural influences.

CHAPTER 4

The determination of shell growth rate in *Nacella concinna*

4.1 Introduction

The recapture of tagged and released individuals of many species has proved to be a successful method in estimating annual and instantaneous rates of population growth (Ricker, 1975; Kirkwood, 1983). The success of the method depends upon the level of physiological stress suffered by the individual upon marking, the efficiency and speed of the marking technique and the rate of recapture of marked individuals over time. With the former factors reduced to a minimum the mortality rate due to the tagging procedure is negligible and the rate of recapture, especially in slow moving or sessile animals, high. The resultant changes in morphological parameters recorded over time may be subsequently used to provide a reliable estimation of the population growth parameters.

4.2 Materials and Methods

603 Individuals representing both morphological forms of *Nacella concinna* were collected from the littoral and sub-littoral zones of Factory Cove during January, February, May, August and October 1988 (Fig. 24a) for long term shell growth analysis in ambient conditions by means of tagging and subsequent recapture.

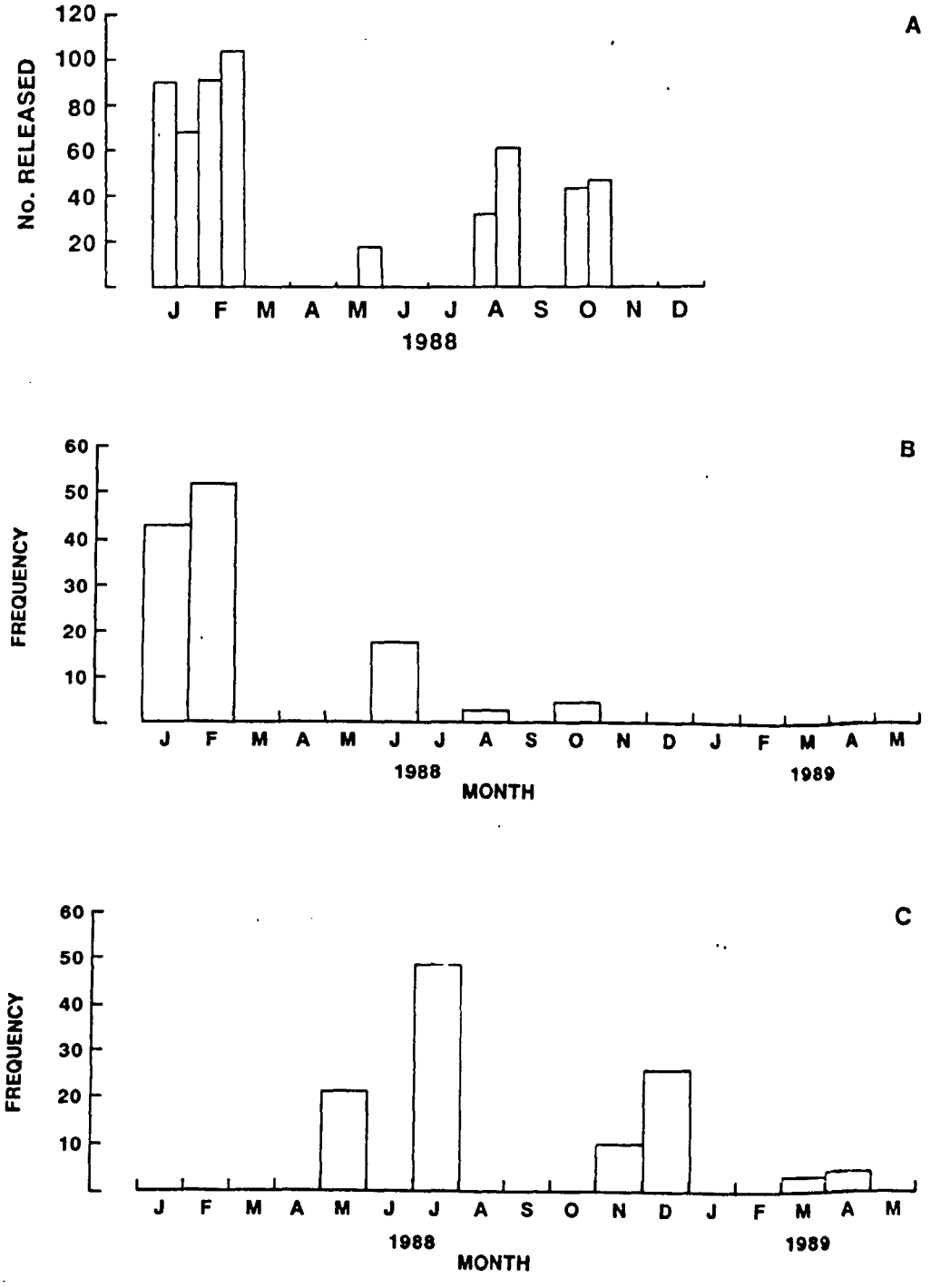


Figure 24. *Nacella concinna*. A : The temporal distribution of release periods and number of individuals released during the period January - December 1988. B : The temporal distribution of release periods for individuals recaptured during the period January - December 1988 and C : The temporal distribution of recapture periods for recaptured individuals during the period January 1988 - May 1989.

The process involved in the marking of individuals developed through time as faster less stressful methods were developed. Ultimately animals upon collection were sanded with fine grade emery paper to remove surface anomalies. This area was then acetone wiped to clean and dry the shell and a light coat of pale coloured emulsion paint applied to this surface. Upon drying an individual identification number was written on the paint surface with black writing ink and a coating of clear nail varnish applied. Once dry a covering of cyanoacrylate *'Superglue'* finished the procedure.

Animals were acclimated in laboratory conditions for 3 days after which time shell length, breadth and height was measured to ± 0.01mm using a Vernier calipers. Animals were liberated close to the point of collection and allowed a minimum time of 60 days in natural conditions before recapture. Upon return to the laboratory length, breadth and height was again recorded.

4.3 Results

Of the 603 animals marked a mortality rate of 8.29% was observed following the marking procedure and before release. There was no significant difference between the mortality rates of littoral and sub-littoral animals. Of the remainder that were released 19% (116) were recovered by the end of the study period comprising 72 animals of littoral origin and 44 animals of sub-littoral origin. Animals on average were

recaptured after 198 days (SD = 82.57) with maxima and minima of 33 and 514 respectively. The temporal distribution of release and recapture periods is presented in Figure 24b and 24c.

Of the shells recovered, abrasion of the shell edge and other physical shell damage was evident in 30% of individuals effecting one or other of the parameters measured. The most acute incidence of shell loss accounted for a reduction in shell length of 2.44mm over a period of 191 days with a great many similar instances of negative or zero shell gain recorded.

Animals whose period of liberty was mainly during the summer showed the greatest incidence of shell loss based on the analysis of daily incremental addition, with those recaptured after winter and yearly release periods showing a lower incidence of negative shell growth. In all cases the mode of daily incremental addition to shell length was contained within the daily increment range of 0.000 - 0.002mm (Fig. 25). Average daily increments over the three release periods were 0.21μm and 0.28μm over the summer and winter periods and 1.35μm in animals released for predominantly a year (Table 9). Animals recaptured after summer growth showed a greater range in incremental values than both winter and yearly growing animals though the positive limit of the range and the positive distribution of incremental values between summer and yearly periods of growth were very similar. This suggests that the majority of shell growth occurs during the

summer months with slower growth occurring in winter. Daily addition to shell length, based on yearly growth periods, may reflect the repair to summer shell damage (caused by increased activity and abrasion) during the winter resulting in the lower overall frequency of negative incremental values within this group. Analysis of the combined data showed no significant relationship with either total shell increment or daily shell increment with period of release (Fig. 26).

Table 9. Daily incremental addition to shell length (mm) in *Nacella concinna* recaptured after periods of predominantly summer, winter and yearly periods of release.

Release Period	N	MEAN	STDEV	MIN	MAX
Summer	70	0.00021	0.00293	-0.01491	0.00509
Winter	14	0.00028	0.00138	-0.00245	0.00341
Yearly	32	0.00135	0.00162	-0.00219	0.00556

The affects of shell abrasion on the accurate measurement of shell increase over time thus precluded a time series analysis of growth using data from recaptured individuals.

The growth of *Nacella* occurs seasonally, with major shell growth occurring during the spring and summer months and decreased winter growth rates (Shabica, 1976; Picken, 1980b). Based on this assumption animals showing large positive growth increments and long, near annual, periods of

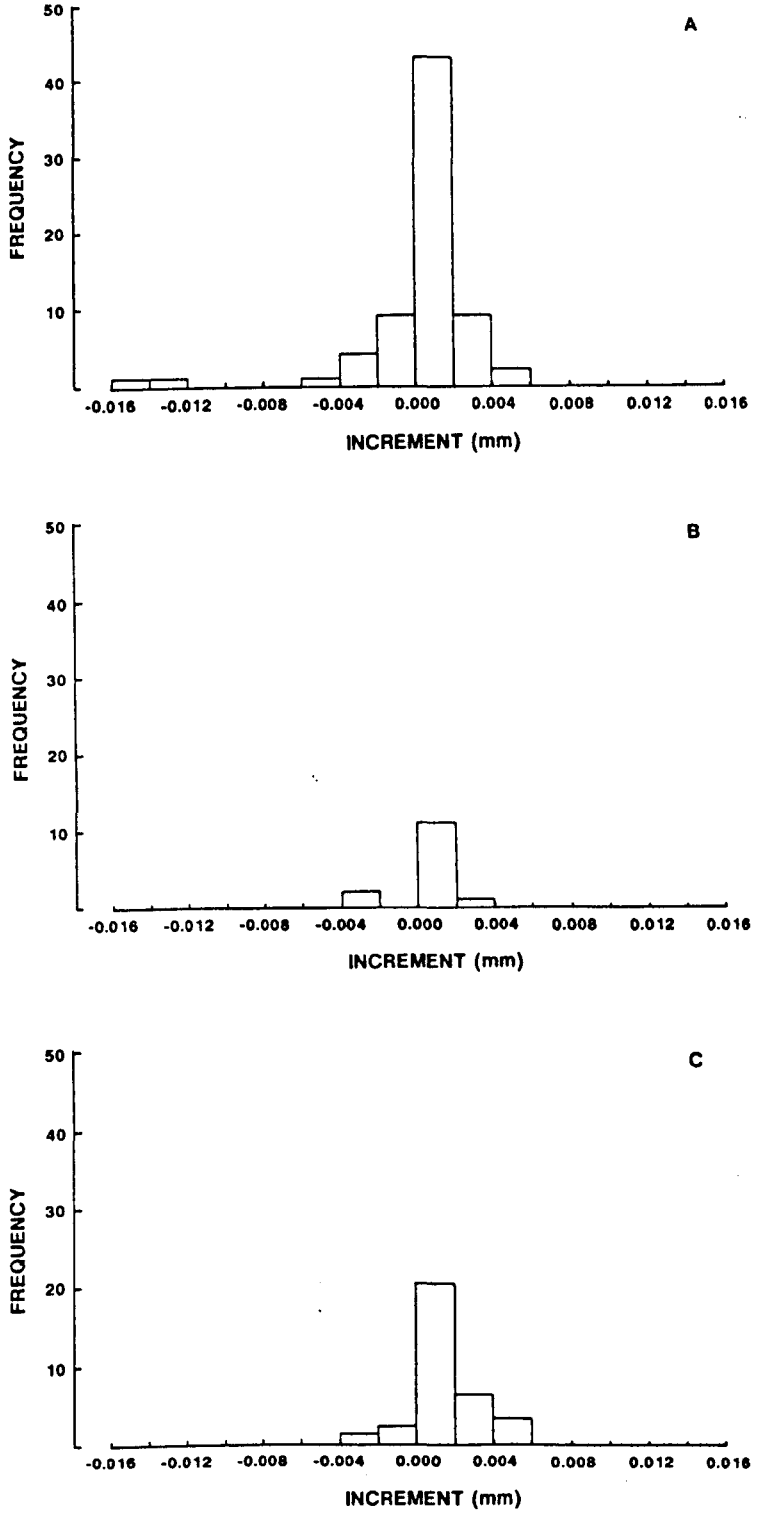


Figure 25. *Nacella concinna*. Frequency histograms of daily incremental growth in shell length from individuals recovered after predominently Summer (A), Winter (B) and Summer and Winter (C) release periods.

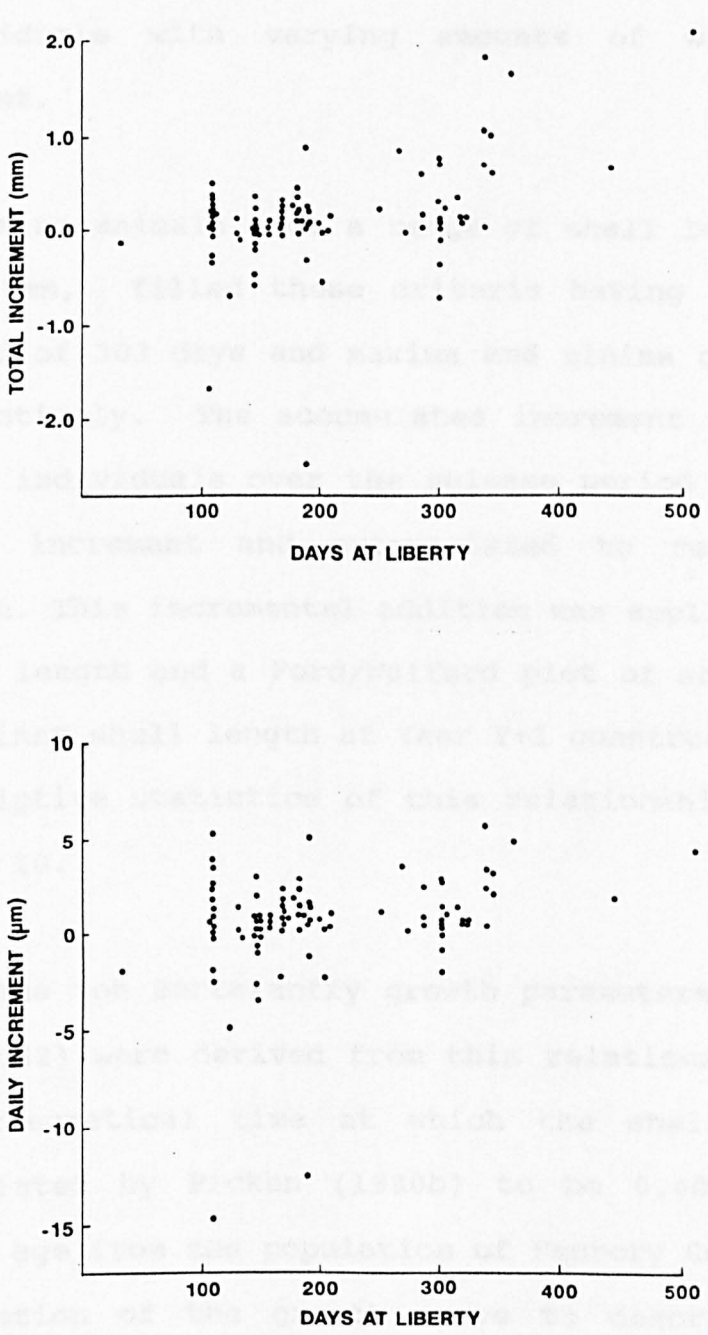


Figure 26. *Nacella concinna*. The relationship between Incremental addition to shell length and days at liberty observed in recaptured individuals. A) Total Increment and B) Daily Increment.

release were selected for growth rate analysis. These criteria ensured that summer growth was represented in all individuals with varying amounts of winter growth also evident.

Nine animals from a range of shell lengths between 18mm and 39mm, filled these criteria having an average release period of 303 days and maxima and minima of 363 and 147 days respectively. The accumulated increment in shell length of these individuals over the release period was converted to a daily increment and extrapolated to represent one years growth. This incremental addition was applied to the original shell length and a Ford/Walford plot of shell length at Year y against shell length at Year Y+1 constructed (Fig. 27). The descriptive statistics of this relationship are presented in Table 10.

The von Bertalanffy growth parameters L_{∞} (45.19mm) and k (0.062) were derived from this relationship. The value t_0, the theoretical time at which the shell length is zero, calculated by Picken (1980b) to be 0.4887 for *Nacella* of known age from the population of Factory Cove was used in the generation of the growth curve to describe the population (Fig. 28). Using these parameters in the von Bertalanffy growth model estimates of size at age were constructed for the *Nacella concinna* population of Factory Cove. (Table 11). Applying the model to the largest animal recorded from this population (40.34mm shell length, present study) an age of 37 years was obtained.

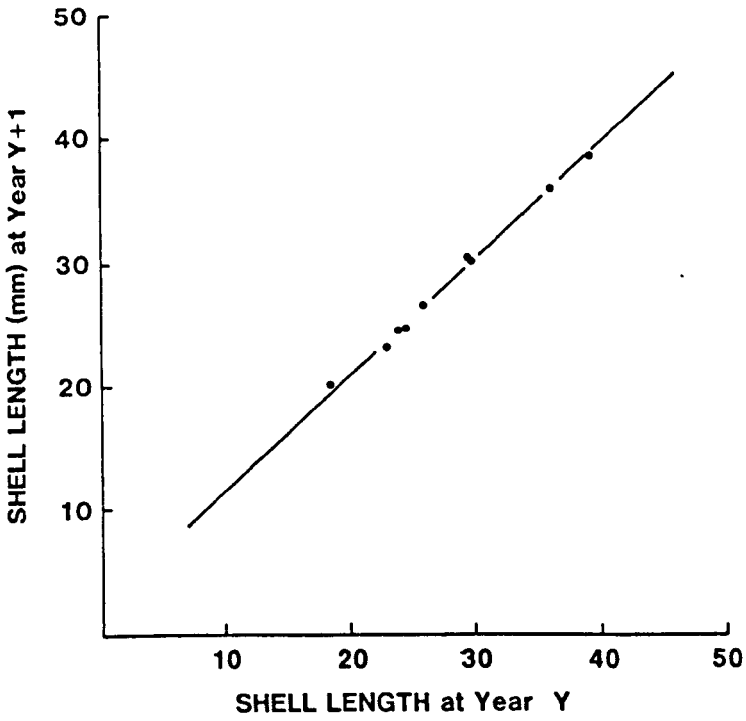


Figure 27. *Nacella concinna*. Ford-Walford plot of shell length at year Y (mm) against shell length at year Y+1 (mm).

Table 10. *Nacella concinna*. Least squares regression and analysis of variance of shell length at year Y (mm) on shell length at year Y+1. p = Probability level, Df = Degrees of Freedom.

Parameter	Estimate	Standard Error	t-ratio	p
Intercept	2.7189	0.6989	3.89	0.006
Slope	0.93984	0.02469	38.07	0.000

Analysis of Variance

Source	Sum of squares	Df	Mean Square	F-ratio	p
Model	302.89	1	302.89	1449.12	0.000
Error	1.46	7	0.21		
Total	304.36	8			

Correlation coefficient = 0.995 Adjusted R^2 = 99.5%

Standard error of the estimate = 0.4572

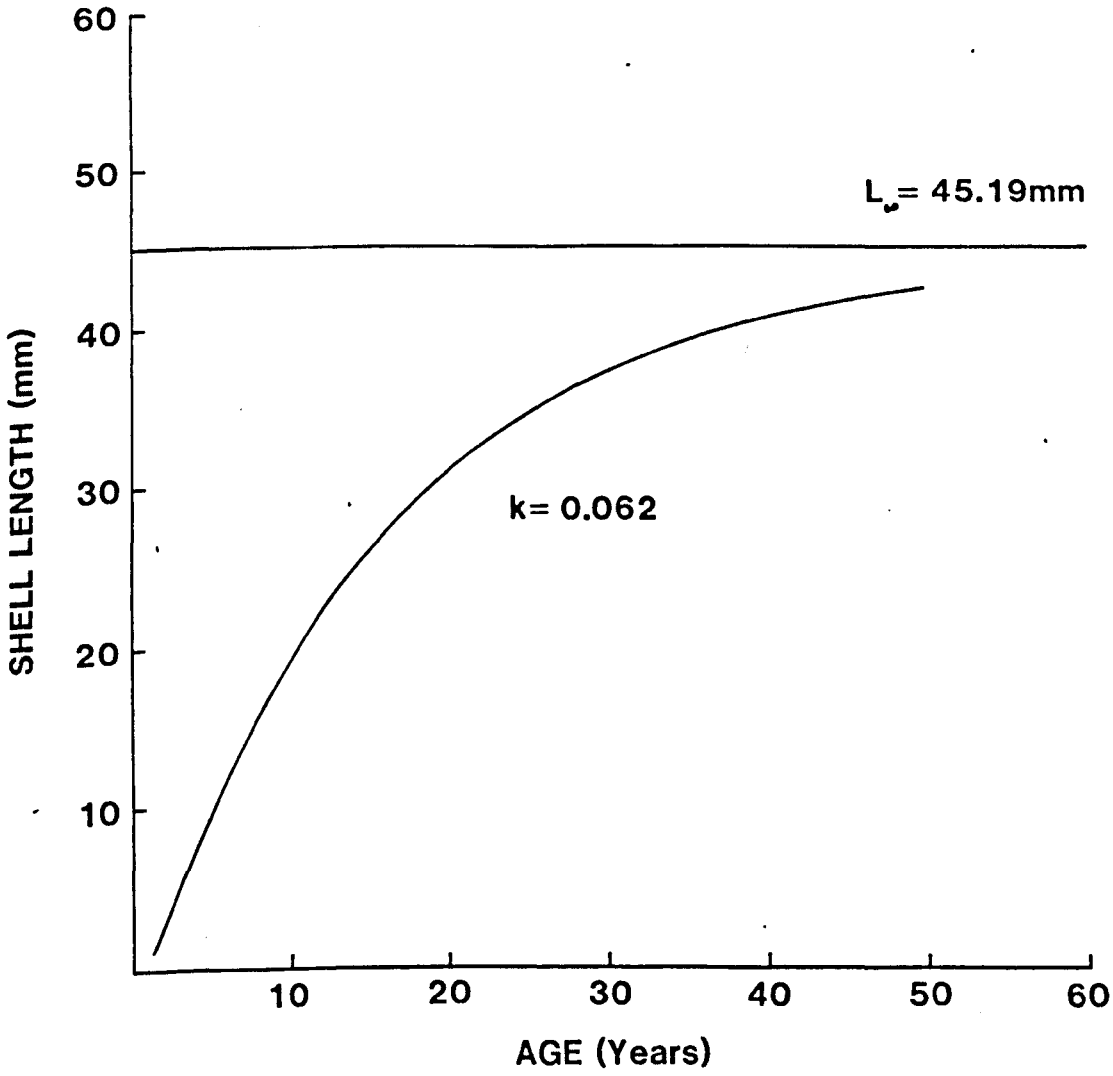


Figure 28. *Nacella concinna*. Growth curve constructed for the Inshore population of *Nacella concinna* from Factory Cove, Signy Island. L_∞ = Maximum predicted shell length, k = von Bertalanffy growth rate coefficient.

Table 11. Shell length (mm) at age (Years) predicted from the von Bertalanffy growth equation constructed for the inshore population of *Nacella concinna* in Factory Cove, Signy Island.

AGE	LENGTH	AGE	LENGTH	AGE	LENGTH	AGE	LENGTH
1	1.41	16	27.92	31	38.37	46	42.50
2	4.04	17	28.95	32	38.78	47	42.66
3	6.52	18	29.93	33	39.17	48	42.81
4	8.84	19	30.85	34	39.53	49	42.96
5	11.03	20	31.71	35	39.87	50	43.09
6	13.08	21	32.52	36	40.19		
7	15.01	22	33.28	37	40.49		
8	16.82	23	34.00	38	40.77		
9	18.53	24	34.67	39	41.04		
10	20.13	25	35.30	40	41.29		
11	21.64	26	35.90	41	41.52		
12	23.05	27	36.46	42	41.74		
13	24.39	28	36.98	43	41.95		
14	25.64	29	37.47	44	42.15		
15	26.81	30	37.94	45	42.33		

4.4 Discussion

The Antarctic limpet *Nacella concinna* has been shown to be long lived and slow growing based on the analysis of external shell growth bands (Picken, 1980b) and mark/recapture studies (Shabica, 1976). These investigations determined maximum age in the populations examined of between 21 and >63 years though differences in population size ranges and sampling environments were evident in each case.

Shabica (1976) in a comprehensive study of the *Nacella concinna* population of Arthur Harbour, Anvers Island (64° 46'S, 64° 05'W) marked 627 animals, released them for a period of 10 months and recaptured 30.94% of the original individuals covering a size range of between 8.13mm and 51.99mm shell length. Absolute growth was calculated for these individuals and adjusted to one year. In all animals recovered in this study no occurrence of negative growth was reported although 28 individuals over 38mm in length showed no measurable length change over the study period. Fitting a polynomial curve to the data, presented as yearly length increase against original shell length, a growth equation which fitted 65% of the population and described the growth rate of animals up to 40mm in length was obtained. The scatter about the fitted curve however showed extreme variability even for individuals of similar size and was suggested to be induced by both physiological and environmental conditions.

Using this relationship Shabica (1976) assigned an age of greater than 63 years for an individual of 39mm shell length, the absolute age uncertain as the polynomial relationship used to describe yearly growth in this study became negative after 40mm shell length was reached. Shabica also estimated an age for an individual of 61mm shell length from a gull midden proximal to the study site of approximately 190 years.

When the von Bertalanffy parameters are extrapolated from this data the Arthur Harbour population is described by a von Bertalanffy growth coefficient k of 0.019 and a length asymptote of 53.68mm. The age of an individual 39mm in length calculated using these parameters and a t_0 value of 0.4887 (Picken, 1980b) is 69 years and this value corresponds closely to that of 63 years predicted by Shabica (1976) using the polynomial growth model. The growth rate of this population described by the von Bertalanffy coefficient is extremely slow in comparison to the present study but may be affected by the reported measurement accuracy of the vernier calipers used of ± 0.12mm.

Picken (1980b) in a study of the *Nacella concinna* population of Factory Cove, Signy Island, used the external, annually deposited (Shabica, 1976) growth bands evident on small individuals to determine population growth rates. Animals within the size range 0.7mm to 26.30mm shell length were examined from a population ranging from 0.7mm to 41.00mm shell length and the rate of growth described using the von

Bertalanffy model. A calculated age of 21 years was ascribed to the largest individual of this population with associated values of L_∞ = 53.0mm, k = 0.0715 and t_0 = 0.4887 determined for the von Bertalanffy parameters.

In the present study the effects of shell loss through abrasion of the shell edges has been shown to prevent an accurate measurement of uniform shell growth in the majority of animals measured. Where the axes of measurement have not been obviously damaged and yearly growth can be assessed the growth parameters for the population are similar to those of Picken (1980b) predicting an L_∞ of 45.19mm and k value of 0.062. The yearly increases in shell length observed and predicted are very similar indicating a good fit of the model to the observed data.

The growth curves for the *Nacella concinna* populations examined by Shabica (1976), Picken (1980b) and the present study are presented in Figure 29. Initially the curves derived form the data of Picken (1980b) and the present study are similar. They seperate, however, with time with the present study predicting slower growth with greater age than that of Picken (1980b). The rate of growth described by the von Bertalanffy curve fitted to the data of Shabica (1976) is considerably slower than either Picken's data or that of the present study. It is likely that a degree of this difference is due to the difficulties of extraction of accurate data from Shabica's work which is complicated by the small size of the increments and annual adjustment to the original

recapture data performed by Shabica. If it can be assumed that these factors have not significantly displaced the growth curve derived from this data, the reduced growth rate may represent the effects of a shorter summer growth period or be indicative of a general difference in environmental regime on the Arthur Harbour population of *Nacella concinna*. Similar variation in longevity and growth rate with specific habitat occupied has been observed in *Patella vulgata* (Lewis and Bowman, 1975) though not of the magnitude described in the present comparison.

The growth coefficient k, is a useful comparative index of growth that is not dependent on body size. In comparison with the relatively few other Antarctic species measured the k value of *Nacella* is extremely low and within a similar range to the bivalve *Yoldia eightsi* (k=0.056). Ralph and Maxwell (1977) in a study of the growth of the Antarctic bivalves *Adamussium colbecki* and *Laternula elliptica* calculated k values of 0.24 and 0.16 for these species. Although these values are low when compared with temperate species, they appear to be high when related to the values for the co-existent species *Nacella concinna* and *Yoldia eightsi* which are under similar environmental controls. A large part of this difference may, however, be explained by the use of external growth lines as the means of aging in this study. This technique is widely criticised particularly with slow growing animals where the ability to resolve external, annual growth lines is extremely difficult.

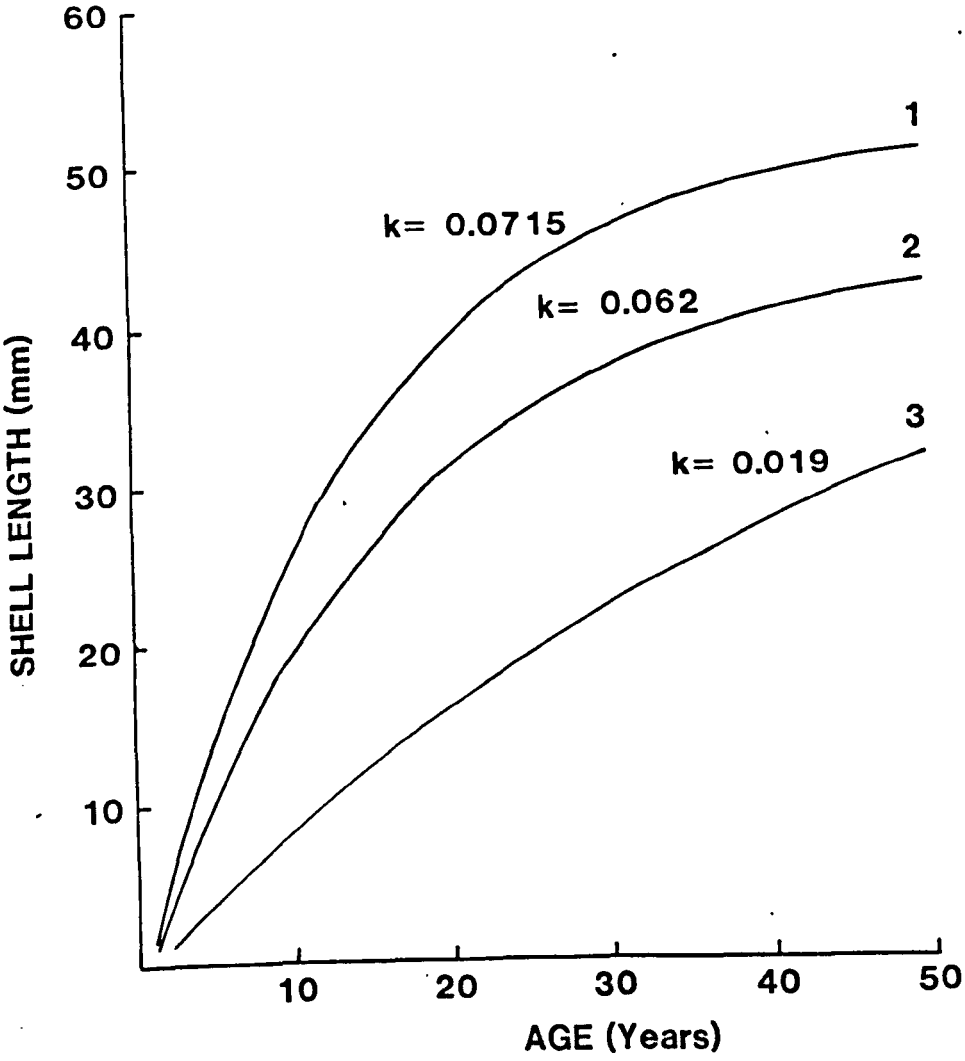


Figure 29. *Nacella concinna*. Comparison of growth curves constructed for populations of *Nacella concinna* from Factory Cove, Signy Island (1 ; Picken, 1980b; 2 ; Present Study) and Anvers Island (3 ; Extrapolated from data presented in Shabica, 1976). k = von Bertalanffy growth rate coefficient.

Within limpet species an inverse correlation between longevity and k has been shown to exist on both an intraspecific and interspecific level (Branch, 1981; Lewis and Bowman, 1975). Different environmental conditions exist to explain this slow growth in species showing low k values with food availability recognised as a highly significant factor.

The effects of seasonal ice cover, annual winter migration and a short, seasonal pulse of algal growth, associated with light attenuation and penetration of the water column, effectively limit the growing season available to the *Nacella concinna* population of Factory Cove. This has the effect of reducing the growth rate to an extremely low level and increasing longevity to a possible maximum of between 40 and 50 years. The rate of growth of Antarctic *Nacella concinna* populations are therefore the lowest recorded for any limpet species so far examined.

CHAPTER 5

The distribution and Morphometric characteristics of the *Yoldia eightsi* population of Factory Cove.

5.1 Sample collection.

Yoldia eightsi were collected from a site in Factory Cove, Signy Island (Fig. 3) using a diver-assisted underwater suction sampler [*'Zotter'* or *'Ivor'*] (modified after Hiscock and Hoare, 1973) at monthly intervals over the period December 1987 - December 1988 (Figs. 30 and 31). The site of collection was determined from a preliminary S.C.U.B.A. survey of the cove area and was positioned as the intersection of the line transects of : 1) the seal exclosure on Waterpipe beach with the centre of the large Billie Rock, with 2) the line of sight between the fume cupboard and kitchen chimneys of Signy Base. The site was buoyed during the summer months and located during the winter by line of sight. The site was accessed during the winter through a hole cut in the sea-ice.

Initial problems in the successful operation of the suction sampler were few and easily overcome. During winter, however, the venturi ports of the air intake in the main riser pipe had a tendency to ice-up, effecting the suction potential and efficient operation of the sampler. This fault was caused by a combination of low air and water temperatures cooling the apparatus prior to operation in combination with an excessively high air pressure entering the venturi

Fig. 30. The author pictured with the modified Hiscock and Hoare (1973) suction sampler assembled in it's working state. An inflatable air-bag was attached to the frame of the sampler to assist lifting to the surface after the sampling session was completed.

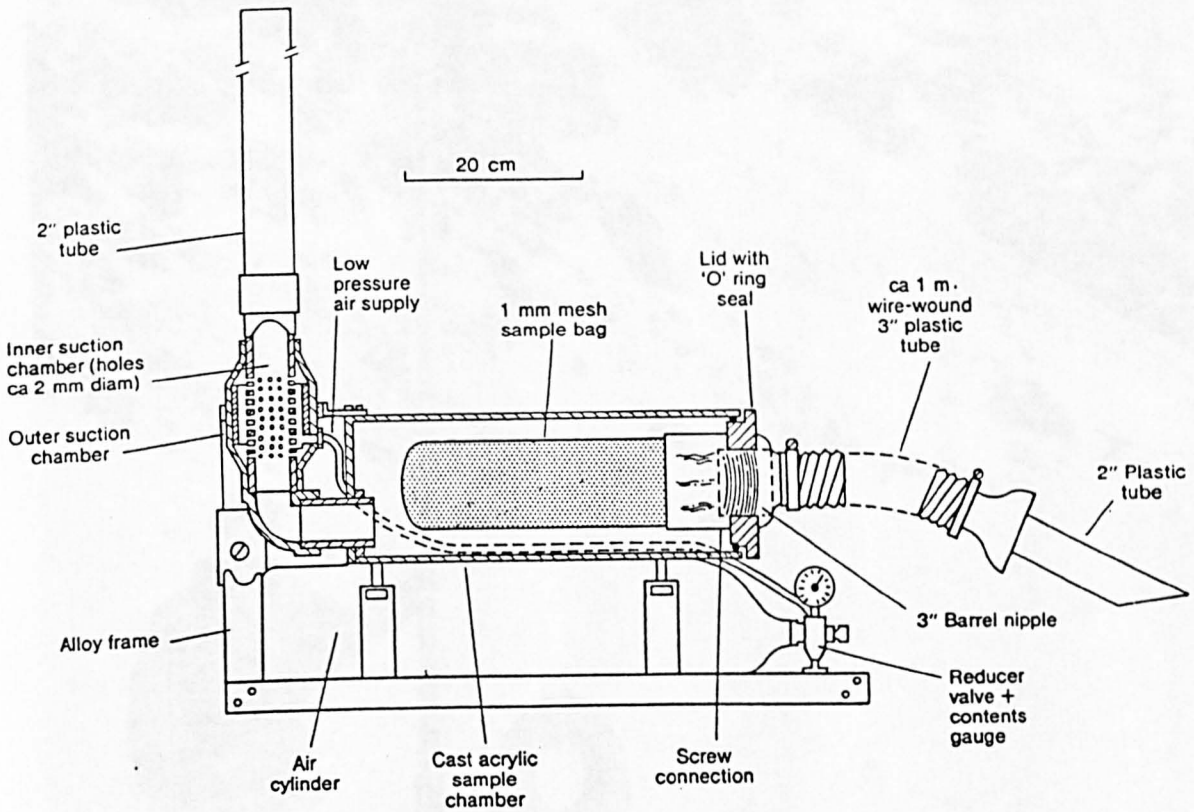


Figure 31. The modified Hiscock and Hoare (1973) suction sampler used to sample the *Yoldia eightsi* populations of Factory Cove, Signy Island. Compressed air is fed to the inner suction chamber and passes up the exhaust tube. In so doing a vacuum is created which draws water and sediment through the sampling nozzle and through the 1mm mesh sample bag. The sample bag is situated within a clear plastic tube and is removed after operation by unscrewing from the inflow hose to which it is secured through the tube lid.

chamber. As no gas regulator was immediately available this problem was eventually solved by introducing the high pressure air to the chamber at a very low rate through the manual adjustment of the pillar valve on the compressed air feeder bottle (Fig. 31).

Once on site a $0.25m^2$ quadrat was placed randomly on the sediment and the sediment therein removed to a depth of 4cms by the suction sampler. On return to the surface the sample bag was removed and placed in a bucket of fresh sea-water. On return to the laboratory animals retained by the 1mm mesh sampling bag were used for both morphometric and experimental analysis.

5.2 *Morphometric methodology*

The length and height of all individuals sampled was measured to ± 0.01mm, and a representative sub-sample taken for ash free dry mass measurements.

Animals were shucked of all tissue, blotted of any excess water, weighed to ± 0.001g and dried at 60°C for 24hrs. Dry masses were determined and the samples placed in a muffle furnace at 550°C for 12hrs. After cooling, ash masses were measured to ± 0.001g and the Ash free dry mass determined for each individual.

5.3 *Morphometric results*

A strong relationship between shell length and shell height was evident in all the shells measured, with the regression explaining 99.6% of the variance (Fig. 32, Table 12). The summary statistics for length, height, dry mass and ash free dry mass are shown in tables 13 and 14 and the length frequency histograms for samples collected from December 1987 - December 1988 in Figs. 33 and 34.

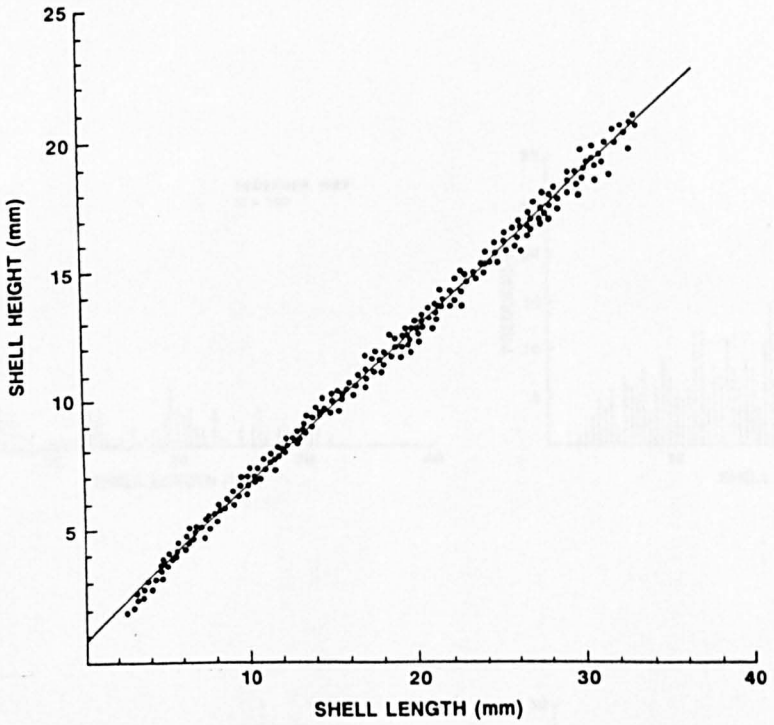


Figure 32. The relationship between shell height and shell length in *Yoldia eightsi* from Factory Cove, Signy Island. The fitted regression line is presented in Table 12. 2,850 points have been omitted to prevent obscuring the diagram.

Table 12. *Yoldia eightsi*. Least squares regression and analysis of variance of shell length (mm) on shell height (mm). p = Probability level, Df = Degrees of freedom.

Parameter	Estimate	Standard Error	t-ratio	p
Intercept	0.74278	0.01097	67.72	< 0.001
Slope	0.60558	0.00068	886.15	< 0.001

Analysis of Variance

Source	Sum of squares	Df	Mean square	F-ratio	p
Model	48689	1	48689	785266	< 0.001
Error	188	3038	0		
Total	48878	3039			

Correlation coefficient = 0.996 Adjusted R^2 = 99.6%

Standard error of the estimate = 0.2490

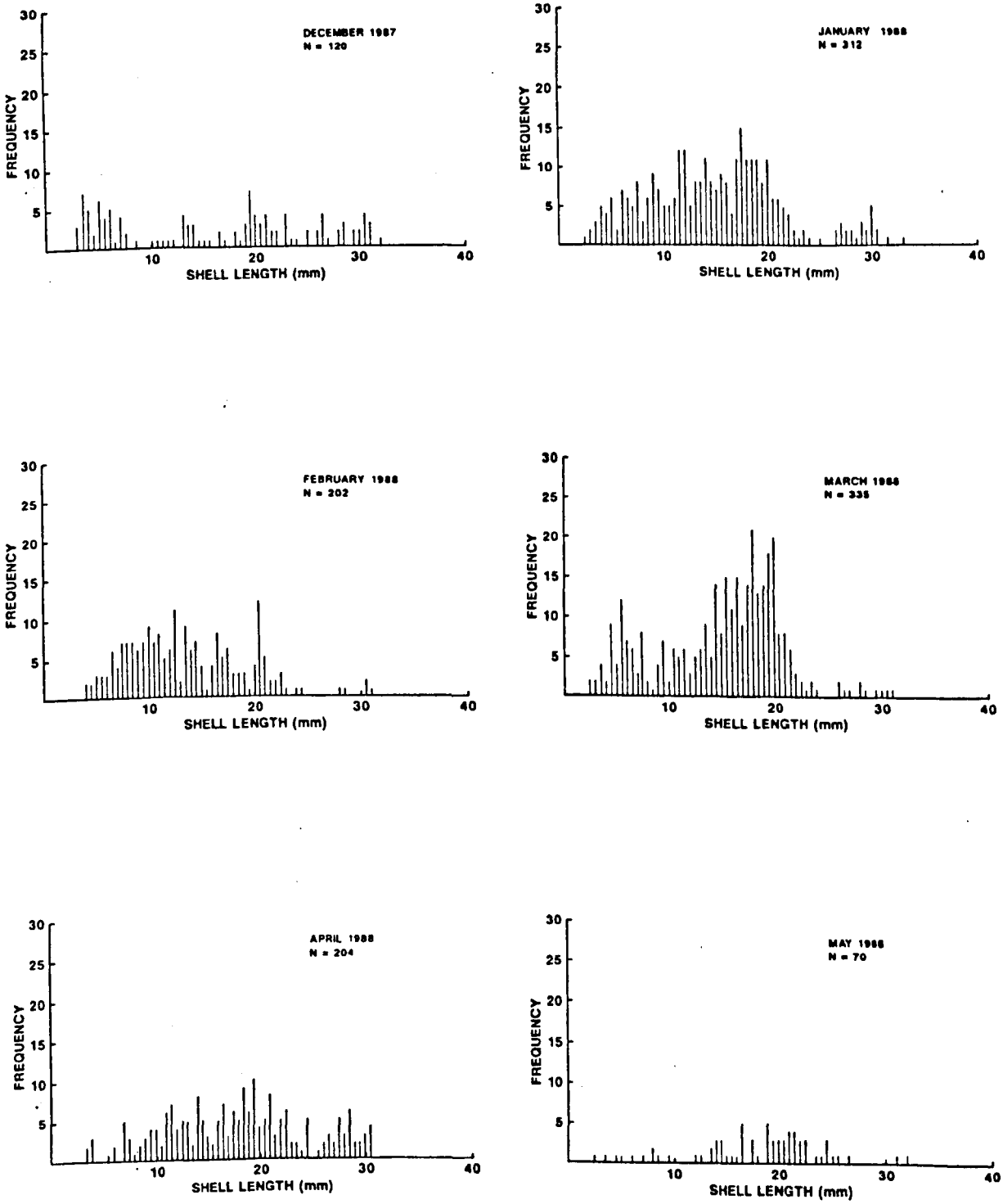


Figure 33. Length/Frequency histograms of monthly *Yoldia eightsi* collections taken over the period December 1987 - May 1988 in Factory Cove, Signy Island.

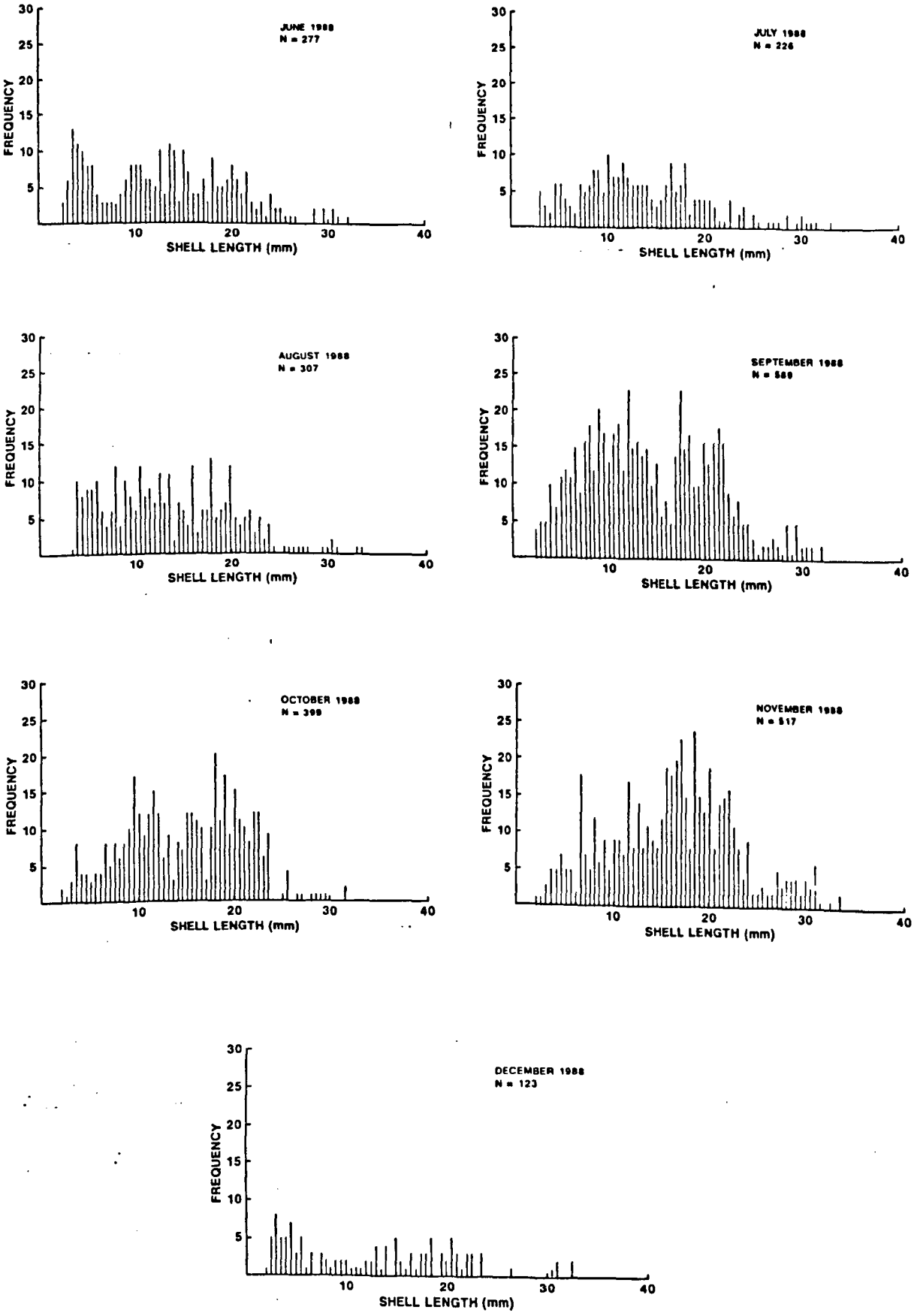


Figure 34. Length/Frequency histograms of monthly *Yoldia eightsi* collections taken over the period June 1988 - December 1988 in Factory Cove, Signy Island.

Table 13. *Yoldia eightsi*. Monthly summary statistics for shell length and shell height of samples taken between December 1987 and December 1988 in Factory Cove, Signy Island.

SHELL LENGTH (mm)

	N	Mean	SE	Min.	Max.
DECEMBER 1987	120	15.88	0.84	03.07	31.85
JANUARY 1988	312	14.97	0.37	02.48	33.01
FEBRUARY	202	13.64	0.40	04.00	30.86
MARCH	335	15.04	0.32	02.58	30.94
APRIL	204	17.66	0.47	03.38	30.60
MAY	70	17.69	0.74	02.47	31.95
JUNE	277	13.12	0.42	02.30	32.05
JULY	226	13.58	0.43	22.92	33.21
AUGUST	307	13.65	0.37	03.66	33.26
SEPTEMBER	589	14.39	0.27	02.28	31.93
OCTOBER	399	14.80	0.30	02.16	31.42
NOVEMBER	517	16.24	0.29	01.83	33.73
DECEMBER 1988	123	12.52	0.71	01.88	32.42

SHELL HEIGHT (mm)

	N	Mean	SE	Min.	Max.
DECEMBER 1987	120	10.29	0.51	02.29	19.36
JANUARY 1988	312	09.77	0.22	01.84	19.73
FEBRUARY	202	09.02	0.24	02.80	19.88
MARCH	335	09.86	0.20	02.00	20.13
APRIL	204	11.47	0.28	02.47	19.10
MAY	70	11.42	0.45	01.85	19.79
JUNE	277	8.67	0.25	01.81	20.46
JULY	226	8.97	0.26	02.16	21.06
AUGUST	307	9.02	0.23	02.58	20.80
SEPTEMBER	589	9.46	0.17	01.68	19.36
OCTOBER	399	9.73	0.19	01.72	19.96
NOVEMBER	517	10.57	0.18	01.33	21.40
DECEMBER 1988	123	8.27	0.44	01.40	20.79

Table 14. *Yoldia eightsi*. Monthly summary statistics for Tissue dry mass and Tissue ash free dry mass of samples taken between December 1987 and December 1988 in Factory Cove, Signy Island.

TISSUE DRY MASS (mg)

	N	Mean	SE	Min.	Max.
DECEMBER 1987	66	219.74	19.49	30.80	572.00
JANUARY 1988	108	110.65	13.92	00.15	595.60
FEBRUARY	204	63.26	6.27	00.74	472.70
MARCH	335	81.19	4.48	00.22	498.10
APRIL	204	128.25	9.05	00.51	527.40
MAY	60	121.00	13.70	00.10	493.30
JUNE	137	83.58	9.51	00.18	493.80
JULY	122	72.73	9.34	00.24	452.10
AUGUST	123	52.97	8.86	00.01	512.20
SEPTEMBER	148	54.51	6.84	00.11	487.80
OCTOBER	123	64.25	8.95	00.12	462.90
NOVEMBER	123	85.48	10.55	00.06	543.90
DECEMBER 1988	123	69.38	9.85	00.11	559.30

TISSUE ASH FREE DRY MASS (mg)

	N	Mean	SE	Min.	Max.
DECEMBER 1987	59	154.13	14.87	18.90	385.40
JANUARY 1988	108	86.49	11.24	00.03	493.20
FEBRUARY	202	40.74	4.36	00.45	348.80
MARCH	334	50.09	2.95	00.05	341.40
APRIL	201	88.13	6.44	00.42	361.00
MAY	60	80.37	9.68	00.10	368.20
JUNE	137	54.78	6.36	00.13	344.60
JULY	122	48.54	6.45	00.21	322.60
AUGUST	123	33.30	5.90	00.01	350.30
SEPTEMBER	148	36.80	4.86	00.08	372.00
OCTOBER	121	38.77	5.60	00.09	273.40
NOVEMBER	122	54.00	6.82	00.13	357.90
DECEMBER 1988	123	41.03	5.94	00.10	336.80

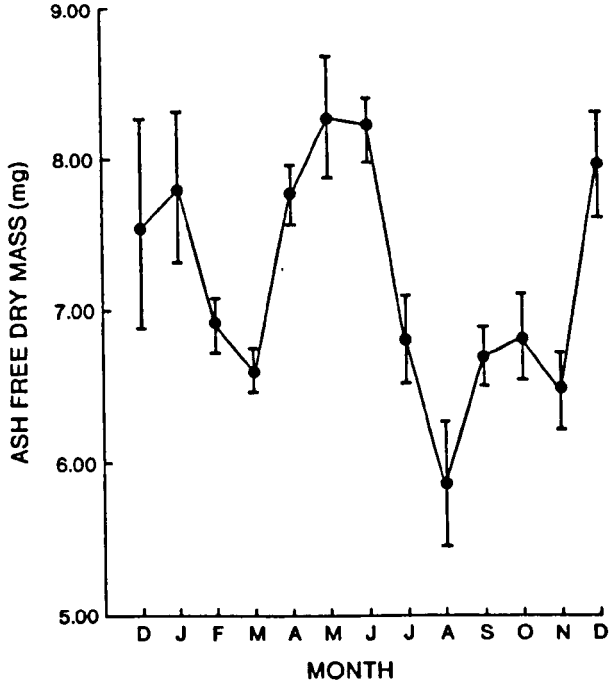


Figure 35. Seasonal variation in Tissue ash free dry mass (mg) of the *Yoldia eightsi* population sampled over the period December 1987 - December 1988 from Factory Cove, Signy Island. Values determined for a standard animal of 10mm shell length derived from monthly regression algorithms (Table 15). 95% confidence limits plotted for each point.

Table 15. Monthly regression parameters for the relationship of Log ash free dry mass (mg) on Log length (mm) in the *Yoldia eightsi* population of Factory Cove, Signy Island, over the period December 1987 - December 1988. Int = Intercept, b = regression co-efficient, SE = Standard error, n = number of observations and F = value of the F statistic.

Month	Int	b	n	F	SEb
December	-2.624	3.502	58	3872	0.056
January	-2.450	3.342	101	6369	0.042
February	-2.665	3.350	201	16170	0.028
March	-2.836	3.656	333	38079	0.019
April	-2.516	3.406	200	28319	0.020
May	-2.404	3.322	59	9043	0.035
June	-2.293	3.207	136	33337	0.018
July	-2.407	3.240	121	10560	0.032
August	-2.627	3.395	122	3585	0.057
September	-2.463	3.289	147	25665	0.021
October	-2.398	3.232	120	12411	0.029
November	-2.505	3.316	121	15897	0.026
December	-2.118	3.019	122	10287	0.030

Tissue ash free dry mass showed a strong relationship with shell length. Monthly regression data of Log ash free dry mass on Log length are presented in table 15 with a graphic representation of seasonal change in tissue biomass based on these data and extrapolated for a standard animal of 10mm shell length presented in fig. 35. This shell size was chosen to represent an individual below the mean size with a relatively fast rate of growth and assimilation efficiency.

Table 16 combines the monthly Ash free dry mass relationships with length with the monthly abundance of *Yoldia* to produce a total biomass and abundance measurement per square metre of sediment over the sample site. Tissue ash free dry mass ranged from 22.04gm^{-2} to 111.27gm^{-2} over the study period, with a yearly average of 52.41gm^{-2}.

5.4 Population density

The analysis of population density was performed using the coefficient of dispersion (CD). This is a standard measure calculated as the ratio of the variance to the mean of population samples (CD = variance/mean) and was applied to the combined density measurements of samples of *Yoldia* taken throughout the study period. Where this ratio is close to 1 the distribution is essentially Poisson and indicative of a randomly distributed population.

Table 16. Monthly biomass of *Yoldia eightsi* from Factory Cove, Signy Island collected over the period December 1987 - December 1988 expressed as Ash free dry Mass (g) and number of individuals per square meter. SD = Standard deviation, N = number of individuals.

Month	g/m²	N/m²
December 1987	46.21	480
January 1988	36.41	1248
February	31.28	808
March	68.08	1340
April	70.43	816
May	22.04	280
June	44.53	1108
July	32.42	904
August	41.96	1228
September	96.94	2356
October	61.86	1596
November	111.27	2068
December 1988	17.85	492
Mean	52.41	1133
SD	28.19	611

Table 17. *Yoldia eightsi*. Oneway analysis of variance of Shell length, Shell height, Dry mass and Ash free dry mass in monthly samples collected over the period December 1987 - December 1988 from Factory Cove, Signy Island. df = degrees of Freedom, SS = Sum of squares, MS = Mean square, F = F statistic value, p = probability level.

Source of Variation	df	SS	MS	F	p
Shell Length					
Among months	12.00	6027.06	502.25	11.59	<0.001
Within months	3668.00	158934.44	43.33		
Total	3680.00				
Shell height					
Among months	12.00	224.72	185.39	11.54	<0.001
Within months	3668.00	58908.08	16.06		
Total	3680.00	59132.80			
Dry mass					
Among months	12.00	2192315	182963	15.99	<0.001
Within months	1836.00	2096712	11422		
Total	1848.00	4289027			
Ash free dry mass					
Among months	12.00	1158676	96556	17.92	<0.001
Within months	1847.00	9951636	5388		
Total	1859.00	11110312			

Where the variance is much greater than the mean value, a clumped or contagious distribution is obtained, which is indicative of a non-random distribution of the population. The results of this test on the monthly density measurements in the Factory Cove population of *Yoldia eightsi*, indicate a highly contagious or clumped density distribution (Coefficient of dispersion = 329.50). No seasonal pattern to the population density is evident with the coefficient of dispersion greater than 1 in each case. The population of *Yoldia* is therefore non-randomly distributed and deviates significantly from the expected monthly observations of density distribution in a randomly dispersed population. Densities of *Yoldia* in Factory Cove ranged from $280m^{-2}$ to $2356m^{-2}$ over the study period with a yearly average of $1133m^{-2}$.

The non-random distribution of the *Yoldia* population in Factory Cove is further supported by the analysis of variance in shell and tissue morphometrics between monthly sample collections (Table 17). With an assumed slow rate of shell growth in *Yoldia* the expected observation, based on the assumption of totally random comparative samples from a single population, is one where no significant difference exists between monthly samples. This, however, is not the case in the *Yoldia* population of Factory Cove and although all monthly samples are generally distributed over similar ranges there is a significant statistical difference in their comparative distributions ($p<0.001$).

This significant degree of variability in shell morphometrics is associated with similar and slightly more significant monthly differences in tissue dry mass and tissue ash free dry mass measurements. A large proportion of these differences must, however, be attributed to temporal changes in the physical condition of the populations sampled.

5.5 Discussion

The seasonal trend in tissue ash free dry mass shows a gradual decrease in body mass through the months of January to March. This coincides with an increase in turbidity of the water column caused by the phytoplankton bloom which has the effect of reducing available light levels to the benthic algae. During the decline of the planktonic algal bloom to winter levels there is an associated downward flux of algal material from the water column to the sediment. This peaks in February and continues through to April. During the majority of this period individual *Yoldia* biomass is in decline increasing only after the complete settlement of the bloom material. This coincides with an increase to pre-bloom levels in the light penetration characteristics of the water column and coincides with a rise in benthic algal biomass at this time. *Yoldia* biomass levels respond immediately to this increase in food supply reaching their maximum condition in June. *Yoldia* has been observed spawning during June (Colman, pers. comm.) and this, associated with the formation of winter sea-ice, may explain the rapid decline in ash free dry mass over July which reaches a yearly low in August. This

decline in condition suggests a metabolic response to the release of gametes, falling water temperatures and a reduced level of light penetration to the benthos. Body condition improves slightly after spawning and remains stable throughout the winter months of September to November when increasing light levels and depth of penetration induces the major bloom of benthic algae. This bloom peaks in December and falls away to winter levels during February. The length and duration of winter sea-ice regulates the seasonal productivity of the benthic bloom by controlling the period of light penetration to the benthos (White, 1973). As the phytoplankton bloom increases in productivity there is a steady decrease in light attenuation through the water column eventually reaching levels which are below the productive threshold levels necessary for benthic algal increase.

It would appear that the magnitude of these two annual events, which supply food to the benthos, are of significant importance to *Yoldia* and serve to dictate the fecundity and growth rate of the population. The growing season of *Yoldia* thus occurs during two intervals : early summer when food is provided by the main period of the benthic algal bloom along with vertical flux from the water column and late autumn when the water column clears and allows a brief period of benthic algal production. Depending on the amount of organic input to the sediment from these sources, a potential growing season of between 2 and 6 months may be estimated for *Yoldia* .

The determination of year classes from the analysis of size frequency distributions depends upon the identification of prominent size classes within sample distributions and the ability to follow their temporal progression through the population. This method of analysis demands consistently random sampling of a single population throughout the study period and shows greatest resolution in relatively fast growing organisms. When applied to relative slow growing organisms the ability to resolve individual size classes becomes increasingly difficult.

The separation of year classes in the *Yoldia eightsi* population of Factory Cove, based on standard length frequency techniques, proved difficult to justify and was compounded by the non-random nature of the population distribution within the study site (Figs. 33 and 34). Alternative techniques were therefore required to determine the annual growth rate and the age structure of the *Yoldia eightsi* population.

CHAPTER 6

The determination of shell growth in *Yoldia eightsi*.

6.1 Introduction.

The nuculanid, protobranch bivalve, *Yoldia (Aequiyoldia) eightsi* (Jay, 1839) is a dominant infaunal member of Antarctic soft bottom communities, with densities in excess of 2,700m^{-2} recorded for inshore sediments (Rabarts, 1970). It is a widely distributed species which, although apparently limited to the western sector of the Antarctic continent, has a range extending northwards through the Scotia arc to the Magellanic region of South America and Southern Chile as far North as 49°S (Dell, 1962; 1971; Powell, 1951; 1960; Rabarts and Whybrow, 1979), with an isolated occurrence at Kerguelen Island (49°32'S, 70°13'E). It occurs in a variety of sediments ranging from muddy gravel to fine mud being concentrated in the top 4cms of the sediment within a depth range of 5m-728m (Dell, 1964). Members of the genus are primarily surface and sub-surface deposit feeders (Yonge, 1939) with an ability to filter feed and can have a significant influence in reworking bottom sediment. *Yoldia eightsi* is particularly noteworthy in this regard with an individual of shell length 30mm capable of processing approximately 4.55g dry wt sediment per day when actively feeding (Davenport, 1988a, 1989).

The shell is completely aragonitic and has a fine grained homogeneous structure. It is essentially constructed of one distinct layer, although there is a small wedge of prismatic structure beneath the hinge plate at the position of the dorsal pallial muscle attachment or that of a pedal muscle (Taylor *et al*, 1969).

Molluscan shell growth rates have received much attention because they form a convenient index of whole body growth, and represent a history of current and past regimes of carbonate deposition within the structure of the shell (Wilbur, 1972; Clark, 1974). Methods commonly used in determining seasonal and long term rates of shell growth have generally been based on following the incremental addition to shell height, length or weight over time. Alternatively methods utilising the microscopic analysis of internal periodicity structures within the shell and incorporation of chemical or isotopic markers into the shell carbonate have been used to determine short term growth rates.

The measurement of increases in linear shell dimensions is an important tool in analysing the structure and longevity of bivalve populations (Orton, 1926; Moore, 1934; Comfort, 1957; Mason, 1957; Eisma, 1965; Andrews, 1972; Ebert, 1973; Gilbert, 1973; Seed, 1973; Hutchings & Haedrich, 1984). Limitations, however, exist with this type of analysis as measurements are generally restricted to the shell margin and may not necessarily reflect total shell growth. More importantly the daily incremental addition to the shell may

be so small as to require lengthy periods of growth to register a significant measurable increment.

External growth lines on the shells of molluscs have long been used to determine growth rates and age structure of many species (Newcombe, 1935; Craig & Hallam, 1963; Rabarts, 1970; Brousseau, 1979; Luckens, 1990). The principal difficulty encountered with this means of analysis arises from an inability to distinguish disturbance and event marks from genuine annual rings (Peterson & Ambrose, 1985; Emerson, 1990). If surface sculpture is used to determine annual periods a similar problem exists as in many cases, within the depth range of a species, the surface sculpture may alter becoming less complex as depth increases (Forbes, 1854). The number of external shell lines therefore, may or may not correspond to the age of bivalves examined (MacDonald & Thomas, 1980)

Periodic increments or growth bands, within bivalve shells have provided a more accurate means of estimating growth rates with much attention focusing on environmental influences associated with their formation and their biological and palaeontological significance (see Rosenberg and Runcorn, 1975; Lutz & Rhoads, 1977; Gordon & Carriker, 1978; Rhoads and Lutz, 1980 for a review)

Increment formation has generally been associated with periods of feeding and metabolic activity. This is especially evident in littoral and shallow sub-sublittoral animals where

there is an associated response to tidal conditions (Mathers, 1976; Loosanoff & Nomejko, 1946; Richardson, 1987, 1988; Richardson *et al.*, 1980), salinity changes (Bøggild, 1930; Lowenstam, 1954b; Eisma, 1966; Richardson, 1987) and temperature fluctuations (Lowenstam, 1954a, 1954b, 1964; Dodd, 1963, 1964, Peck, 1989). Also the degree of exposure to environmental extremes correlates strongly with growth line prominence (Clark, 1974).

The formation of first order or annual lines has been attributed to temperature cycles (Barker, 1964), the spawning cycle (Thompson *et al*, 1980; Jones *et al*, 1978), food pulses (Rhoads & Pannella, 1970, Gilkinson *et al*, 1986) and decreased winter growth (MacDonald & Thomas, 1980). Generally there is no evidence of complete cessation of shell growth throughout the year but rather a variation in the extent of increment size (Kennedy *et al*, 1969). It has been shown that crystal size and density decrease as growth rates slow (Wada, 1961; MacClintock, 1967; Pannella & MacClintock, 1968; Lutz, 1976; Deith, 1985), resulting in the deposition of narrower growth increments in winter.

The incorporation of isotopic calcium into shell carbonate has been used extensively to determine shell accretion, dissolution and growth rates on a gross level (Bevelander, 1952; Wilbur & Jodrey, 1952; Jodrey, 1953; Crenshaw & Neff, 1969; Zischke *et al*, 1970; Wheeler *et al*, 1975; Dillaman & Ford, 1982). However, decrease of growth with age, calcium concentration and temperature (Kado, 1960)

and differences in the uptake rate of discrete shell regions (Wheeler *et al*, 1975) effect the gross incorporation of isotopic calcium and make the determination of incremental growth per unit area of shell difficult to define quantitatively. A recent development of the this technique through the incubation and controlled etching of specific shell regions allows the incremental addition to axes of shell growth to be measured over extremely short periods (Dillaman & Ford, 1982).

6.2. The analysis of Shell growth using ^{45}Ca.

6.2.1 Materials and Methods

I. Shell preparation and Etching procedure.

Five experimental animals were selected from the collection taken in January 1988 within the size ranges of 14-17mm and 20-23mm. Internal anatomical examination revealed these size classes to be representative of immature and mature individuals respectively.

Each group of animals was measured to ± 0.01mm using a vernier callipers, acclimated for 5 days in 0.5 litre jars of freshly collected sediment, and placed in running seawater at ambient temperature prior to the experimental procedure.

To investigate the short term incorporation of calcium separately contained samples of five immature and mature individuals were incubated together in a medium containing 0.130 $\mu Ci\ ml^{-1}$ (4.8 $kBq\ ml^{-1}$) ^{45}Ca and animals removed and sacrificed after 48, 72, 96, 120 and 144 hours. Freshly shucked and cleaned animals were placed in the containing jar of each incubation group as controls. After incubation 3 animals were selected from each group, the tissues excised and the shells washed and air dried. The right valve was selected for analysis.

Pieces of shell approximately 5mm x 5mm were cut from the edge of the shell and external to the pallial line using a hand held mini-drill with fine saw blade attachment taking care to include and not damage the growing edge. All pieces were taken from a central position of the right valve (Fig. 36). The periostracum was removed, after soaking in water for 30 minutes, due to the likelihood of it becoming detached during the experimental procedure causing an unwanted exposure of shell material. Once removed and the shell piece dried at 50°C for 30 minutes, all edges were lightly ground using fine emery paper. Special attention was paid to the growing edge of the shell margin in this regard. This particular area was removed because Dillaman and Ford (1982) had found that ^{45}Ca was spread over a large number of fractions when etched in the presence of the shell tip. This effect was due to the upturned nature of the shell edge (which incorporated the labelled layer) and the single plane of action of the etching solution upon the shell material. If not removed, the curved edge releases the label over a longer period than that of the flat inner area.

Shell pieces were coated with nail varnish on their exposed edges and external surfaces and glued to 0.5mm x 1mm x 10mm wooden strips by their painted surface (Fig. 36b). The strip was then glued in a central position to the tapered end of the etching chamber shaft (Fig. 36c) and the shaft placed in the chamber to a depth of 43mm, equivalent to a sample chamber volume of 1ml.

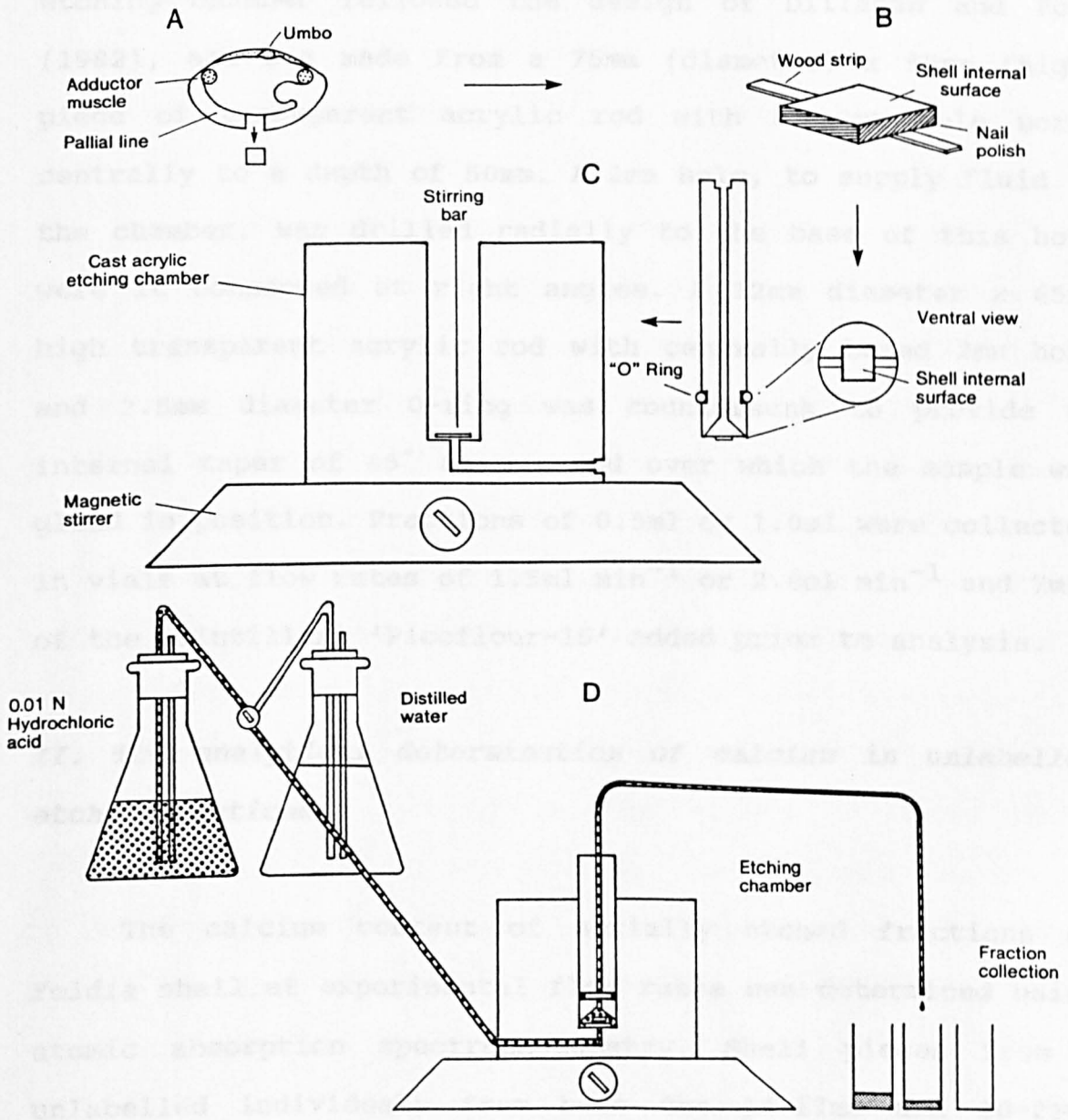


Figure 36. The controlled etching procedure: **A**, Shell piece cut from valve post pallial line; **B**, Section painted with Nail polish and mounted on wooden strip; **C**, Wooden strip glued to the base of central chamber rod; **D**, Etchate flows over sample and fractions are collected at pre-determined intervals.

The etching apparatus consisted of a regulated gravity fed supply of 0.01N HCl or distilled water to the sample chamber passing over the mounted sample (Fig 36d). The etching chamber followed the design of Dillaman and Ford (1982), and was made from a 75mm (diameter) x 55mm (high) piece of transparent acrylic rod with a 12mm hole bored centrally to a depth of 50mm. A 2mm hole, to supply fluid to the chamber, was drilled radially to the base of this hole were it connected at right angles. A 12mm diameter x 65mm high transparent acrylic rod with centrally bored 2mm hole and 2.5mm diameter O-ring was countersunk to provide an internal taper of 45° at one end over which the sample was glued in position. Fractions of 0.5ml or 1.0ml were collected in vials at flow rates of 1.5ml min^{-1} or 2.0ml min^{-1} and 7mls of the scintillant 'Picoflour-15' added prior to analysis.

II. The analytical determination of calcium in unlabelled etched fractions.

The calcium content of serially etched fractions of *Yoldia* shell at experimental flow rates was determined using atomic absorption spectrophotometry. Shell pieces from 3 unlabelled individuals from both the 14-17mm and 20-23mm length size classes, were cut and prepared similarly to the procedure used for labelled individuals. Thirty serial fractions of 1ml volume, at flow rates of 1.5ml min^{-1} and 2.0ml min^{-1} 0.01N HCl, were taken and the calcium concentration of the elutant measured on an *Instrumentation*

Laboratories Video 11 spectrophotometer using an air/acetylene flame and a wavelength of 422.7nm.

6.2.2 *Results*

I. Fraction calcium analysis.

The pattern of calcium elution from pieces of non-labelled *Yoldia* shell etched at flow rates of 1.5mls and 2.0ml min^{-1} 0.01N HCl are presented in Fig. 37. Flow rates lower than 1.5ml min^{-1} and particularly at 1.0ml min^{-1}, produced an erratic elution of calcium from the shell pieces due in the main part to the formation of substantial amounts of carbon dioxide which tended to adhere to the surface under etch and come off when bubble size reached unstable proportions. This varied the surface area available to etching throughout the procedure and produced variable concentrations of calcium in the etched fraction. This problem, unmentioned in the original protocol and results of Dillaman and Ford (1982), was overcome by increasing the flow rate over the specimen thus reducing variation between replicates (Table 18).

Calcium content of serial fractions at 1.5ml and 2ml min^{-1} etch rate show an increase over the first four fractions reaching a maximum of 37.8μg Ca/ml/cm^2 and 36.7μg Ca/ml/cm^2 respectively. At the slower flow rate the calcium content decreases from this maximum and settles to a serial mean of 31.35μg Ca/ml/cm^2, with that of the faster etch rate

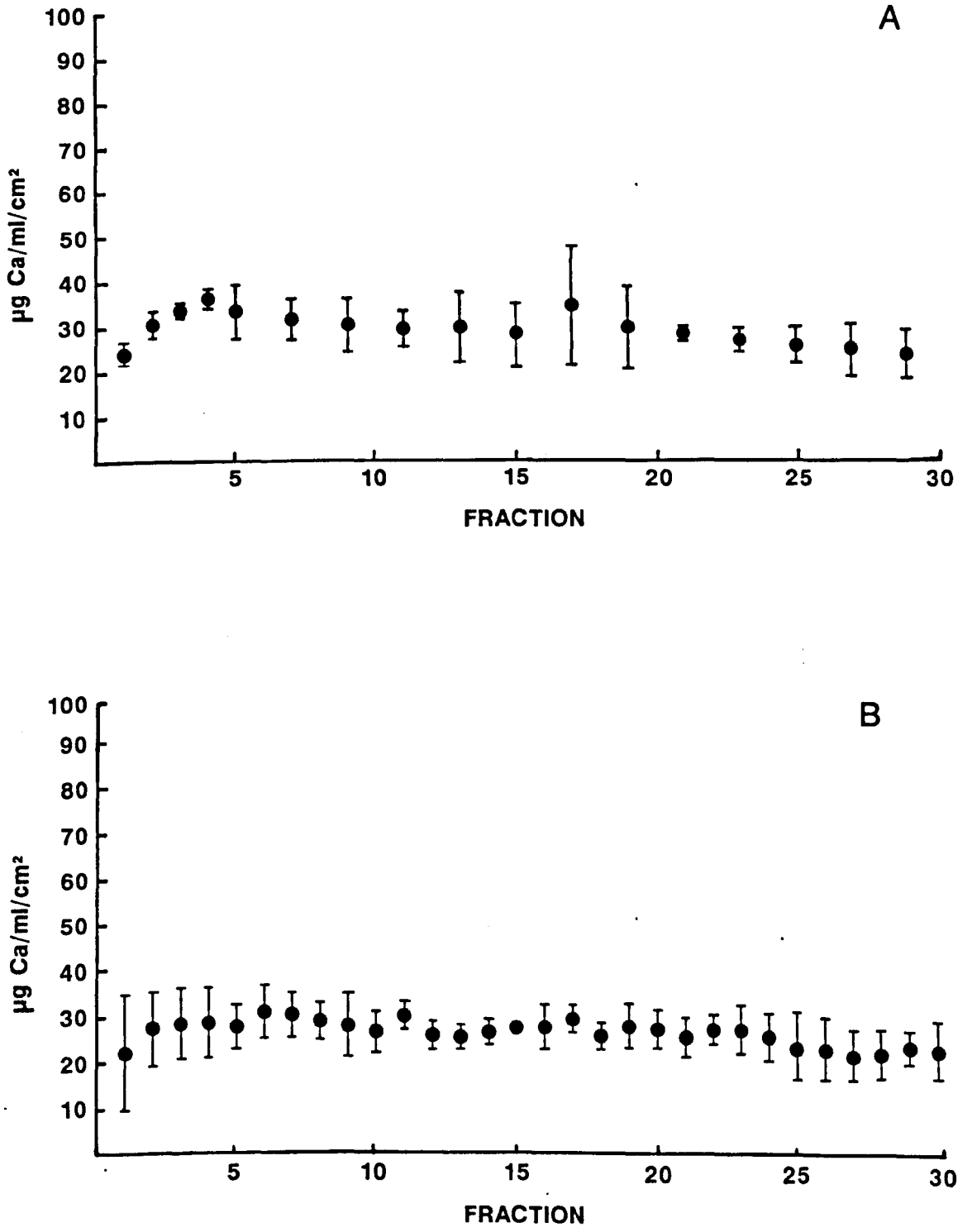


Figure 37. The pattern of elution of calcium (µg/Ca/cm²) from the controlled etch of unlabelled pieces of *Yoldia eightsi* shell at flow rates of 1.5ml/min HCl (A) and 2.0ml/min HCl (B).

following the same trend but maintaining a tighter range of values giving a mean of 26.86μg Ca/ml/cm^2 over the fraction range. Summary statistics are presented in Table 18.

Table 18. *Yoldia eightsi.* Fraction calcium content of replicate shell pieces under differing etch rates with 0.01N HCl. N = Sample size, SD = Standard deviation, CV = Coefficient of variation (%).

Flow rate (mls/min)	N	Mean	SD	CV	Range
1.5	17	31.35	3.48	11.10	25.62 - 37.78
2.0	30	26.86	2.00	7.44	23.34 - 30.45

II. Etching of experimental animals.

Shell pieces prepared from incubated animals ranged from 10.20mm² to 18.96mm² in surface area having a mean of 14.21mm² and a standard deviation of 2.37mm². Typical patterns of radioactivity within the fractions of etched shell pieces showed a peak in concentration in the second to third fraction falling to baseline levels after 4 - 11 fractions, dependent on incubation time (Fig. 38).

The calcium content of experimental fractions containing radioactive label was calculated from the fraction concentrations of calcium determined from the etching of unlabelled shell pieces at similar etch rates. The resulting data was standardised and used to estimate the incremental

addition to the shell height of experimental animals through the application of the formula suggested by Dillaman and Ford (1982):

If T is the thickness of the shell increment in height (cm), then

$T = 1/D \times R \times Ca/A$

where D = Density of aragonite ($2.93 g/cm^3$), R = ratio of the molecular mass of $CaCO_3$ to Ca (2.5), Ca is the total mass of calcium contained in the fractions from the beginning of the etching procedure up to and including the peak fraction, and A is the experimental surface area of the sample (cm^2).

Total incremental addition to the shell over the period of incubation was very variable between individuals although an overall relationship of incubation period to total increment was evident (Fig. 39). Over the entire incubation series incremental addition ranged from 0.14μm/hr to 0.19μm/hr giving a mean increase of 0.16μm/hr over the combined incubation series (Table 19).

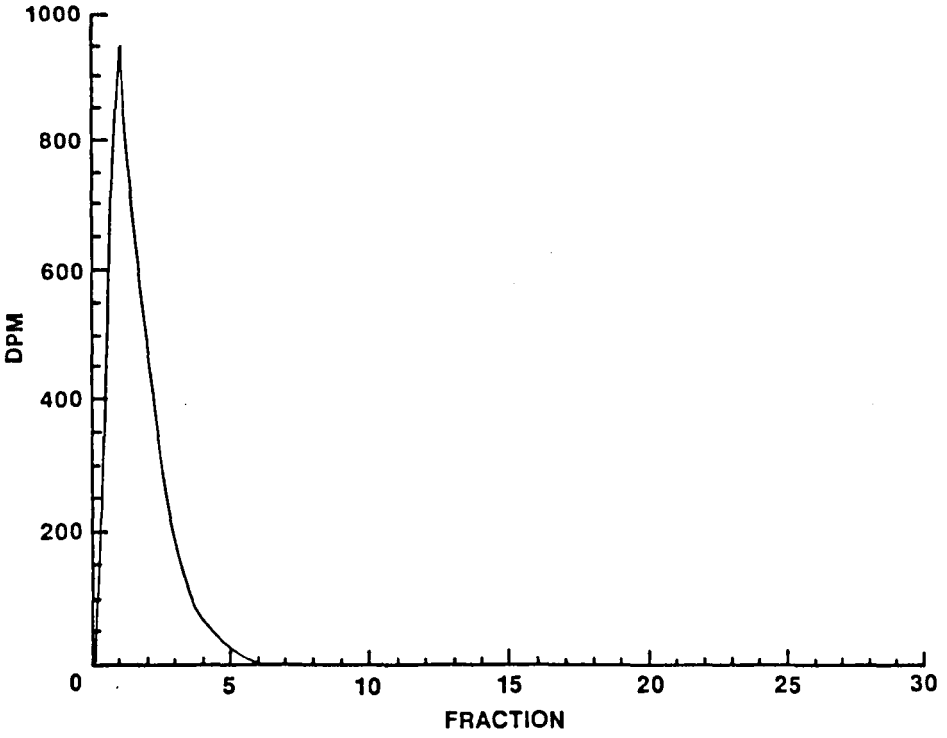


Figure 38. The typical distribution pattern of 1ml fractions showing ^{45}Ca activity of shell pieces, etched with 0.01N HCl, after experimental periods of up to 144 hours. DPM = Disintegrations per minute.

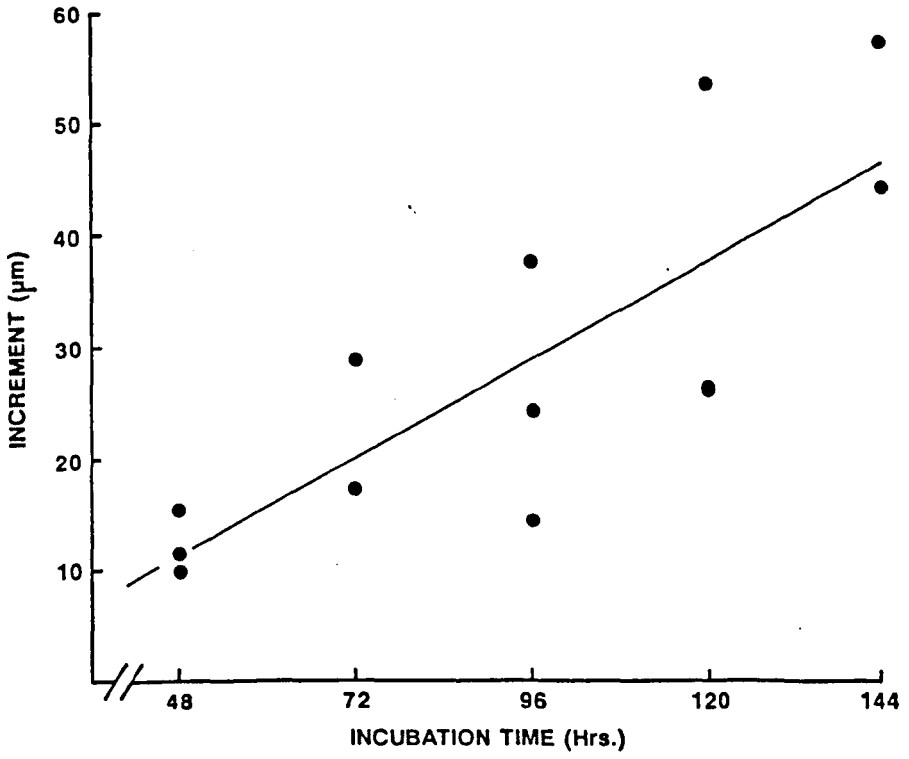


Figure 39. The relationship between total calculated increment in shell height and incubation period for *Yoldia eightsi*, based on the analysis of ^{45}Ca incorporation with time.

Table 19. *Yoldia eightsi*. Calculated total and hourly increments in shell height (μm) determined by the experimental incorporation of ^{45}Ca over increasing incubation periods (hours).

Total addition over incubation

Incubation period (Hours)	Mean (μm)	Standard deviation (μm)	Range (μm)	N
48	9.07	2.21	7.25 - 11.52	3
72	11.61	3.96	8.81 - 14.41	2
96	13.69	6.78	7.67 - 21.04	3
120	17.55	7.57	13.14 - 26.30	3
144	25.04	4.47	21.88 - 28.20	2

Hourly addition over incubation period.

Incubation period (Hours)	Mean (μm)	Standard deviation (μm)	Range (μm)	N
48	0.19	0.046	0.15 - 0.24	3
72	0.16	0.057	0.12 - 0.20	2
96	0.14	0.071	0.08 - 0.22	3
120	0.15	0.064	0.11 - 0.22	3
144	0.18	0.035	0.15 - 0.20	2
Total	0.16	0.051	0.08 - 0.24	13

The analysis of incremental shell addition with incubation time shows a significant positive, though weakly correlated, relationship (Table 20). The slope of the relationship, 0.151, represents the predicted overall mean increment in shell height (μm/hr) of incubated animals and is in accordance with that of 0.16μm/Hr determined from individual measurements.

Table 20. *Yoldia eightsi*. Least squares regression and analysis of variance of incubation time (hours) on incremental shell addition (μm).

Parameter	Estimate	Standard deviation	t-ratio	p
Intercept	0.757	4.213	0.18	0.861
Slope	0.1507	0.042	3.57	0.004

Analysis of Variance

Source	Sum of Squares	Df	Mean	F-ratio	p
Model	325.80	1	325.80	12.75	0.004
Error	281.13	11	25.56		
Total	606.93	12			

Adjusted R^2 = 49.5%

Experimental animals ranged from 14.34mm to 21.34mm in shell length and showed no significant relationship between shell length and calculated hourly incremental addition ($F = 0.25$, $p = 0.63$, $n = 12$).

If it is assumed that shell material in *Yoldia* is deposited at a constant rate during periods of growth, the overall annual gain in shell material may be calculated. The data on water column chlorophyll and benthic algal biomass (Fig. 5a & 5b) and the seasonal variation in the biomass of a standard animal (Fig. 35) suggest that there is an annual period of three to four months during which the Factory Cove population of *Yoldia* have access to an abundant food supply

and are actively increasing in biomass. Measurements of incremental addition to shell height in experimental animals over such an active metabolic period suggest that this increase occurs at a constant rate of 0.16μm per hour. Extrapolation of this rate allows an annual increment in shell height of 346μm - 461μm to be predicted for animals within the size range examined (9.43 - 13.12mm shell height, 14.34 - 20.72mm shell length).

6.3 The determination of shell growth in *Yoldia eightsi* using internal periodicity structures.

6.3.1 Materials and Methods

A random sample of individuals from each monthly collection was taken for the analysis of internal periodicity structures. Individuals were shucked of all tissue and the shells washed and allowed to air dry prior to further processing.

In preparation for growth ring analysis shells were hand-ground to the axis of maximum growth from the umbo to the shell edge, washed in acetone, dried and embedded upright in *'Metset SW'* resin (Agar Scientific, U.K.). Resin was poured into 40mm (Diameter) x 30mm (Depth) circular moulds to a depth of approximately 5mm. Valve halves were stood, on end, in this resin layer and the resin allowed to set to a gel-like consistency. The mould was then filled with resin and allowed to set fully. This procedure was developed as a response to initial problems of resin contraction during the resin curing process. This lead to the separation of the resin from the surface of the embedded shell resulting in a gap which collected abrasive material and acid to detrimental effect in later stages. The shell material exposed in this manner often showed major structural damage typically having inner and outer shell layers pulled apart as the resin contracted, and as a result proved unusable for incremental analysis. Following many attempts to solve this problem the

above procedure proved successful and was adopted for the majority of shells examined.

Once cured, the blocks were lapped to flatness on 600 grit (9μm) Carborundum pads and brought to a final polish using a series of abrasive diamond pastes from 6μm through to 1μm on a standard geological polishing machine. The blocks were then cleaned in Propan-2-ol alcohol and etched with 1% HCl for a period of between 30 and 90 seconds. After a gentle emersion in distilled water and air drying, an acetate peel of the resultant etched surface was taken and dry mounted prior to microscopic examination under transmitted light at 100x and 200x magnification.

6.3.2 Results

I. Shell increment analysis.

Of 300 embedded individuals processed, 130 successful peels were produced. This low success rate of the peels and the difficulty in resolving anything other than the most prominent growth lines is attributed to the homogeneous nature of the shell material and the depositional regime experienced by *Yoldia* for shell carbonate. These factors have been shown to adversely effect the positive delineation of anything but the strongest lines of greatest contrast in other molluscs (MacClintock, 1967; Pannella & MacClintock, 1968) and are further complicated in *Yoldia* by its thin and fragile shell.

Increments were examined in all peels to determine if an characteristic obvious structure existed. Prominent series of growth lines were observed in all individuals examined and in the more detailed peels consisted of regularly repeating units of varying size and intensity. Incremental units corresponding to those of Barker (1964) were identified within the shell sections examined and generally showed strong presence of First order, major, increments (Barker, 1964) containing two 2nd order and finer scale 3rd and 4th order increments. On the basis of these observations strong first order growth increments, as suggested by Barker (1964), were assumed to be annual in occurrence.

The distance from the umbo to prominent, or first order shell increments was measured for 1043 growth increments (Fig. 44).

A Ford/Walford plot of this data was constructed relating shell height at increment t, to shell height at increment t+1 (Fig. 40). This provided a statistically significant model of shell growth (table 21). The slope of this line is e^{-k}, it's intercept on a 45° line (that is where $y = x$) is H, the theoretical maximum shell height, and the intercept on the y axis is $H(1-e^{-k})$. k is the coefficient of catabolism of von Bertalannfy's (1938) growth equation, and describes the rate at which the maximum or asymptotic shell height of the growth curve is reached (Beverton and Holt, 1959).

Table 21. *Yoldia eightsi*. Least squares linear regression and analysis of variance of shell height (mm) at first order increment t+1 on shell height (mm) at first order increment t.

Parameter	Estimate	Standard Error	t-ratio	p
Intercept	1.204	0.029	41.37	< 0.001
Slope	0.946	0.002	423.28	< 0.001

Analysis of Variance

Source	Sum of squares	Df	Mean square	F-ratio	p
Model	15268	1	15268	179163	< 0.001
Error	89	1042	0		
Total	15357	1043			

Adjusted R^2 = 99.4%

The construction of Manzer/Taylor (1947) plots relating individual increases in incremental addition proved difficult as few individual shell sections contained more then 2 or 3 consecutive first order lines. All incremental data was therefore pooled prior to further analysis.

A number of growth rate equations are commonly used to fit curves to growth data. Of these one of the most widely employed is that developed by von Bertalannfy (1938). This expression is given as ;

$$H_t = H\ (1-e^{-k(t-to)})$$

where H_t is the shell height at time t, H is the maximum theoretical shell height determined empirically through

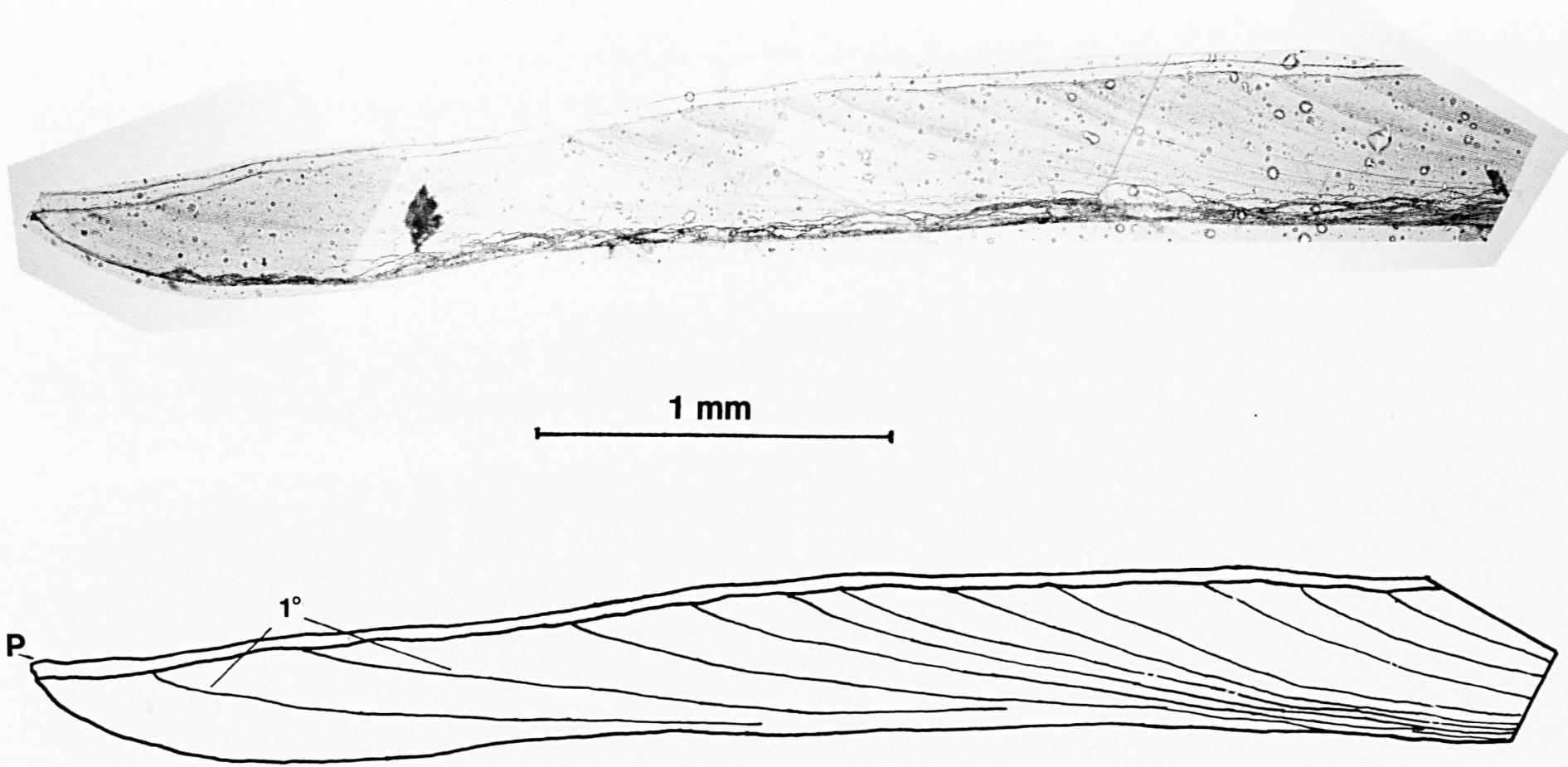


Fig. 44. *Yoldia eightsi*. A composite photomicrograph and corresponding line drawing of a typical acetate peel from the growing margin of a sectioned, polished and etched shell surface. Shell height = 19.00mm, P = periostracum, 1° = First order periodicity lines, (Barker, 1964).

intensive sampling or graphically using the Ford/Walford technique. k is the coefficient of catabolism determined from the slope of the Ford/Walford plot (e^{-k}) and t_0 is the theoretical time at which the shell width of the animal is zero.

The von Bertalanffy parameters of maximum shell height (H) and rate of shell growth towards this asymptotic value (k) were calculated from the relationship of H_t on H_{t+1} to be 22.22mm and 0.056, respectively (Fig. 41). Using the known settlement size (H_{t0}) for *Yoldia* of 0.32mm in height (Colman, pers. com.) a value for t_0, of -0.26, was obtained from the von Bertalanffy equation.

Incorporating the values of H, k and t_0 into the von Bertalanffy growth equation a size at age relationship for the Factory Cove population of *Yoldia eightsi* was determined. These data are presented in table 22.

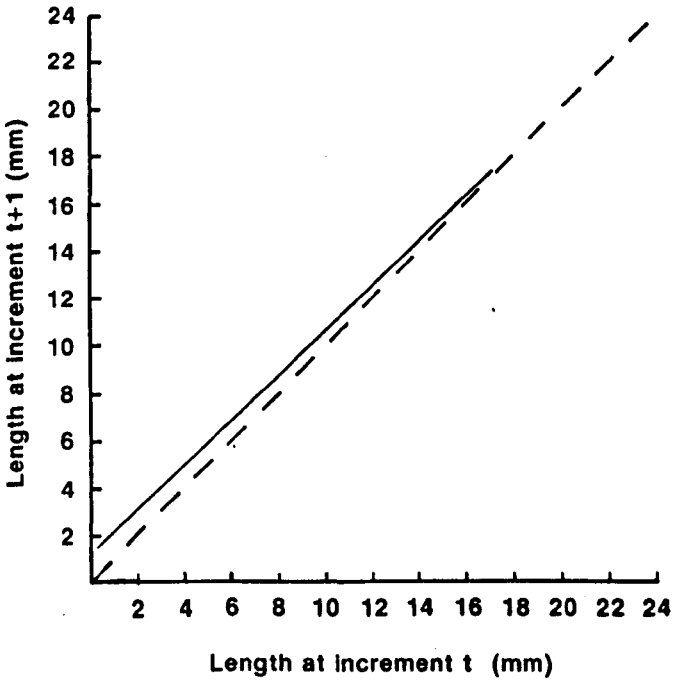


Figure 40. *Yoldia eightsi*. Ford-Walford plot of shell height at first order internal shell increment (t) to shell height at following first order increment (t+1).

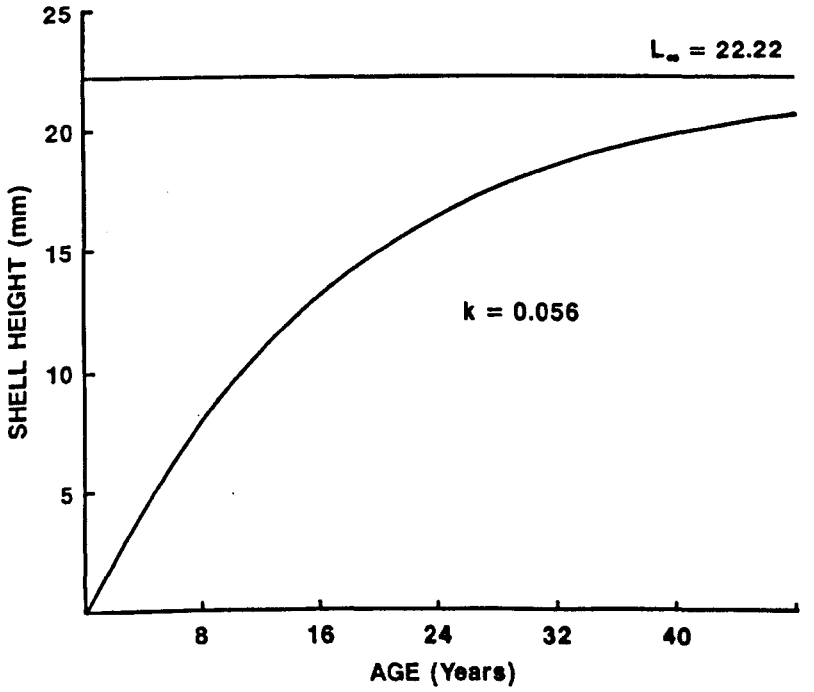


Figure 41. Growth curve constructed for the inshore population of *Yoldia eightsi* at Factory Cove, Signy Island. L_∞ = Maximum predicted shell height, k = von Bertalannfy growth rate coefficient.

Table 22. Predicted shell height (mm) at age (years) extrapolated from the von Bertalannfy growth equation derived for the inshore population of *Yoldia eightsi* in Factory Cove, Signy Island. Shell lengths (mm) have been extrapolated from the population length/height relationship.

AGE	PREDICTED HEIGHT	PREDICTED LENGTH	AGE	PREDICTED HEIGHT	PREDICTED LENGTH
0	0.32	0.36	28	17.59	28.01
1	1.50	1.91	29	17.84	28.44
2	2.62	3.51	30	18.08	28.86
3	3.68	5.09	31	18.30	29.24
4	4.68	6.61	32	18.51	29.61
5	5.63	8.09	33	18.71	29.95
6	6.52	9.49	34	18.90	30.29
7	7.37	10.85	35	19.08	30.60
8	8.17	12.14	36	19.25	30.90
9	8.93	13.38	37	19.41	31.18
10	9.65	14.56	38	19.56	31.44
11	10.33	15.68	39	19.71	31.70
12	10.97	16.74	40	19.84	31.93
13	11.58	17.76	41	19.97	32.16
14	12.15	18.71	42	20.09	32.37
15	12.69	19.62	43	20.21	32.58
16	13.21	20.50	44	20.31	32.76
17	13.69	21.31	45	20.42	32.95
18	14.15	22.09	46	20.52	33.13
19	14.59	22.84	47	20.61	33.28
20	15.00	23.54	48	20.69	33.43
21	15.39	24.21	49	20.78	33.58
22	15.76	24.84	50	20.85	33.71
23	16.11	25.45	51	20.93	33.85
24	16.44	26.02	52	21.00	33.97
25	16.75	26.55	53	21.06	34.08
26	17.05	27.07	54	21.13	34.20
27	17.33	27.5			

II. Population age structure

Although the determination of the growth rate of the Factory Cove population of *Yoldia* and the environmental constraints thereon was a primary objective of this study some additional features of the population may be deduced from the monthly data collected.

The patchy nature of the distribution of the *Yoldia* population within Factory Cove precluded an accurate estimate of the population age structure based on the analysis of individual monthly samples.

As the post-spawning body biomass of representative individuals of the population stabilised from July to October (Fig. 35) the assumption of slow to insignificant shell growth was made for this period. The morphometric data of samples taken during this period were pooled to provide a more representative sample of the population for age structure analysis.

A sample size of 1521 individuals was thus obtained (Fig. 42) and the von Bertalanffy growth equation for the population, derived from incremental growth data, used to back-calculate the age of each individual. Back-calculation from the peels of individual shell sections proved impossible due to the incomplete registration of all growth increments on acetate replicas. Abrasion of the umbo on the majority of specimens of all ages further compounded this approach.

The age of individuals calculated in this manner is representative of a mean size at age and recognises the variation in growth rates contained by any individual age cohort which is confined by this procedure. It is inherent that the calculation of age from size data will introduce such a bias, though it is suggested that the size on age distribution derived from this procedure provides a reliable estimate.

The resulting population structure (Fig. 43) shows very few individuals within the first year class. The dearth of individuals within these size classes may represent the episodic spawning of the population or be indicative of adverse environmental influences on the survival of a regularly spawned annual brood. This feature of the length frequency distribution of *Yoldia* from Factory Cove has been previously noted (Rabarts, 1970) and agrees with observations of poor veliger settlement and survival from a successful spawning event (Colman, pers. com.). The variation in the frequency of the early age classes may represent such episodic spat survival.

Alternatively a sampling bias, effectively precluding the successful collection of the smallest individuals, may be present.

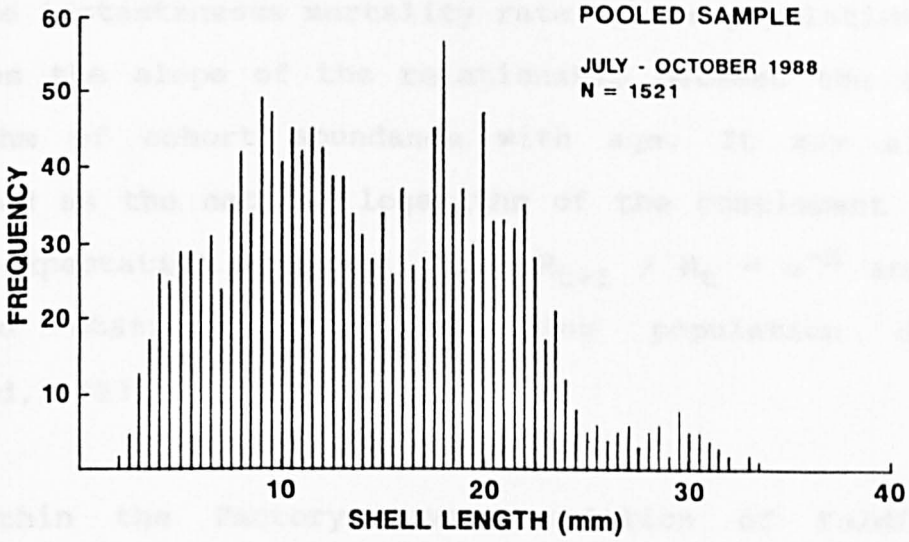


Figure 42. *Yoldia eightsi*. Length frequency distribution of the pooled length data for the July - October 1988 samples.

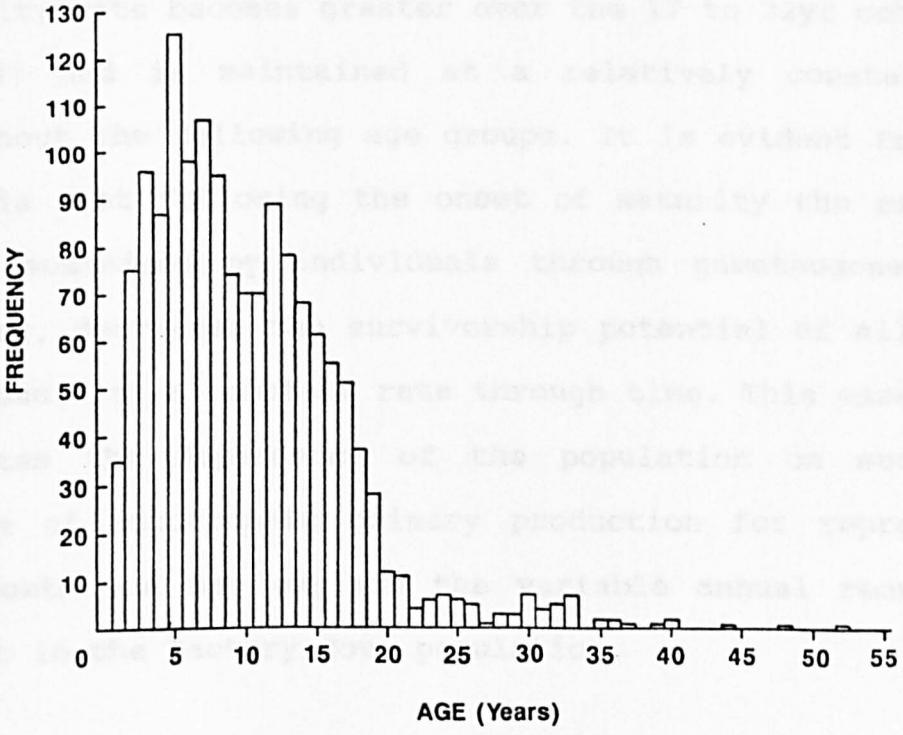


Figure 43. *Yoldia eightsi*. Age frequency histogram constructed for the pooled data of the July - October 1988 samples, based on the extrapolation of the von Bertalannfy equation derived for the Factory Cove population.

The instantaneous mortality rate of the population, Z is given as the slope of the relationship between the natural logarithm of cohort abundance with age. It may also be expressed as the natural logarithm of the complement of the annual expectation of death, i.e. $N_{t+1} / N_t = e^{-Z}$ and is a standard statistic for describing population decline (Gulland, 1983).

Within the Factory Cove population of *Yoldia* the mortality rate becomes constant over the ages of 12 to 17yrs ($Z = 0.11$) (Fig. 45). This lower age cohort approximates to the onset of maturity in this population (Shell height >10mm, Age > 12yrs.). Following this initial period of decline the mortality rate becomes greater over the 17 to 22yr cohorts ($Z = 0.49$) and is maintained at a relatively constant rate throughout the following age groups. It is evident from this analysis that following the onset of maturity the metabolic stress sustained by individuals through gameteogenesis and spawning, decreases the survivorship potential of all mature individuals at a constant rate through time. This essentially indicates the dependence of the population on successful periods of autotrophic primary production for reproduction and growth and may explain the variable annual recruitment evident in the Factory Cove population.

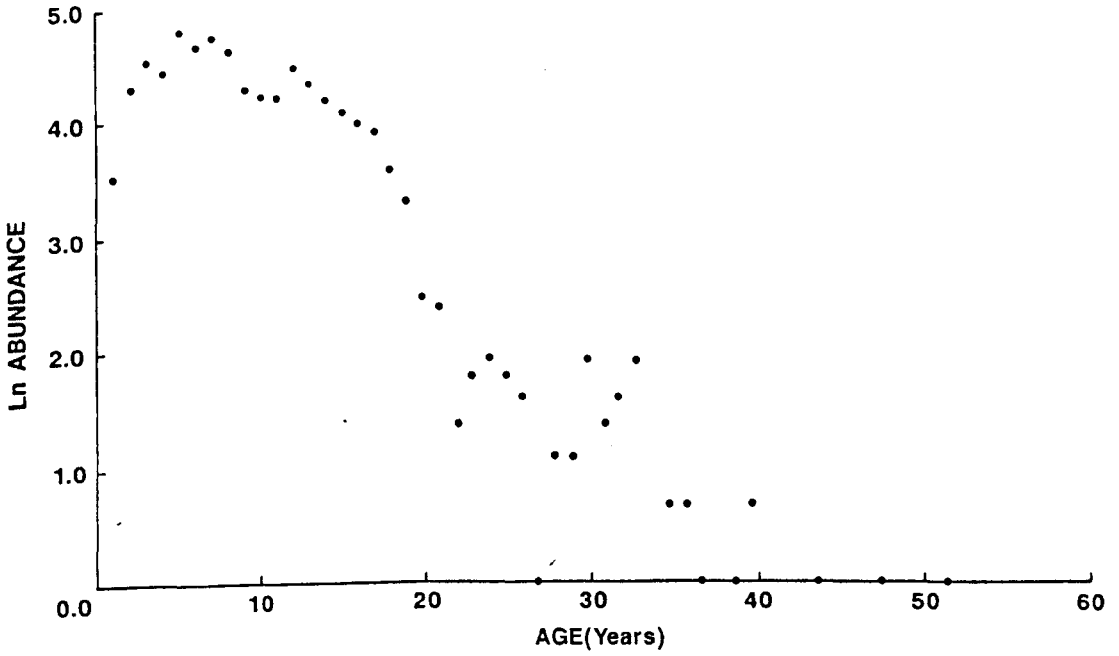


Figure 45. The relationship between the natural logarithm of cohort abundance and age in the Factory Cove population of *Yoldia eightsi* at Signy Island.

III. Determination of growing season.

Incorporation of ^{45}Ca in a range of experimental individuals from 9.43mm to 13.59mm shell height predicted hourly incremental rates within the range of 0.08μm to 0.24μm in shell height. The application of the von Bertalannfy growth equation, determined from the incremental growth band analysis of the Factory Cove *Yoldia* population, predicts an annual shell height increment related to individual size, ranging from 0.48mm to 0.72mm for these animals. Application of the Ford/Walford incremental relationship estimates an increase of between 0.47mm and 0.69mm for these same individuals (Table 23).

Using the hourly shell accretion rates determined for these individuals from the analysis of ^{45}Ca uptake, the length of the available growing season may be calculated from the predicted gross annual increase in shell height. Periods of shell growth determined using this method estimate an average growing season length of 159 days. The high coefficients of variation in growing days (Ford/Walford: 42%; von Bertalannfy: 43%) are evidence of variations in individual growth rates caused by differing physiological rates of growth and possible experimental stress. The average growing season predicted from this analysis however, concurs with the annual period of active biomass increase observed within the Factory Cove population of *Yoldia* (Fig. 35). From these data it can be concluded that the Factory Cove population of *Yoldia* has an approximate annual growing season

of 5 months and an annual shell growth rate described by the von Bertalannfy equation determined from internal shell growth increments.

Table 23. Growth rate and growing season length predicted from measured hourly uptake rates of ^{45}Ca and extrapolation of the Ford/Walford plot (FW) and von Bertalannfy equation (Von B) constructed for the inshore population of *Yoldia eightsi* at Factory Cove, Signy Island. SD = Standard deviation, CV = Coefficient of variation.

Experimental period (hrs.)	Shell height (mm)	Hourly Increment (μm/hr)	Increment predicted FW	Increment predicted VonB	Growing season (days) FW	Growing season (days) VonB
48	13.57	0.18	0.467	0.480	108	111
	13.30	0.15	0.482	0.480	134	133
	12.41	0.24	0.530	0.540	92	94
72	13.12	0.20	0.492	0.480	103	100
	12.88	0.12	0.504	0.480	175	167
96	12.48	0.13	0.526	0.540	169	173
	12.32	0.08	0.535	0.540	279	281
	11.83	0.22	0.561	0.570	106	108
120	9.43	0.11	0.691	0.720	262	273
	9.72	0.22	0.675	0.680	127	129
	9.93	0.11	0.664	0.680	252	258
144	13.59	0.15	0.466	0.480	129	133
	13.55	0.20	0.468	0.480	98	100
				Mean	157	159
				SD	66.61	68.48
				CV	42.4%	43.1%

6.3.3 Discussion

The factors effecting the growth rate and longevity of many species of bivalves have received much attention. Of these, the tendency for increasingly slow rates of growth as latitude increases in species with wide geographical ranges has attracted particular interest (Weymouth *et al.*, 1931; Ansell, 1968; Gilbert, 1973; Graus, 1974; Harrington, 1986). In an intensive study of the bivalve genus *Protothaca* (Veneridae) from the Gulf of Alaska to Panama a change in growth rate was evident as water temperature increased. Within Alaskan waters (60°N) the von Bertalannfy parameter k for *P.staminea* ranged between 0.094 and 0.139 in waters of approximately 7.5°C. The same species at the southern part of its range (30°N) in waters of 15.0°C had a much greater growth rate with k values ranging between 0.528 and 1.238. Examination of the daily growth increments within the shell of this species showed that in Alaska the maximum number of daily increments was about 150 suggesting that *P.staminea* was metabolically growth active for only about 5 months out of each year. Progressing southward, the number of daily increments increased gradually such that at the southern range end-point of the species, the number of increments was about 330. These values correlate well with the productivity patterns in the oceans at these latitudes which suggests that growth is controlled primarily by food supply rather than temperature.

Gilbert (1973) has shown a similar trend in a study on the bivalve *Macoma balthica* over the geographical range of 38°N - 60°N. Individuals in this study showed decreased rates of growth and greater longevity as latitude increased which was associated with a steady decline in ocean temperature and length of the growing seasons as the northerly end of the range was reached.

The importance of the coupling of active metabolic growth in bivalves to the seasonal pulse of primary production is also evident in deep-sea bivalves. Lightfoot *et al.* (1979) suggested that the timing of reproductive cycles in deep-sea bivalves and other invertebrates was coupled to this pulse. This response has also been reported in deep-sea echinoderms (Tyler *et al.*, 1982) and has been the subject of comprehensive review (Tyler, 1988).

In a study of the internal shell banding patterns in the deep-sea bivalves *Yoldia thraciaeformis* and *Nuculana pernula* (Gilkinson *et al.*, 1986) strong shell growth bands were taken to indicate that a major annual event effects the growth pattern of these animals. Growth bands, assumed to be annual, were very small in these species being recorded as 13μm in the inner shell layer of *Nuculana pernula* and between 80 - 100μm in the outer shell layer of *Yoldia thraciaeformis* though the shell size and position of measurement were not reported. These growth bands were suggested to represent shell-mediated changes in growth rate resulting from

fluctuations in food supplied from surface waters (Valentine, 1983).

Food supply rather than low ambient temperature and high ambient pressure therefore appears to be the major limiting factor for growth and productivity in the deep sea (Horne *et al*, 1969; Ikeda & Hing Fay, 1981). Where this is the case great ages may be attained by resident bivalves. *Tindaria callistiformis*, a nuculoid bivalve from 3800m, has been aged from ^{228}Ra measurements at about 100 years (Turekian *et al.*, 1975) whilst *Arctica islandica* from approximately 200m has been shown to attain an age of 150 years (Thompson *et al.*, 1980).

In those few places in the deep-sea where food supply is constant, growth rates of bivalves may be much higher than in related shallow water forms. The dense suspensions of chemosynthetic microbes around deep sea hydrothermal vents and harboured within the gills of bivalves are supported by photoautotrophically produced material from surface waters that is concentrated by convection cells created by the vents themselves. These communities support rates of growth of 120-500 times that of deep-sea bivalves away from hydrothermal vents (Rhoads *et al.*, 1981, Turekian *et al.*, 1981).

The growth of *Mytilus edulis* from the seasonally ice-locked Disko and Thule district of Greenland has been shown to be slower than that recorded in most temperate areas with values of k ranging from 0.022 to 0.155. When the growth

rate was related to the number of ice free days with temperatures above 0°C however, growth at the Greenland site almost equalled that recorded for *Mytilus edulis* populations in temperate regions (Theisen, 1973).

Growth curves calculated from annual data obscure seasonal variation and provide an average of the seasonal and environmental fluctuations of the growth parameter, k. Richardson *et al.* (1980) have analysed the variations in short term growth rates evident in populations of the bivalve *Cardium edule* from Menai Bridge, North Wales and Ramfjord, Norway. The populations experience very different growing seasons with those in North Wales exhibiting growth almost around the year and those in Norway showing most of their growth during a period of approximately 160 days from May to October. The comparison of the short term coefficient of growth k_{14} (Growth coefficient measured over 14 days) during the periods of maximum growth in both these populations however, was very similar with values of k_{14} ranging from 3 - 4 x 10^{-3} day^{-1} in the temperate population and a maximum value of 2.5 x 10^{-3} day^{-1} in the sub-Arctic population. Annual k values extrapolated from this data for temperate (k=0.70) and sub-Arctic (k=0.20) populations reflect the differing biological and environmental regimes present at each site and the control these exert on the population growth rates.

Although studies on the rate of growth of Antarctic bivalves have been few, the general synopsis of the data

gathered from all the species examined to date has been one indicating very slow rates of growth. Rabarts (1970) assigned an age structure to the *Yoldia eightsi* population within Factory Cove based on the interpretation of external pairs of winter check marks on individual shells. The maximum age class predicted by this study was 19 years with a relationship suggested to exist between yearly variation in sea water temperature and shell height increase.

Rabarts (1970) assumed that the nutritional requirements of the inshore populations of *Yoldia* from Factory Cove must be adequately met by the annual phytoplankton production and detrital accumulation. This was accepted to be reasonably constant from one year to the next and it was suggested that annual differences in growth rate, independent of the nature of the substratum, were most likely induced by yearly fluctuations in sea water temperature.

In order to quantify the effects of sea water temperature on shell growth Rabarts (1970) applied temperature data from an adjacent, deep water site (30m) at Normanna straits to the shallow water *Yoldia* community of Factory Cove. The annual variation evident in this data was correlated with annual shell height increases over a range of shell sizes.

Temperature effects were not shown to be consistent over the entire shell size range and a seasonal effect, implicit in the presence of check rings, was not established.

The bivalves *Laternula elliptica* and *Adamussium colbecki* collected from Antarctic waters exhibit values of the von Bertalannfy growth parameter k, of 0.16 and 0.24 respectively (Ralph and Maxwell, 1977). Although these values are low in relation to temperate water species they are high in comparison with those of ; Picken (1980b) and the present study, for *Nacella concinna* (k=0.0715 and k=0.062 respectively) and the values presented in this study for *Yoldia eightsi* (k=0.056). The values of k presented by Ralph and Maxwell (1977) may be artificially high, however, and may reflect the difficulty in resolving annual periods of shell secretion from the examination of external rings. This technique is of little use, particularly in slow growing organisms. The values of k, suggested by Picken (1980b) and the present study, compare favourably with those presented for Arctic specimens of *P. staminea*, k = 0.094 - 0.139, (Harrington, 1986) and *M. edulis*, k = 0.022 - 0.155 (Theisen, 1973).

The Antarctic inshore marine environment, in common with these studies from northerly latitudes, has an extremely seasonal pulse of primary production which dictates a short growing season for the majority of dependent herbivores and detritivores. The prediction of an average growing season of 157 days for the population of *Yoldia eightsi* from Factory Cove, derived from ^{45}Ca incorporation and internal shell increment analysis, is similar to that reported for populations of *Cardium edule* from Ramfjord in Norway

(Richardson *et al*, 1980), *Mytilus edulis* from Greenland, Theisen (1973) and *Protothaca staminea* from Alaska (Harrington, 1986). This interval accounts for the periods of biomass increase occurring during the summer months which is evident as an increase in ash free dry mass of the population over this period. Under these conditions the population dynamics of *Yoldia* are very similar to those of other detritivores found in deep sea environments with similar limited seasonal food input and growth rates. Sediment processing and turnover rates are high with efficient sorting removing a high proportion of the available organic material at a constant, temperature independent, metabolic rate (Davenport 1988a, 1988b). That food supply is the limiting factor to the growth rate is further supported by the fast average growth rate observed of 3.84μm day^{-1} (0.16μm hr^{-1}) in shell height during January. This agrees with the mark/recapture studies of Davenport (1989) who recorded a daily growth rate of approximately 3μm day^{-1} (SD 2.30μm day^{-1}) in animals of between 19.10 and 32.50mm shell length. This rate of growth, however, does not appear to be sustained throughout the year.

The slow yearly growth observed in *Yoldia* affects the period of time taken to reach maturity and hence the longevity of the population. The population age structure is indicative of variable yearly recruitment with the onset of sexual maturity at an age of approximately 12 years and a maximum age within the population of Factory Cove of 52 years. These observations are supported by the slow growth

rates reported for the Antarctic shrimp *Chorismus antarcticus* (Clarke & Lakhani, 1979), the isopods *Serolis polita* and *Serolis polita* (Luxmoore, 1982) the echinoderm, *Odontaster validus* (Pearse, 1965) and the patellid limpet *Nacella concinna* (Picken, 1980b) which are all also characterised by a relatively long life-span.

Longevity and gigantism are characteristics of deep sea bivalves. Growth has been shown to be restricted by limitations in the annual food supply rather than temperature variation, resulting in a clearly defined growing season of variable duration (Turekian *et al.*, 1975; Thompson *et al.*, 1980, Richardson *et al.*, 1980a, 1981). The great age attained by the inshore population of *Yoldia eightsi* is consistent with the general observation that eurythermal bivalves live longer and grow larger in the colder parts of their ranges, due to restricted periods of primary production (Nicol, 1964). In Factory Cove it is unlikely that water and air temperature variations play an important role in the seasonal alteration of the benthic environment. Chemical and biological data collected from the site, suggest that shell growth is directly influenced by periods of food availability rather than variations in water temperature. Annual variations in the level of benthic and phytoplanktonic primary production, therefore, serve to regulate and dictate the growth and fecundity of the *Yoldia eightsi* population.

CHAPTER 7

Summary and suggestions for further study

7.1 Summary

The growth and calcification rates of the Antarctic limpet *Nacella concinna* and the infaunal bivalve *Yoldia eightsi* are directly affected by variations in environmental parameters, morphology and behaviour.

Successful growth to maturity in *Nacella concinna* is influenced by individual behaviour. The population consists of two discrete groups with affinities with either the littoral or sub-littoral zones. In each of these zones survivorship is affected by differing circumstances. The height, strength and general shell morphology in sub-littoral animals is altered through the grazing of other limpets on endolithic algae which infests the shell material. The shell is severely weakened through this process and in some instances may be completely eroded. Those animals resident in the littoral zone are subjected to greater extremes of temperature and avoid infection by endolithic algae and the loss of shell material through intraspecific grazing. They are, however, subject to the predatory attentions of the Dominican Gull, *Larus dominicanus*. Limpets are preferentially selected on the basis of shell shape with animals of a pear-shaped, basal profile predominating in gull middens.

Recapture of marked limpets revealed a rate of growth described by the von Bertalannfy coefficient k, of 0.062 to a maximum shell length of 45.19mm. The age of the largest individual recorded during this study was predicted to be 37 years.

The chemical environment of the inshore waters of Signy Island is rich in calcium, strontium and magnesium and is in no way limiting to shell secretion. The Carbonate cycle is affected by the proliferation of phytoplankton during the spring bloom, with a non-limiting depletion in total alkalinity occurring at this time in the inshore waters. Following the spring bloom the flux of senescent phytoplankton to the sediment along with an increase in benthic algal biomass, as a consequence of increased light penetration, provides the major annual input of organic material to the sediment.

The growth rate of the *Yoldia eightsi* population of Factory Cove is directly influenced by annual variations in food supply. The patchily distributed population utilises algae and detritus from both benthic and planktonic sources and reflects this period of active metabolism through the secretion of an annual band of shell carbonate. Shell secretion rates determined experimentally using ^{45}Ca reveal a rate of growth coincident with that predicted from periodicity structures within the shell, along with periods of increasing biomass and primary production.

The growth rate for *Yoldia* determined by the analysis of internal shell growth increments is described by the von Bertalannfy coefficient k of 0.056 with a maximum predicted shell size of 22.22mm shell height. This rate of growth is similar to that recorded for the population of *Nacella concinna* in Factory Cove.

The predicted annual increment in shell height in *Yoldia*, for an individual of between 9 and 13mm shell height, is within the range of 346μm and 461μm. This assumes a constant growth rate of 0.16μm per hour and extrapolates to an average growing season of 159 days. The maximum age for the largest individual sampled was determined as 53 years lying within the predicted age size class of 21.06-21.13mm shell height and 34.08-34.20mm shell length.

Although the overall rate of growth is slow the growth rate recorded during periods of peak productivity is comparable to peak rates of growth in many temperate and warmer water species. The growth rate of the population of *Yoldia eightsi* in Factory Cove is also comparable to that recorded for members of deep-sea communities and other high latitude species whose growth is similarly regulated by food supply.

From these data it is evident that food supply is the limiting factor to growth in the Factory Cove population of *Yoldia eightsi* at Signy Island.

7.2 Suggestions for further study

There are a number of areas, brought to light in this study, which would benefit from the application of advanced techniques and be independent of resident time in the Antarctic.

For both the species examined the analysis of internal shell growth and crystal growth patterns could be examined to better resolution using standard electron microscopy techniques. A study of this type would provide a better understanding of the temporal variation in shell secretion and if comprehensive environmental data were collected over a similar period more accurate interpretations of the environmental controls to growth would be possible.

It may also be possible to determine to a more finite extent the exact periods of shell deposition using the isotopic analysis of shell carbonate. This would necessitate development of standard techniques and may be occluded by background 'biological' noise. The technique if successful however, would predict the water temperature at the time of shell deposition and would be of great value in determining the true relationship between food supply and growth.

A study of the feeding ecology of both species would provide much more information on food selection processes, dietary content, periods of food availability and feeding criteria for successful spat fall and recruitment. In

association with feeding studies the ecological relationship of the endolithic alga with *Nacella concinna* would be of interest. The growth rate and nutritional comparison with other available food sources would provide a data set which would determine the relative importance of this food source and could further elucidate feeding and behavioural differences between the littoral and sub-littoral populations.

CHAPTER 8

REFERENCES

ALDERMAN, D.J. and JONES, E.B.G., 1967. Shell disease of *Ostrea edulis* L. *Nature*, 216, 797-798.

ANDREWS, J.T., 1972. Recent and fossil growth rates of marine bivalves, Canadian Arctic, and late Quaternary Arctic marine environments. *Paleobiol. Paleoclim., Paleoecol.*, 11, 157-176.

ANSELL A.D., 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L) throughout the geographical range. *J. Cons. perm. int. Explor. Mer.*, 31, (3), 364-409.

BARKER, R.M., 1964. Microtextural variation in pelecypod shells. *Malacologia*, 2, (1), 69-86.

BATHURST, R.G.C.,1966. Boring algae, micrite envelopes and lithification of molluscan biosparites. *Geol. J.*, 5, 15-32.

BERGMAN, K.M., ELNER, R.W. and RISK, M.J., 1982. The influence of *Polydora websteri* borings on the strength of the sea scallop, *Placopecten magellanicus*. *Can. J. Zool.*, 60, 2551-2556.

BERRY, R.J. and RUDGE, P.J., 1973. Natural selection in Antarctic limpets. *Br. Antarct. Surv. Bull.*, No. 35, 73-81.

BERTALANFFY, L. von., 1938. Basic concepts in quantitative biology of metabolism. *Helgoländer wiss. Meeresunters.*, 9, 5-37.

BEVELANDER, G., 1952. Calcification in molluscs. III. Intake and deposition of Ca^{45} and P^{32} in relation to shell formation. *Biol. Bull.*, 102, 9-15.

BLACK, R., LYMBERY,A. and HILL, A., 1988. Form and function : size of radular teeth and inorganic content of faeces in a guild of grazing molluscs at Rottnest Island, Western Australia. *J. Exp. Mar. Biol. Ecol.*, 121, 23-35.

BLANKLEY, W.O., 1981. Marine food of kelp gulls, lesser sheathbills and imperial cormorants at Marion Island (Sub-Antarctic). *Cormorant*, 9, 77-84.

BLANKLEY, W.O., 1982. Feeding ecology of three inshore fish species at Marion Island (Southern Ocean). *S. Afric. J. Zool.*, 17, 164-170.

BLANKLEY, W.O. and BRANCH, G.M., 1985. Ecology of the limpet *Nacella delesserti* (Phillipi) at Marion Island in the sub-Antarctic Southern ocean. *J. Exp. Mar. Biol. Ecol.*, 92, 259-281.

BOGGILD, O.B., 1930. The shell structure of the mollusks. *K. danske Vidensk. Selsk. Skr.*, **2**, 232-325.

BRANCH, G.M., 1981. The biology of limpets: physical factors, energy flow and ecological interactions. *Oceanog. Mar. Biol. Ann. Rev.*, **19**, 235-380.

BRANCH, G.M., 1985. The impact of predation by kelp gulls *Larus dominicanus* on the sub-Antarctic limpet *Nacella delesserti*. *Polar Biol.*, **4**, 171-177.

BRANCH, G.M. and BRANCH, M.L., 1980. Competition between *Cellana tramoserica* (Sowerby) (Gastropoda) and *Patiriella exigua* (Lamarck) (Adteroidea) and their influence on algal standing stocks. *J. Exp. Mar. Biol. Ecol.*, **48**, 35-49.

BRANCH, G.M. and MARSH, A.C., 1978. Tenacity and shell shape in six patella species: adaptive features. *J. Exp. Mar. Biol. Ecol.*, **34**, 111-130.

BRIAN, M.V. and OWEN, G., 1952. The relation of the radula fraction to the environment in *Patella*. *J. Animal Ecol.*, **21**, 241-249.

BRIGGS, J.C., 1974. *Marine Zoogeography*. McGraw-Hill, New York.

BROUSSEAU, D.J., 1979. Analysis of growth rate in *Mya arenaria* using the Von Bertalanffy equation. *Mar. Biol.*, 51, 221-227.

CAILLEAUX, A., 1961. Endemicité actuelle et passée de l'Antarctique. *C. r. Séanc. Soc. Biogeogr.*, Nos. 332-4, 65-71.

CAVALIERE, A.R. and ALBERTE, R.S.,1970. Fungi in animal shell fragments. *J. Elishia Mitchell Soc.* 86,203-206.

CLARK, G.R., 1974. Growth lines in invertebrate skeletons. *Annu. Rev. Earth Planet. Sci.*, 2, 77-79.

CLARKE, A., 1983. Life in cold water : the physiological ecology of polar marine ectotherms. *Oceanogr. Mar. Biol. Ann. Rev.*, 21, 341-453.

CLARKE, A., 1988. Seasonality in the Antarctic marine environment. *Comp. Biochem. Physiol.*, 90B, 461-473.

CLARKE, A., 1989 . Faecal production and an estimate of food intake in the wild of the Antarctic limpet *Nacella concinna* (Strebel). *J. Moll. Stud.*, 55, 261.

CLARKE, A., HOLMES, L.J. and WHITE, M.G., 1988 The annual cycle of temperature, chlorophyll and major nutrients at Signy island, South Orkney Islands, 1969-82. *Br. Antarct. Surv. Bull.*, No. 80, 65-86.

CLARKE, A. and CRAME, J.A., 1989. The origin of the southern ocean marine fauna. In : *Origins and Evolution of the Antarctic Biota*, (J.A. Crame, (ed)), pp. 253-268. Geological Society Special Publication No. 47.

CLARKE, A. and LAKHANI, K.H., 1979. **Measuires** of biomass, moulting behaviour and the pattern of early growth in *Chorismus antarcticus* (Pfeffer). *Br. Antarctic Surv. Bull.*, **47**, 61-88.

COMFORT, A., 1957. The duration of life in molluscs. *Proc.the Malacol. Soc. Lond.*, 32, 219-241.

CRAIG, G.Y. and HALLAM, A., 1963. Size frequency and growth-ring analyses of *Mytilus edulis* and *Cardium edule*, and their Paleoecological significance. *Paleontology*, 6, (4), 731-750.

CRENSHAW, M.A. and NEFF, J. M. 1969. Decalcification at the mantle shell interface in molluscs. *Amer. Zool.*, 9, 881-885.

CRENSHAW, M.A., 1980. Mechanisms of shell formation and dissolution. In : *Skeletal Growth of Aquatic Organisms*. (D.C. Rhoads and R.A. Lutz, eds.) pp. 115-132. Plenum Press, New York.

CUSHING, D.H., 1959. The seasonal variation in oceanic production as a problem in population dynamics. *J. Cons. Int. Explor. Mer.* 24, 455-464.

DAVENPORT, J., 1988a. The feeding mechanism of *Yoldia* (= *Aequiyoldia*) *eightsi* (Courthouy). *Proc. Roy. Soc. Lond.* B, 232, 431-442.

DAVENPORT, J., 1988b. Oxygen consumption and ventilation rate at low temperatures in the Antarctic protobranch bivalve mollusc *Yoldia* (= *Aequiyoldia*) *eightsi* (Courthouy). *Comp. Biochem. Physiol.*, **90A**, (3), 511-513.

DAVENPORT, J., 1988c. Tenacity of the Antarctic limpet *Nacella concinna*. *J. Moll. Stud.*, **54**, 355-356.

DAVENPORT, J., 1989. Feeding, oxygen uptake, ventilation rate and shell growth in the Antarctic protobranch bivalve mollusc *Yoldia eightsi* (Courthouy). In *University Research in Antarctica*, Proceedings of the British Antarctic Survey Antarctic special awards scheme symposium, 9-10 November 1988 (R. B. Heywood, ed.).

DEITH, M.R., 1985. The composition of tidally deposited growth lines in the shell of the edible cockle, *Cerastoderma edule*. *J. mar. biol. Ass. U.K.*, 65, 573-581.

DELL, R.K., 1962. Zoogeography of Antarctic benthic mollusca. *Polar Rec.*, 11, (72), p327.

DELL, R.K., 1964. Antarctic and sub-Antarctic mollusca : Amphineura, Scaphopoda and Bivalvia. *'Discovery' Rep.*, 33, 99-250.

DELL, R.K., 1971. The marine mollusca of the Royal Society expedition to southern Chile, 1958-1959. *Rec. Dom. Mus. Wellington*, 7, 155-233.

DELL, R.K., 1972. Antarctic Benthos. *Adv. mar. Biol.*, 10, 1-216.

DELL, R.K., 1990. Antarctic Mollusca. *Roy. Soc. N. Zeal.*, Bulletin No. 27, 1-311.

DILLAMAN, R.M. and FORD, S.E. 1982 Measurement of calcium carbonate deposition in molluscs by controlled etching of radioactively labelled shells. *Mar. Biol.*, 66, 133-143.

DODD, J.R., 1963. Paleoecological implications of shell mineralogy in two pelecypod species. *J. Geol.*, 71, 1-11.

DODD, J.R., 1964. Environmentally controlled variation in the shell structure of a pelecypod species. *J. Paleont.*, 38, 1065-1071.

EBERT, T.A., 1973. Estimating growth and mortality rates from size data. *Oecologia*, 11, 281-298.

EBLING, F.J., SLOANE, J.F., KITCHING, J.A. and DAVIES, H.M., 1962. The ecology of Lough Ine. XII. The distribution and characteristics of *Patella* species. *J. Animal Ecol.*, 31, 457-470.

EISMA, D., 1965. Shell characteristics of *Cardium edule* L. as indicators of salinity. *Neth. J. Sea Res.*, 2, (4),493-540.

EISMA, D., 1966. The influence of salinity of mollusk shell mineralogy : a discussion. *J. Geol.*, 74, 89-94.

EKMAN, S., 1953. *Zoogeography of the Sea*. Sidgwick and Jackson, London.

El-SAYED, S.Z., 1968. Primary Productivity. *Am. Geogr. Soc. Antarctic Map Folio Series*, 10, 1-6.

El-SAYED, S.Z. and TURNER, J.T., 1977. Productivity of the Antarctic and tropical/sub-tropical regions : A comparative study. In : *Polar Oceans* (M.J. Dunbar, ed.), pp. 463 - 503, Arctic Institute of North America, Calgary, U.S.A..

EMERSON, C. W., 1990. Influence of sediment disturbance and water flow on the growth of the soft shell clam, *Mya arenaria* L. *Can. J. Fish. Aquat. Sci.*, 47, 1655-1663.

FORBES, E., 1954. Note on an indicator of depth of primaeval seas afforded by the remains of colour in fossil testacea. *Proc. Roy. Soc. Lond.*, 7, 21-23.

FRETTER,V. and GRAHAM A., 1962. *British prosobranch molluscs, their functional anatomy and ecology*. Ray Society, London.

GILBERT, M.A., 1973. Growth rate, longevity and maximum size of *Macoma balthica* (L.). *Biol. Bull.*, 145, 119-126.

GILBERT, N.S.G., (1990 - in press). Primary production by benthic algae in the nearshore marine marine environment of Antarctica. *Polar Biol.*, 11.

GILKINSON, K.D., HUTCHINGS, J.A, OSHEL, P.E. and HAEDRICH, R.L., 1986. Shell microstructure and observations on internal banding patterns in the bivalves *Yoldia thraciaeformis* Storer, 1838, and *Nuculana pernula* Müller, 1779 (Nuculanidae), from a Deep-sea environment. *Veliger*, 29, (1), 70-77.

GOLUBIC, S., 1969. Distribution, taxonomy, and boring patterns of marine endolithic algae. *Amer. Zool.*, 9, 747-751.

GOLUBIC, S., BRENT, G. and LECAMPION, T.,1970. Scanning electron microscopy of endolithic algae and fungi using a multipurpose casting-embedding technique. *Lethaia*, 3, 203-209.

GORDON, J. and CARRIKER, M.R., 1978. Growth lines in a bivalve mollusk: Subdaily patterns and dissolution of the shell. *Science*, 202, 519-521.

GRAUS, R.R., 1974. Latitudinal trends in the shell characteristics of marine gastropods. *Lethaia*, 7, 303-314.

GRÉGOIRE, C., 1972. Structure of the molluscan shell. In : *Chemical Zoology*, Volume VII, *Molluscs*, (M. Florkin and B. Scheer, eds.) pp. 45-102, Academic Press, New York, U.S.A..

GULLAND, J.A., 1983. *Fish Stock Assessment : A Manual of Basic Methods*. FAO/Wiley Series on Food and Agriculture, vol. 1., FAO, Rome, Italy.

HAIN, S., 1990. Die beschalten benthischen Mollusken (Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. *Ber. Polarforsch.*, 70, 1-185.

HARGENS, A.R. and SHABICA, S.V., 1973. Protection against lethal freezing temperatures by mucus in an Antarctic limpet. *Cryobiol.*, 10, 331-337.

HARRINGTON, R. J., 1986. Growth patterns within the genus Protothaca (Bivalvia : Veneridae) from the gulf of Alaska to Panama : Paleotemperatures, Paleobiogeography and Paleolatitudes. *Ph. D. Thesis*, University of California, Santa Barbara, 235pp.

HART, T.J., 1942. Phytoplankton periodicity in Antarctic waters. *Discovery Reps.*, 21, 263-348.

HAWKINS, S.J., WATSON, D.C., HILL, A.S., HARDING, S.P., KYRIAKIDES, M.A., HUTCHINSON, S. and NORTON, T.A., 1989. A comparison of feeding mechanisms in microphagous herbivorous intertidal prosobranchs in relation to resource partitioning. *J. Moll. Stud., 55*, 151-165.

HEDGPETH, J.W., 1969a. Introduction to Antarctic zoogeography. In : *Distribution of selected groups of marine invertebrates in waters south of 35°S latitude.* Antarctic map folio series (V.C. Bushnell (ed.), Folio 11, American Geographic Society, New York.

HEDGPETH, J.W., 1969b. Preliminary observations between the tidemarks at Palmer station, 64°45'S. *Antarct. J. U.S.*, 4, 106-107.

HEYWOOD, R.B. and WHITAKER, T.M., 1984. The Antarctic marine flora. In : *Antarctic Ecology*, (R.M. Laws, (ed)), Vol. 2, pp. 273-419. Academic Press, London.

HICKS, G.R.F., 1974. Variation in zooplankton biomass with hydrological regime beneath the seasonal sea ice, McMurdo Sound, Antarctica. *New Zealand J. Mar. Fresh. Res.*, 8, 67-77.

HISCOCK, K. and HOARE, R., 1973. A portable suction sampler for rock epibiota. *Helg. wiss. Meeres.*, 25, 35-38.

HOCKEY, P.A.R. and BRANCH, G.M., 1983. Do oystercatchers influence limpet shell shape? *Veliger*, 26, 139-141.

HOLDGATE, M.W., 1967. Signy Island. *Phil. Trans. Roy. Soc. Lond., Ser. 3*, 252, 173-177.

HOLM-HANSEN, O., 1985. Nutrient cycles in Antarctic marine ecosystems. In : *Antarctic Nutrient Cycles and Food Webs*, (W.R. Siegfried, P.R. Condy and R.M. Laws (eds.), pp. 6-10. Springer-Verlag, Berlin.

HORNE, A.J., FOGG, G.E. and EAGLE, D.J., 1969. Studies *in situ* of the primary productivity of an area of inshore Antarctic sea. *J. mar. biol. Ass. U.K.*, 49, 393-405.

HUTCHINGS, J.A. and HAEDRICH, R.L., 1984. Growth and population structure in two species of bivalves (Nuculanidae) from the deep sea. *Mar. Ecol. Prog. Ser.*, 17, 135-142.

IKEDA, T. and HING FAY, E., 1981. Metabolic activity of zooplankton from the Antarctic ocean. *Aust. J. Mar. Freshwater Res.*, 32, 921-930.

JENNINGS, J.C., GORDON, L.I. and NELSON, D.M., 1984. Nutrient depletion indicates high productivity in the Weddell Sea. *Nature*, **309**, 51-54.

JODREY, L.H., 1953. Studies on shell formation. III. Measurement of calcium deposition in shell and calcium turnover in mantle tissue using the mantle-shell preparation and Ca^{45}. *Biol. Bull.*, **104**, 398-407.

JOHNSON, T.W. and ANDERSON, W.R., 1962. A fungus in *Anomia simplex* shell. *J. Elisha Mitchell Sci. Soc.*, **78**, 43-47.

JONES, D. S., THOMPSON, I. and AMBROSE, W. G., 1978. Age and growth rate determinations for the Atlantic surf clam *Spisula solidissima* (Bivalvia : Mactracae), based on internal growth lines in shell cross sections. *Mar. Biol.*, **47**, 63-70.

JONES, N.S., 1946. Browsing in *Patella*. *Nature, London*, **158**, 557-558.

JONES, N.V., 1963. The sheathbill, *Chionis alba* (Gmelin), at Signy Island, South Orkney Islands. *Br. Antart. Surv. Bull.*, No. 2, 53-71.

KADO, Y., 1960. Studies on shell formation in mollusca. *J. Sci. Hiroshima Univ., Series B*, **19**, 163-210.

KALLE, K., 1971. Salinity. In : *Marine Ecology*. (O. Kinne, ed.) Vol. 1, pt. 2, pp. 683-688, John Wiley & Sons, New York.

KENNEDY, W.J., TAYLOR, J.D. AND HALL, A., 1969. Environmental and biological controls on bivalve shell mineralogy. *Biol. Rev.*, **44**, 499-530.

KIRKWOOD, G.P., 1983. Estimation of von Bertalanffy growth curve parameters using both increment and age-length data. *Can. J. Fish. Aquat. Sci.*, **40**, 1405-1411.

KNOX, G.A. and LOWRY, J.K., 1977. A comparison between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the amphipods and the polychaeta. In : *Polar Oceans*, (M.J. Dunbar, (ed.)). Arctic Institute of North America, Calgary, 423-462.

KNOX, G.A., 1960. Littoral ecology and biogeography of the Southern Ocean. *Proc. Roy. Soc. Lond. B*, **152**, 577-624.

KOHLMEYER, J., 1969. The role of marine fungi in the penetration of calcareous substances. *Amer. Zool.*, **9**, 741-746.

KOHLMEYER, J., 1972. Marine fungi deteriorating chitin of hydrozoa and keratin-like annelid tubes. *Mar. Biol.*, **12**, 277-284.

KOPCZYNSKA, E.E., 1981. Periodicity and composition of summer phytoplankton in Ezcurra Inlet, Admiralty Bay, King George Island, South Shetland Islands. *Polish Polar Res.*, 2, 55-70.

LEWIS, J.R. and BOWMAN, R.S., 1975. Local habitat induced variations in the population dynamics of *Patella vulgata* L. *J. Exp. Mar. Biol. Ecol.*, 77, 197-207.

LIGHTFOOT, R.H., TYLER, P.A. and GAGE, J.D., 1979. Seasonal reproduction in deep-sea bivalves and brittlestars. *Deep-Sea Res.*, 26A, 967-973.

LIPPS, J.H. and HICKMAN, C.S., 1982. Origin, age and evolution of Antarctic and deep-sea faunas. In : *The environment of the deep sea (Rubey Volume II)* (W.G. Ernst and J.G. Morin, (eds.)), pp. 325-356. Prentice-Hall, Englewood Cliffs, New Jersey.

LITTLEPAGE, J.A., 1965. Oceanographic investigations in McMurdo sound, Antarctica. *Antarctic Res. Ser.*, 5, 1-37.

LOOSANOFF, V. L. and NOMEJKO, C. A., 1946. Feeding of Oysters in relation to tidal changes and to periods of light and darkness. *Biol. Bull. mar. biol. Lab. Woods Hole*, 90, 244-267.

LOWELL, R.B., 1984. Desiccation of intertidal limpets: effects of shell size, fit to substratum, and shape. *J. Exp. Mar. Biol. Ecol.*, 77, 197-207.

LOWENSTAM, H.A., 1954a. Environmental relations of modification compositions of certain carbonate secreting marine invertebrates. *Proc. Nat. Acad. Sci. U.S.A.*, 40, 39-48.

LOWENSTAM, H. A., 1954b. Factors effecting the aragonite : calcite ratios in carbonate secreting marine organisms. *J. Geol.*, 62, 284-322.

LOWENSTAM, H.A., 1962. Geothite in radular teeth of recent gastropods. *Science*, 137, 279-280.

LOWENSTAM, H.A., 1964. Coexisting calcites and aragonites from skeletal carbonates of marine organisms and their strontium and magnesium contents. In : *Recent Researches in the Fields of Hydrosphere Atmosphere and Nuclear Geochemistry*, pp. 373-404. Marnzen, Tokyo.

LUCKENS, P. A., 1990. Distribution, size-frequency, and growth ring analysis of *Tawera mawsoni* (Bivalvia : Veneridae) at Macquarie Island. *N. Z. J. mar. freshw. Res*, 24, 59-73.

LUTZ, R. A., 1976. Annual growth patterns in the inner shell layer of *Mytilus edulis* L. *J. mar. biol. Ass. U.K.*, 56, 723-731.

LUTZ, R. A. and RHOADS, D.C., 1977. Anaerobiosis and a theory of growth line formation. *Science*, 198, 1222-1227.

LUXMOORE, R.A., 1982. Moulting and growth in serolid isopods. *J. Exp. Mar. Biol. Ecol.*, 56, 63-85.

MacCLINTOCK, C., 1967. Shell structure of patelloid and blerophontoid gastropods (Mollusca), *Peabody Mus. Nat. Hist. Yale Univ. Bull.*, 22, 1-140.

MacDONALD, B.A. and THOMAS, M.L.H., 1980. Age determination in the soft-shell clam *Mya arenaria* using shell internal growth lines. *Mar. Biol.*, 58, 105-109.

McCLINTOCK, J.B. and PEARSE, J.S., 1987. Reproductive biology of the common Antarctic crinoid *Promachocrinus kerguelensis* (Echinodermata : Crinoidea). *Mar. Biol.*, 96, 151-155.

MANZER, J.I. and TAYLOR, F.H.C., 1947. The rate of growth of the lemon sole in the strait of Georgia. *Prog. Rep. Pacif. Cst. Stns.*, 72, 24-27.

MARR, J.W.S., 1935. The South Orkney Islands. *Discovery Rep.*, 10, 283-382.

MASON, J., 1957. The age and growth of the scallop *Pecten maximus* (L.), in Manx waters. *J. mar. biol. Ass. U.K.*, 36, 473-492.

MATHERS, N.F., 1976. The effects of tidal currents on the rhythm of feeding and digestion in *Pecten maximus* L. *J. Exp. Mar. Biol. Ecol.*, 24, 271-283.

MILLERO, F.J., 1974. Seawater as a multicomponent electrolyte solution. In : *The Sea*, (E. D. Goldberg, ed.), pp. 3-80, John Wiley AND Sons, New York.

MINITAB, INC., 1987. Minitab statistical software, release 6.1.1. *Minitab Incorporated, 3081 Enterprise Drive, State College, PA. 16801 , United States of America.*

MOORE, H.B., 1934. The relation of shell growth to environment in *Patella vulgata*. *Proc. Malacol. Soc. Lond.*, 21, 217-222.

NEWCOMBE, C.L., 1935. Growth of *Mya arenaria* from the Bay of Fundy region. *Can. J. Res.*, 13, 97-137.

NICOL, D., 1964. An essay on size of marine pelecypods. *J. Paleontol.*, 38, 968-974.

NICOL, D., 1967a. Some characteristics of cold water marine pelecypods. *J. Paleontol.*, 41, (6), 1330-1340.

NICOL, J.A.C., 1967b. *The Biology of Marine Animals*. 2nd. edition, Pitman, London.

ORTON, J.H., 1926. On the rate of growth of *Cardium edule*. Part I. Experimental observations. *J. mar. biol. Ass. U.K.*, **14**, 239-279.

ORTON, J.H., 1932. Studies on the relation between organism and environment. *Proc. Trans. Liverpool Biol. Soc.*, **46**, 1-16.

ORTON, J.H., SOUTHWARD, A.J. and DODD, J.M., 1956. Studies on the biology of limpets. II. The breeding of *Patella vulgata* L.in Britain. *J. mar. biol. Ass. U.K.*, 35, 149-176.

PALMISANO, A.C., SOO HOO, J.B., MOE, R.L. and SULLIVAN, C.W., 1987. Sea ice microbial communities VII. Changes in under-ice spectral irradience during the development of Antarctic sea ice microalgal communities. *Mar. Ecol. Prog. Ser.*, 35, 165-173.

PANNELLA, G. and MacCLINTOCK, C., 1968. Biological and environmental rhythms reflected in molluscan shell growth. *J. Paleontol.*, **42** (Supplement to No. 5, Memoir 2), 64-80.

PEARSE, J.S., 1963. Marine reproductive periodicity in polar seas : A study of two invertebrates at McMurdo sound, Antarctica. *Bull. Ecol. Soc. Amer.*, **44**, 43.

PEARSE, J.S., 1965. Reproductive periodicities in several contrasting populations of *Odontaster validus* Kohler, a common Antarctic asteroid. *Antarctic Res. Ser.*, 5, 39-85.

PEARSE, J.S. and GIESE, A.C., 1966. Food, reproduction and organic constitution of the common Antarctic echinoid *Sterechinus neumayeri*. *Biol. Bull.*, 130, 387-401.

PECK, L.S., 1989. Temperature and basal metabolism in two Antarctic marine herbivores. *J. Exp. Mar. Biol. Ecol.*, 127, 1-12.

PECK, L.S., CLARKE, A. and HOLMES, L.J., 1987. Size, shape and the distribution of organic matter in the recent Antarctic brachiopod *Liothyrella uva*. *Lethaia*, 20, 33-40.

PERRIN, R.A., LU, P. and MARCHANT, H.J., 1987. Seasonal variation in marine phytoplankton and ice algae at a shallow Antarctic coast site. *Hydrobiol.* 6, 33-46.

PETERSON, C.H. and AMBROSE, W. G., 1985. Potential habitat dependence in deposition rate of presumptive annual lines in shells of the bivalve *Protothaca staminea*. *Lethaia*, 18, (3), 257-260.

PICKEN, G.B., 1979. Non-pelagic reproduction of some Antarctic prosobranch gastropods from Signy Island, South Orkney Islands. *Malacologia*, 19, 109-128.

PICKEN, G.B., 1980a. Reproductive adaptations of Antarctic benthic invertebrates. *Biol. J. Linn. Soc.*, 14, 67-75.

PICKEN, G.B., 1980b. The distribution, growth and reproduction of the Antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1908). *J. Exp. Mar. Biol. Ecol.*, 42, 71-85.

PICKEN, G.B., 1985. Marine habitats - benthos. In : *Antarctica* (W.N. Bonner and D.W.H. Walton (eds.)), pp. 154-172. Pergammon Press, Oxford.

PICKEN, G.B. and ALLAN, D., 1983. Unique spawning behaviour by the Antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1908). *J. Exp. Mar. Biol. Ecol.*, 71, 283-287.

POWELL, A. W. B., 1951. Antarctic and sub-Antarctic mollusca : Pelecypoda and Gastropoda. *'Discovery' Rep.*, 26, 47-196.

POWELL, A. W. B., 1960. Antarctic and sub-Antarctic mollusca (catalogue). *Rec. Auk. Inst. Mus.*, 5, (3-4), 117-193.

POWELL, A.W.B., 1965. Mollusca of Antarctic and sub-Antarctic seas. In *Biogeography and Ecology in Antarctica*. pp 333-380. (J. van Meighem & P. van Oye, eds.). Dr. W. Junk Publishers, The Hague.

POWELL, A.W.B., 1973. The patellid limpets of the world (Patellidae). *Indo-Pacific Mollusca*, 3, 75-206.

PRIDDLE, J., HAWES, I. and ELLIS-EVANS, J.C., 1986. Antarctic aquatic ecosystems as habitats for phytoplankton. *Biol. Rev.*, 61, 199-238.

RABARTS, I. W., 1970. Physiological aspects of the ecology of some Antarctic lamellibranchs. British Antarctic Survey Base report N9b/1970/H, British Antarctic Survey, Cambridge.

RABARTS. I.W. and WHYBROW, S., 1979. A revision of the Antarctic and sub-Antarctic members of the genus *Yoldia* Möller, 1842 (Bivalvia : Nuculanidae). *J. Nat. Hist.*, 13, 161-183.

RALPH, R. and MAXWELL, J.G.H., 1977. Growth of two Antarctic lamellibranchs : *Adamussium colbecki* and *Laternula elliptica*. *Mar. Biol.*, 42, 171-175.

RHOADS, D.C. and PANNELLA, G., 1970. The use of molluscan shell growth patterns in ecology and paleoecology. *Lethaia*, 3, 143-161.

RHOADS, D.C. and LUTZ, R.A. (eds.), 1980. *'Skeletal growth of aquatic organisms'*, Plenum Press, New York, 750pp.

RHOADS, D.C., LUTZ, R.A., REVELAS, E.C. and CERRATO, R.M., 1981. Growth of bivalves at deep-sea hydrothermal vents along the Galapagos Rift. *Science*, 214, 911-913.

RICHARDSON, M.G., 1979. The ecology and reproduction of the brooding Antarctic bivalve *Lissarca miliaris*. *Br. Antarct. Surv. Bull.*, 49, 91-115.

RICHARDSON, C.A., 1987. Microgrowth patterns in the shell of the Malaysian cockle *Anadara granosa* (L.) and their use in age determination. *J. Exp. Mar. Biol. Ecol.*, 111, 77-98.

RICHARDSON, C.A., 1988. Exogenous and endogenous rhythms of band formation in the shell of the clam *Tapes philippinarum* (Adams et Reeve, 1850).

RICHARDSON, C.A., CRISP, D.J. and RUNHAM, N.W., 1980a. Factors influencing shell growth in *Cerastoderma edule*. *Proc. R. Soc. Lond. Ser. B*, 210, 513-531.

RICHARDSON, C.A., CRISP, D.J. and RUNHAM, N.W., 1981. Factors influencing shell deposition during a tidal cycle in the intertidal bivalve *Cerastoderma edule*. *J. mar. biol. Ass. U.K.*, **61**, 465-476.

RICHARDSON, C.A., CRISP, D.J., RUNHAM, N.W. and GRUFFYDD, Ll. D, 1980b. The use of tidal growth bands in the shell of *Cerastoderma edule* to measure seasonal growth rates under cool temperate and sub-Arctic conditions. *J. mar. biol. Ass. U.K.*, **60**, 977-989.

RICKER, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, **191**, 382pp.

RILEY, J.P. and SKIRROW, G. (eds.) 1975. *Chemical Oceanography*. Vol. 2., 2nd. ed., Academic Press, New York.

RODIN, L.E., BRAZILEVICH, N.I. and ROZOV, N.N., 1975. Productivity in the world's main ecosystems. In : *Productivity of World Ecosystems* (D.E. Reichle, J.F. Franklin and D. Goodall, eds.), National Academy of Sciences, Washington, D.C., U.S.A..

ROSENBERG, G.D. and RUNCORN, S.K. (eds.), 1975. *Growth Rhythms and the History of the Earth's Rotation*. 559pp, John Wiley & Sons, London.

RUSSELL, E.S., 1907. Environmental studies on the limpet. *Proc. Roy. Zool. Soc.*, 77, 856-870.

SAKSHAUG, E. and HOLM-HANSEN, O., 1984. Factors governing pelagic production in polar oceans. In : *Marine Phytoplankton and Productivity* (Holm-Hansen, O., Bolis, L and Gilles, R., (eds.)), Lecture notes on Coastal and Estuarine Studies, 8, pp. 1-18, Springer Verlag, Berlin.

SAVIN, S.M., DOUGLAS, R.G. and STEHLI, F.G., 1975. Tertiary marine paleotemperatures. *Geol. Soc. Amer. Bull.*, 86, 1499-1510.

SEAGER, J.R., 1979. Reproductive biology of the Antarctic opisthobranch mollusc *Philine gibba*. *J. Exp. Mar. Biol. Ecol.*, 41, 51-74.

SEED, R., 1973. Absolute and allometric growth in the mussel, *Mytilus edulis* L. (Mollusca Bivalvia). *Proc. Malacol. Soc. Lond.*, 40, 343-357.

SHABICA, S.V., 1971. The general ecology of the Antarctic limpet *Patinigera polaris*. *Antarct. J. U.S.*, 6, 160-162.

SHABICA, S.V., 1976. The natural history of the Antarctic limpet *Patinigera polaris* (Hombron & Jacquinot). *Ph.D.* thesis, University of Oregon, United States of America., 294pp.

SHACKLETON, N.J. and KENNETT, J.P., 1975. Paleotemperature history of the cenozoic and the initiation of the Antarctic glaciation - oxygen and carbon isotope analyses in DSPP sites 277, 279 and 281: Initial report of the deep sea drilling project, U.S.G.P.O., Washington, D.C., 29, 743-755.

SIEG, J. and WÄGELE, J.W.(eds.), 1990. *Fauna der Antarctis.* Paul Parey, Berlin.

SIMPSON, R.D., 1976. Physical and biotic factors limiting the distribution and abundance of littoral molluscs on Macquarie Island (sub-Antarctic). *J. Exp. Mar. Biol. Ecol.*, 21, 11-49.

SIMPSON, R.D., 1985. Relationship between allometric growth, with respect to shell height, and habitats for two patellid limpets, *Nacella (Patinigera) macquariensis* Findlay, 1927, and *Cellana tramoserica* (Holten, 1802). *Veliger*, 28, 18-27.

STENECK, R.S. and WATLING, L., 1982. Feeding capabilities and limitations of herbivorous molluscs: A functional group approach. *Mar. Biol.*, 68, 299-319.

STRICKLAND, J.D.H. and PARSONS, T.R., 1972. *A Practical Handbook of seawater analysis.* Fisheries Research Board of Canada, Bulletin No. 167 (2nd edition), Ottawa, Canada, 310pp.

SVERDRUP, H.U., 1955. The place of physical oceanography in oceanographic research. *J. Mar. Res.*, 14, 287-294.

SVERDRUP, H.U., JOHNSON, M.W. and FLEMING, 1942. *The Oceans : Their Physics, Chemistry and General Biology.* Prentice-Hall, Eaglewood Cliffs, N.J., U.S.A..

TAYLOR, J.D., KENNEDY, W.J. and HALL, A., 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea - Trigonacea. *Bull. Br. Mus. Natur. Hist. (Zool.) Suppl. 3.* 125pp.

THEISEN, B.F., 1973. The growth of *Mytilus edulis* L. (Bivalvia) from Disko and Thule district, Greenland. *Ophelia*, 12, 59-77.

THOMAS, I.M., 1948. The adhesion of limpets. *Aust. J. Sci.*, 11, 28-29.

THOMPSON, I., JONES, D.S. and DREIBELBIS, D., 1980. Annual internal growth banding and life history of the Ocean Quahog *Arctica islandica* (Mollusca: BIvalvia). *Mar. Biol.*, 57, 25-34.

THOMPSON, T.G., 1932. The physical properties of seawater. In : *Physics of the Earth*, Vol. 5, *Oceanography*, p63-94. National Research Council Bulletin No. 85.

THORSON, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25, 1-45.

TUREKIAN, K., COCHRAN, J.K., KHARKAR, D., CERRATO, R., VAISNYS, J.R., SANDERS, H., GRASSLE, J.F. and ALLEN, J., 1975. Slow growth rate of a deep-sea clam determined by ^{228}Ra chronology. *Proc. natn. Acad. Sci. U.S.A.*, 72, 2829-2832.

TUREKIAN, K.K. and COCHRAN, J.K., 1981. Growth rate of a Vesicomyid clam from the Galapagos spreading center. *Science*, 214, 909-910.

TYLER, P.A., 1988. Seasonality in the deep-sea. *Oceanog. Mar. Biol. Ann. Rev.*, 26, 227-258.

TYLER, P.A., GRANT, A., PAIN, S. and GAGE, J., 1982. Is annual reproduction in deep-sea echinoderms a response to variability in their environment? *Nature*, 300, 747-749.

VALENTINE, J.W., 1983. Seasonality : Effects in marine benthic communities. In : *Biotic Interactions in Recent and Fossil Benthic Communities.*(M.J.S. Tevesz and P.L. McCall, eds.), pp 121-156. Plenum Press, New York.

VAN der WAL, P., 1989. Structural and material design of mature mineralised radula teeth of *Patella vulgata* (Gastropoda). *J. Ultrastr. Mol. Struct. Res.*, 102, 147-161.

VERMEIJ, G.J., 1978. *Biogeography and Adaptation : Patterns of Marine Life*. Harvard University Press, Cambridge, Mass., U.S.A..

VINCENT, W.F. 1988, *Microbial Ecosystems of Antarctica*, Studies in Polar research, Cambridge University Press.

VOOUS, K.H., 1965. Antarctic birds. In *Biogeography and Ecology in Antarctica*. pp 649-689. (J. van Meighem & P. van Oye, eds.). Dr. W. Junk Publishers, The Hague.

WADA, K., 1961. Crystal growth of molluscan shells. *Bull. Natnl. Pearl Res. Lab.*, Kashikojima, 7, 703-828.

WALKER, A.J.M., 1972. Introduction to the ecology of the Antarctic limpet *Patinigera polaris* (Hombron and Jaquinot) at Signy Island, South Orkney Islands. *Br. Antarct. Surv. Bull.*, No. 28, 49-71.

WEI, J.H.C., 1988. Morphological and genetic variation in natural populations of Antarctic limpet *Nacella concinna*. *M.Sc.* thesis, University College of North Wales, Wales.

WEYMOUTH, F.W., McMILLAN, J.C. and RICH, W.H., 1931. Latitude and relative growth in the razor clam *Siliqua patula*. *J. Exp. Biol.*, 8, 228-641.

WHEELER, A.P., BLACKWELDER, P.L. and WILBUR, K.M., 1975. Shell growth in the Scallop *Argopecten irradians*. I. Isotope incorporation with reference to diurnal growth. *Biol. Bull.*, 148, 472-482.

WHITAKER, T.M., 1982. Primary production of phytoplankton off Signy Island, South Orkneys, the Antarctic. *Proc. Roy. Soc. Lond.* B, 214, 169-189.

WHITE, M.G., 1973. Aspects of the biological significance of ice in the marine environment. *Proc. Challenger Soc.*, 4, 145-146.

WHITE, M.G., 1977. Ecological adaptations by Antarctic poikilotherms to the polar marine environment. In : *Adaptations within Antarctic Ecosystems*, (G.A. Llano, (ed.)), pp. 197-208. Gulf Publication Company, Houston.

WHITE, M.G., 1984. Marine benthos. In : *Antarctic Ecology*, (R.M. Laws, (ed)), Vol. 2, pp. 421-461. Academic Press, London.

WILBUR, K.M., 1964. Shell formation and regeneration. In : *Physiology of Mollusca* I, (K.M. Wilbur and C.M. Yonge, eds.), pp. 243-282, Academic Press, New York, U.S.A..

WILBUR, K.M., 1972. Shell formation in molluscs. In : *Chemical Zoology VII. Mollusca*. (M. Florkin and B.T. Sheer (eds.)), p103 - 145. Academic Press, New York.

WILBUR, K.M., 1984. Biochemical aspects of molluscan shell mineralization. In : *Marine Biodeterioration : An Interdisciplinary Study*, (J.D. Costlow and R.C. Tipper (eds.)),Proceedings of the Symposium on Marine Biodeterioration, Uniformed Services University of Health Sciences, 20-23 April, 1981. Naval Institute Press, Annapolis, Maryland, U.S.A..

WILBUR, K.M. and JODREY, L.H., 1952. Studies on shell formation. I. Measurement of the rate of shell formation using ^{45}Ca. *Biol. Bull.*, **103**, 269-276.

WILBUR, K.M. and SIMKISS, K., 1968. Calcified shells. In : *Comprehensive Biochemistry 26A*. (M. Florkin and E.H. Stotz, eds.) pp. 229-295, Elsevier, Amsterdam.

YONGE, C. M., 1939. The protobranchiate mollusca ; A functional interpretation of their structure and evolution. *Phil. Trans. Roy. Soc. Lond. Ser. B*, **230**, (566), 79-147.

ZISCHKE, J.A., WATABE, N. and WILBUR, K.M., 1970. Studies on shell formation : measurement of growth in the gastropod *Ampullarius glaucus*. *Malacologia*, **10**, 423-439.