

INTRODUCTION TO THE ECOLOGY OF THE ANTARCTIC LIMPET *Patinigera polaris* (Hombron and Jacquinot) AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS

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ABSTRACT. At Signy Island in summer the patellid species *Patinigera polaris* occurs in the littoral and sub-littoral zones but in winter it is found in the littoral zone only under certain conditions. The species is able to withstand freezing temperatures but only for a limited time; prolonged subjection to low air temperatures causes mortality. However, limpets in the littoral zone avoid the harsh winter climate by a downward movement in autumn. In spring there is a return movement up into the littoral zone. Such behavioural adaptations, or the ability to tolerate low air temperatures, or both, are typical of polar littoral organisms.

The environmental factor eliciting downward movement appears to be correlated with air temperature, and may be the ice film that forms on littoral rocks in autumn when the air temperature falls below the freezing point of the sea. On some shores fast ice later insulates the lower littoral zone from the prevailing air temperature at low tide, the ice film on the rocks then disappears, and limpets may return to the littoral zone. After the break-up of the fast ice these limpets again experience the generally prevailing air temperatures; if these are below freezing, those limpets exposed to air return to below low-water mark.

At Signy Island there are two main populations. The numerically smaller of these exhibits seasonal movement as described, while the other remains in the sub-littoral zone all year round. They can be distinguished by differing shell characteristics.

THE Southern Ocean is an exceedingly productive environment (Hardy, 1967) but this is not evident on polar shores, where the diversity and abundance of organisms is considerably less than in the sub-littoral zone (Price and Redfearn, 1968). The littoral zone, which in warmer regions is rich in species and biomass (Fischer, 1961), is exposed in high latitudes to fluctuating and freezing temperatures as well as to ice, which most species do not survive. This reduction in littoral faunal diversity in high latitudes is exemplified by the distribution of limpet species. The Falkland Islands have a comparatively rich littoral fauna with many mollusc species including several species of limpet (Powell, 1960). At South Georgia two species of littoral limpets occur, whereas at the South Orkney Islands the only limpet species is *Patinigera polaris* (Hombron and Jacquinot). This is usually the only large invertebrate found exposed to the air in the littoral zone of regions south of lat. 60°S. Knox (1960) pointed out that air and sea temperatures at the South Orkney Islands are similar to those in the high Arctic where faunal diversity is also poor; Arctic conditions in north-east Greenland support no molluscs or barnacles in the littoral zone (Madsen, 1936; Thorson, 1944). Adaptations to the effects of low air temperatures are thus important to the survival of *P. polaris*.

The taxonomy and zoogeography of the genus *Patinigera* Dall (1905) have been reviewed by Powell (1951, 1960, 1965), Knox (1960) and Dell (1964). Species of *Patinigera* (Patellidae) are circum-polar and are all found south of lat. 30°S. *P. polaris* is an Antarctic species which was first described by Hombron and Jacquinot (1841) from collections made during the expedition of *Astrolabe* and *Zélée* under Dumont d'Urville in 1838. It is now known to be restricted to west Antarctica where it is a dominant shallow-water species. Two sub-species have been recognized: *P.p. concinna* (Strebel, 1908) which has only been found at South Georgia, and *P.p. polaris* which forms the subject of this paper and which occupies the greater geographical range. It is found on the Antarctic Peninsula, at South Georgia, the South Shetland Islands, South Orkney Islands, Bouvetøya, Seymour, Paulet, Wandel, Anvers and Petermann Islands (Dell, 1964).

The shell of *P. polaris* is usually drab brown or black externally, with variable sculpturing, while the interior has a dark bronze lustre. Specimens up to 58 mm. long have been obtained from the Melchior Islands off Graham Land (Powell, 1951); however, during the present study on Signy Island, limpets over 40 mm. were rarely found.

From 1963 to the beginning of 1965 a general ecological survey of inshore fauna and flora was undertaken at Signy Island (Price and Redfearn, 1968). Apart from some preliminary observations, the following paper on *P. polaris* is based on work done during March–November 1965.

ENVIRONMENT AT SIGNY ISLAND

Geography and climate

The South Orkney Islands are well south of the Antarctic Convergence and within the limits of winter pack and fast ice. Sea ice generally surrounds the islands for more than half the year. They are influenced by the West Wind Drift and to a lesser extent by a northerly component of the cold East Wind Drift (Knox, 1960). Signy Island (lat. $60^{\circ}43'S$, long. $45^{\circ}38'W$.) experiences Weddell Sea currents for the greater part of the year but for a short period during the summer (1-3 months) the Bransfield Current (modified Bellingshausen Current) penetrates to the south of the South Orkney Islands.

Signy Island is triangular, 8 km. long and 5 km. wide, and has an area of 18 km.^2 (Fig. 1).

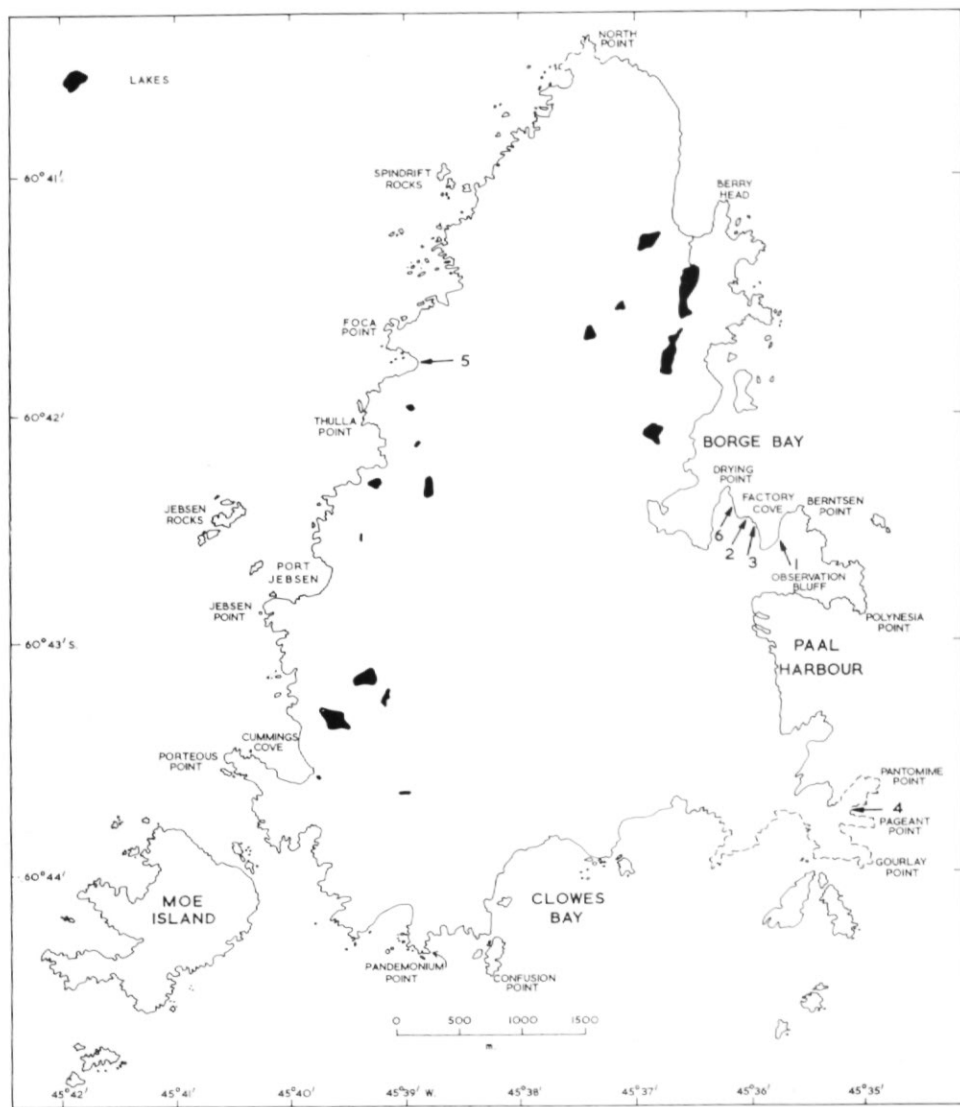


Fig. 1. Map of Signy Island showing the three transects: 1. Factory Cove, 2. Mooring Point, 3. Knife Point; and the other areas of investigations: 4. Gourlay Peninsula, 5. The cove south of Foca Point, 6. The littoral zone between Mooring Point and Drying Point.

TABLE I. MONTHLY PHYSICAL CONDITIONS AT SIGNY ISLAND, MARCH-NOVEMBER 1965

Month	Dates of full and new moon	Air temperatures (°C)			Properties of sea-water						Fast ice in Factory Cove		
		Mean	Max.	Min.	In mouth of Borge Bay				Inshore (mean)		Formed (date)	Broke up (date)	
					Date of sample	Temperature (°C)		Salinity (parts ‰)		Temperature (°C)			Salinity (parts ‰)
					Surface	30 m.	Surface	30 m.					
March	3, 17	+1.8	+7.1	-3.0	1	+1.25	+0.60	33.2	33.2	—	—		
April	2, 5	-0.8	+4.5	-12.4	15	-0.05	-0.04	33.8	33.8	—	—		
May	1, 5, 30	-1.1	+6.0	-9.0	18	-0.39	-0.40	33.8	33.9	-1.2	33.3		
June	14, 29	-3.9	+7.0	-16.0	1	-0.32	-0.33	33.8	33.8	-1.2	33.9		
July	13, 28	-9.1	+5.0	-24.0	22	-1.85	—	33.8	—	-1.8	34.3	12	16
August	12, 26	-10.3	+2.2	-25.7	17	-1.80	-1.82	33.7	33.7	-1.9	34.6	4	1
September	10, 25	-3.4	+6.0	-16.0	1	-1.70	-1.74	33.9	34.0	-1.8	33.6		
October	10, 24	-4.0	+4.0	-23.7	1	-1.80	-1.76	34.0	33.7	-1.7	33.5		
November	9, 23	-0.7	+6.0	-10.7	14	-1.50	-1.50	33.6	34.0	—	—		11

The physiography and geology have been described by Matthews and Maling (1967). The climate is maritime Antarctic (Holdgate, 1964). Sea temperatures vary between about $+1^{\circ}\text{C}$ and just above -2°C , whilst salinity between the surface and 30 m. depth usually varies between 33 and 34‰ (Everson, 1970, fig. 2). Readings at Signy Island show that the tides are semi-diurnal, with diurnal inequality; the range may be as much as 2.29 m. at springs and the lowest spring tides occur at about mid-day or midnight.

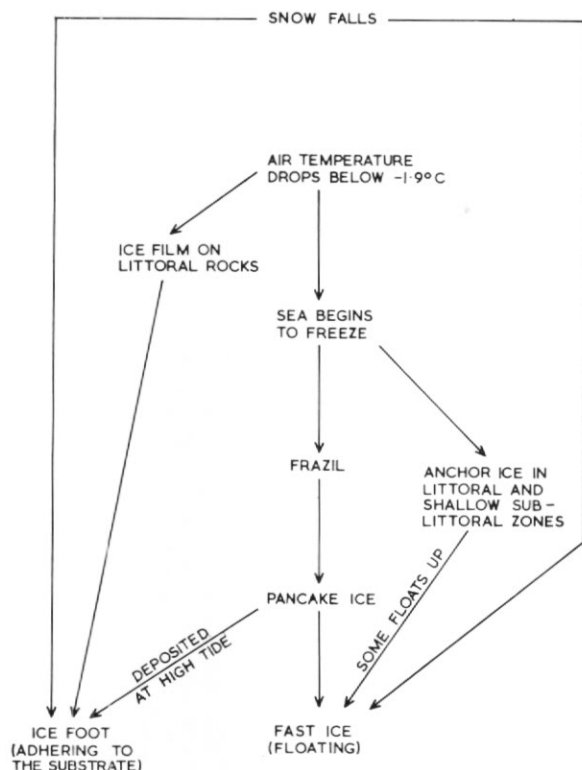


Fig. 2. Sea-ice formation in the littoral zone.

Physical conditions in 1965

Air temperatures for the period of study were obtained from the routine meteorological records at Signy Island. Sea temperatures and salinities in the mouth of Borge Bay were measured monthly at the surface and at 30 m. depth. Similar surface data were obtained from inshore sites and littoral pools in three sampling areas which were visited at about low-water spring tides from two to three times a month. These areas were the littoral pools at Berntsen Point, two sites at Elephant Flats (at the mouth and at about half-way into this bay), and an inlet on the east coast about half-way between Berry Head and Borge Bay. Physical conditions at Signy Island from March to November 1965 are summarized in Table I.

Sea ice

The autumn (April–June) drop in air temperature has two primary effects on the littoral zone (Fig. 2). As waves break during an ebbing tide, a film of ice forms on the rocks and the sea begins to freeze with the formation of ice crystals. These may either float (frazil) or form on the cold substrate (anchor ice). (For definitions of types of sea ice see Armstrong and Roberts (1956).) From frazil is derived pancake ice, and this later consolidates to form fast ice

(which rises and falls with the tide). Some anchor ice may become detached and float up to the underside of the fast ice. The ice foot forms earlier than the fast ice, and its height above low-water springs depends on meteorological conditions, currents and the gradient of the littoral zone. On a steep shore it may extend from low-water springs to high-water springs, while on a less steep shore it may only extend down to mid-tide level as in 1965 (Fig. 3). In colder years it extends farther down the shore.

During and after August 1965, there was a reduction in the amount of anchor ice and of the film of ice adhering to the littoral rocks. This ice was absent in the lower littoral zone in some areas in September, and an observation at Factory Cove (Fig. 1) at low tide on 24 September (1 day before new moon) suggested that the fast ice was insulating the air space above the water level in the littoral zone from outside air temperatures. Holes were cut in the ice and no ice film was visible either on the rocks or on the surface of pools, even though the outside air temperature was -9°C .

Algal zonation at Signy Island

The vertical distribution of the dominant inshore biota at Signy Island has been investigated by Price and Redfearn (1968, personal communication). The general distribution of algae is summarized below.

Littoral zone. In the littoral zone in summer the red alga *Porphyra* occurs on vertical surfaces about 2 m. above chart datum (approximately extreme low-water springs). Where *Porphyra* is not present, the highest colonization in the littoral zone is a more or less continuous band of *Ulothrix* and *Urospora* on firm substrates at about mid-tide level (M.T.L.). Below this, down to low-water springs (L.W.S.), is a band devoid of larger algae.

Sub-littoral zone. The lower boundary of the littoral zone is marked by the upper edge of the red coralline algae *Lithothamnion* and *Lithophyllum*. This calcareous crust is almost ubiquitous on rock in the upper sub-littoral zone and it also occurs in some littoral pools near L.W.S. The upper sub-littoral zone down to about 1 m. below chart datum contains many other red algae, such as *Iridaea*, *Leptosomia*, *Curdia* and *Gigartina*. The brown *Adenocystis* is often present, below which may be found *Ascoseira* and *Desmarestia* species (especially *D. anceps* Montagne),

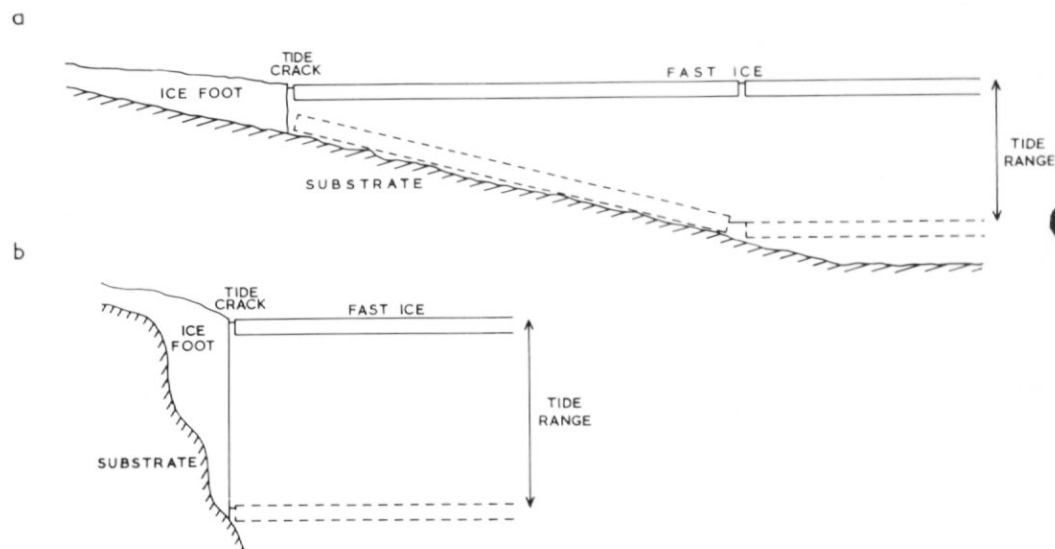


Fig. 3. Diagrams showing the position of the ice foot in 1965 on shores of shallow (a) and steep (b) gradient. The position of fast ice at low tide is shown dotted.

though *D. menziesii* J. Ag. penetrates the upper sub-littoral zone in deep crevices. *Phyllogigas* is found at 8–9 m. below chart datum. Many of the larger plants carry an epiphytic flora, and their holdfasts, axes and branches often provide shelter for a considerable fauna.

METHODS

Preliminary observations in 1964 had indicated seasonal variations in limpet density in the littoral zone, and in 1965 these variations were further investigated. Data were obtained in two ways: from counting limpets on transects and from collected samples. Scuba diving was adopted for counting and collecting limpets in the sub-littoral zone.

Transects

Three marked transects were chosen in a sheltered part of Borge Bay (Fig. 1), because the counting of limpets in the sub-littoral zone required that the sea be as still as possible and almost perpetual swell precludes work in most other areas. Three transects (Fig. 4) were selected as follows:

Transect 1 (Factory Cove). The substrate in the littoral zone here consisted of small boulders less than 1 m. across. In the sub-littoral zone were boulders, whalers' debris and bedrock in sand at the deepest part.

Transect 2 (Mooring Point). The littoral zone here consisted of bare rock with a small pool but few crevices, leading down to exposed bedrock in the sub-littoral zone and then sand at the deepest part.

Transect 3 (Knife Point). The littoral zone here was similar to that at Mooring Point. In the sub-littoral zone there was a vertical underwater cliff, 5 m. high, at the bottom of which was sand.

The transects were laid at the end of February 1965, and in March transect counting began.

Along each transect limpets were counted at 1 m. intervals in the littoral zone and for the first 5 m. of the sub-littoral zone; the remaining counting sites were at 5 m. intervals. The transects at Factory Cove and Mooring Point terminated 40 m. from L.W.S., and at Knife Point, 10 m. from the bottom of the underwater cliff.

A square 0.5 m. quadrat (0.25 m.²) was used for counting limpets, this being the only practical size for underwater work in these conditions. Limpets were counted in the quadrat placed to the left and right of each site and the two counts were added together.

Transect work was often prevented by high seas and failure of an air compressor stopped diving after April. Counting was then initially possible only in the littoral zone of each transect, and in the shallow sub-littoral zone at Factory Cove. However, after the formation of fast ice, holes were cut in the ice above the sites of the Mooring Point and Factory Cove transects; the quadrat was lowered on a line and limpets were counted from above. This method could not be applied to the Knife Point transect as most sites were on the vertical cliff.

Additional observations on limpets were made at other parts of the island (Fig. 1) and also by "snorkelling" in shallow water.

Collection of samples

In order to study the possible effect of habitat factors on *Patinigera polaris*, three samples of 100 or more limpets each were collected each month from three different levels as follows: the littoral zone, the shallow sub-littoral zone (0–2 m. depth below L.W.S.) and the deep sub-littoral zone (more than 4 m. depth below L.W.S.).

Samples were collected from the east coast of Signy Island, in particular in Borge Bay, although weather and ice conditions made it impossible to collect the samples from precisely the same place each month. Collection was by shore collecting, diving (and "snorkelling") and dredging. The samples were preserved in 70 per cent alcohol or 5 per cent formalin.

SEASONAL PRESENCE OF LIMPETS IN THE LITTORAL ZONE

Limpets are found in the littoral and sub-littoral zones in summer. They occur below the *Ulothrix/Urospora* band in pools and on shaded vertical surfaces, especially in crevices and

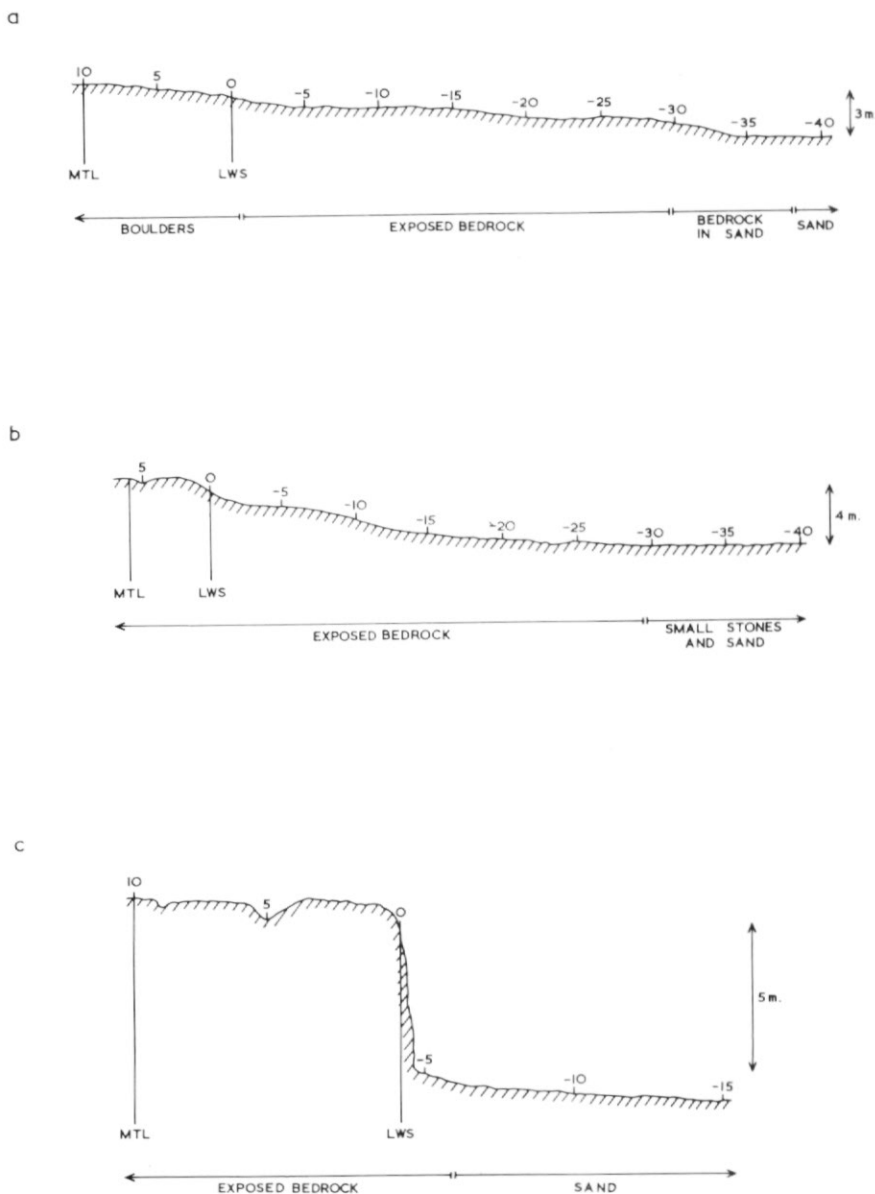


Fig. 4. Vertical sections of the three transects: a. Factory Cove, b. Mooring Point, c. Knife Point. Depths are approximate. The numbers indicate positions in metres *along* the transects, and not level relative to chart datum or low-water springs. (Vertical and horizontal scales of (c) are $\times 2$ those for (a) and (b)).

other sheltered places. They are seldom found on horizontal surfaces which become exposed to the air, but may occur in fresh-water melt streams running through the littoral zone. In the sub-littoral zone limpets have been found down to 60 m. depth (Powell, 1951). Population density in the upper sub-littoral zone is greater than in the littoral zone (Fig. 5) but, as in the littoral zone, distribution varies with substrate, concave surfaces and crevices being preferred, especially with rough seas. They may sometimes be found on the fronds of algae but generally they occur on rocky substrates and encrusting coralline algae.

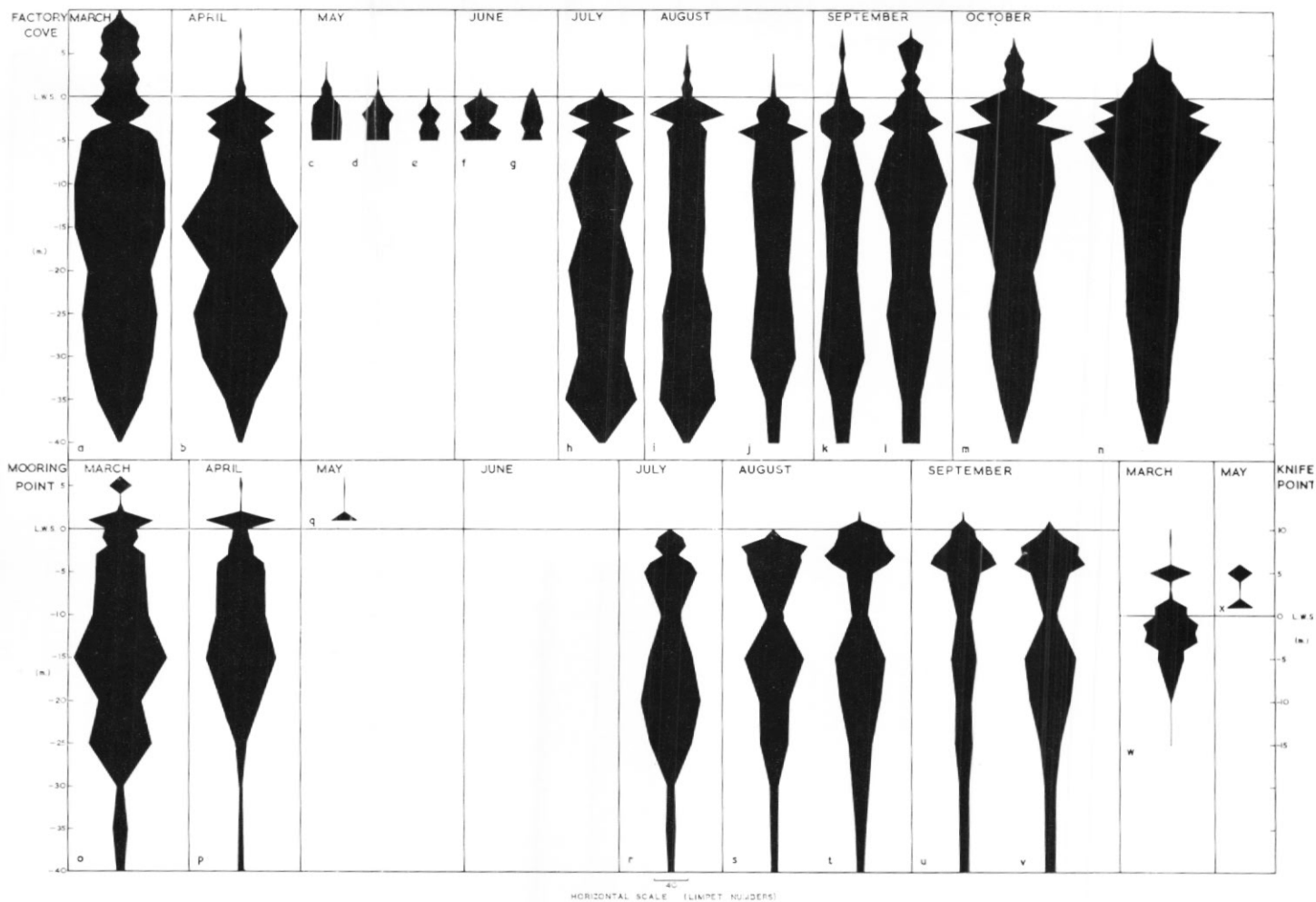


Fig. 5. Kite diagrams of the transect counts.

Factory Cove

- a. 1 March.
- b. 16 April.
- c. 2 May.
- d. 16 May.
- e. 31 May.
- f. 15 June.
- g. 30 June.
- h. 12 July.
- i. 5 and 7 August.
- j. 27-28 August.
- k. 3 September.
- l. 11 September.
- m. 15-16 October.
- n. 19-20 October.

Mooring Point

- o. 3 and 5 March.
 - p. 15 and 19 April.
 - q. 1 May.
- No limpets were seen in the littoral zone in the latter half of May or in June.
- r. 13 July.
 - s. 14 August.
 - t. 21-22 August.
 - u. 20 September.
 - v. 26 September.

Knife Point

- w. 3-4 March.
 - x. 1 May.
- No limpets were seen in the littoral zone in the latter half of May or in June. Thereafter this transect was not investigated.

The vertical scale (m.) indicates the sites of counting *along* the transects (not depth). 0 represents L.W.S., also indicated by a horizontal line. Numerals preceded by a minus sign represent sites in the sub-littoral zone. The horizontal scale shows the numbers of limpets/0.5 m.² at each site. In May and June no counting was possible in deeper water because of failure of the air compressor.

Preliminary observations in 1964 and early 1965 showed seasonal variation in the littoral population of limpets, indicating possible movements. In autumn 1964 the littoral population was observed to decline from 28 March until 12 April, and on 21 April no limpets were seen in the littoral zone. They were still common below L.W.S. When the fast ice broke up on 18 October 1964 no limpets were seen in the littoral zone at Factory Cove, but an upward movement followed and limpets reached the upper limit of their vertical distribution (M.T.L.) in January 1965.

The results of transect counts are shown as kite diagrams in Fig. 5. Important points arising from the counts and from additional observations are presented in Table II. As in 1964, limpets occupied the littoral and sub-littoral zones in summer. A considerable reduction in the littoral population occurred in mid-April, and this was associated with a rough sea, a sudden drop in air temperature and the presence of more bird predators (Appendix A) than usual. Also, many empty limpet shells appeared at this time in the littoral zone. As the winter progressed, limpet numbers further decreased until none was found exposed to the air at low tide. However, at neap tides, though they remained below low-water mark, limpets moved above L.W.S. Full re-colonization of the littoral zone began at Factory Cove after the formation of fast ice. At Mooring Point, a brief occupation of the littoral zone occurred then, but later in the winter no limpets were seen above L.W.S. Observations in ice-free areas in October and November revealed few limpets exposed to air in the littoral zone, except between Drying Point and Mooring Point on 9 November and at Factory Cove on 11 November. The 1964 observations presented above indicate that there is an upward movement into the littoral zone in spring and summer.

From the appearance of large numbers of empty limpet shells in the littoral zone at the time of the sudden reduction of the littoral population in April (Table II), it seems that the decrease in limpet numbers in the littoral zone was at least partly due to mortality. The possibility of a downward movement into the sub-littoral zone must now be considered.

SEASONAL DOWNWARD MOVEMENT OF LIMPETS

Shell shape (height relative to length) and the presence or absence of epibiotic organisms or their remains on the shell appear to be correlated with exposure to air or wave action, and to be suitable characters for separating a population of limpets that regularly visits the littoral zone from one which stays in the sub-littoral zone. Evidence for downward movement is provided by the presence of limpets with littoral characteristics in the autumn and winter *sub-littoral* samples. Let us now examine the evidence for the validity of this proposition by comparing the littoral with the deep sub-littoral samples.

Shell shape

The height to length ratios of the shells of *Patella vulgata* L. vary with habitat (Russell, 1907, 1909; Orton, 1928, 1932; Moore, 1934). On high-level open rocks and on wave-beaten shores, limpets have taller shells than those living low down the shore (especially those under algae). Moore (1934) considered that these differences were environmentally caused. It was therefore decided to analyse the height to length ratios of the samples of *Patinigera polaris* in relation to habitats from which these samples were collected.

Before comparing samples from different habitats, it was necessary to determine the minimum length above which the exposure factor might give rise to consistent variation. In both the littoral and sub-littoral zones, limpets occurred in all length groups except the very smallest (<4 mm.), which were found just below L.W.S. In younger limpets in the littoral zone the exposure factor might not have been operative long enough to cause variation. Therefore, for all samples, shell-shape scatter diagrams (height/length) were prepared. Shell dimensions were measured with vernier calipers to 0.1 mm. In some cases the curve steepened with increasing length (an example is shown in Fig. 6). The graphs showed that the height of the shell of *P. polaris* up to 20 mm. long did not appear to vary consistently with the environment, but above this length the points fell approximately about straight lines with slopes that appeared to be consistently different for littoral and sub-littoral samples.

Monthly samples from the littoral and deep sub-littoral (≥ 4 m. depth) zones were analysed

TABLE II. SUMMARY OF THE MONTHLY DISTRIBUTION OF LIMPETS IN THE LITTORAL ZONE AND ASSOCIATED ENVIRONMENTAL FACTORS

Month	Conditions in the littoral zones	Distribution of limpets
<i>a. Before the formation of fast ice</i>		
March	Ice-free. <i>Ulothrix/Urospora</i> band at M.T.L.	Limpets in both the littoral and sub-littoral zones.
April	Littoral zone began to ice up. <i>Ulothrix</i> and <i>Urospora</i> present. On 13 April air temperature -12° C, and there was a heavy sea. Many Dominican gulls and sheathbills (predators of limpets) seen in the littoral zone.	Reduction of limpets in the littoral zone, especially on 13 April, when many empty shells were also found.
May	Littoral rocks covered by a film of ice at low tide. <i>Ulothrix</i> and <i>Urospora</i> band in decline.	No limpets in the littoral zone by the end of the month.
June	Thickening of ice film on rocks in littoral zone.	Limpets no longer exposed to the air at low tide.
<i>b. During the presence of fast ice</i>		
July	Ice foot permanent. 8 July anchor ice and pancake ice. 12-16 and from 17 July onwards fast ice present.	8 July, limpets observed above L.W.S. but below the water level at low-water neap tides. No limpets on the littoral transects during the following count at spring tides.
August	1 August, fast ice broke out. 4 August, fast ice permanent until November. Later in month a reduction in the ice film adhering to littoral rocks.	Limpets in littoral zone under ice at both transects at neaps and springs, though more above L.W.S. at neaps.
September	Fast ice present.	Limpets reduced in the littoral zone at Mooring Point, but increased at Factory Cove.
October	Fast ice present.	At Factory Cove an increase in limpets at all parts of the transect. Mooring Point not investigated because of weather.
<i>c. After the departure of fast ice</i>		
October (contd)	Gourlay Peninsula and Foca Point (see Fig. 1) ice-free. Investigated at the end of the month.	Much fewer limpets at these two sites than at ice-covered Factory Cove.
November	Ice-free areas at Gourlay Peninsula (4 November) and near Drying Point (9 November; see Fig. 1) only, investigated. Fast ice left Factory Cove 11 November.	No increase in limpets at Gourlay Peninsula. Limpets abundant in littoral zone near Drying Point. Many limpets in littoral zone at Factory Cove after departure of ice.

in order to determine whether there were significant differences in shell shape between samples from the different habitats. Regression lines were calculated for the height/length data for limpets ≥ 20 mm. long in each monthly sample (Table III; Fig. 7). The slope calculated from the total combined samples of littoral limpets (slope 0.53; range of samples 0.52-0.55) was

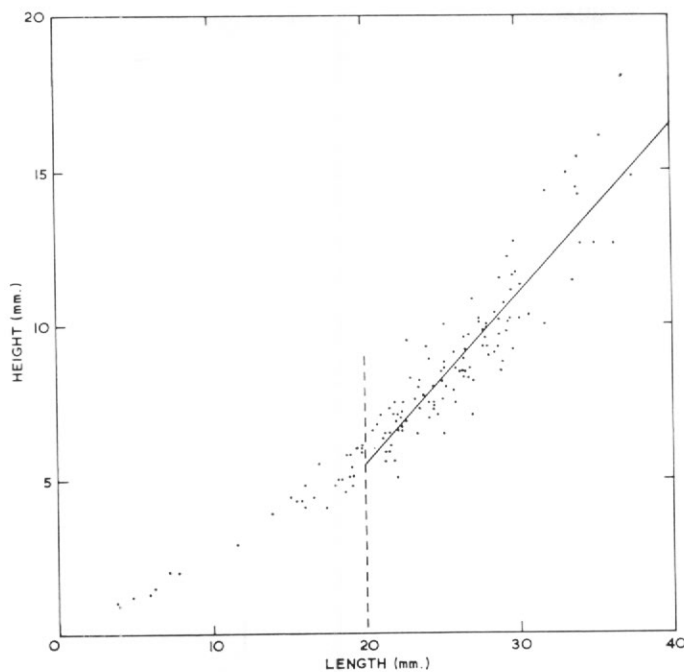


Fig. 6. Scatter diagram showing the relationship between height and length of a littoral sample of limpets (April). A regression line has been fitted to points representing limpets 20 mm. in length and over.

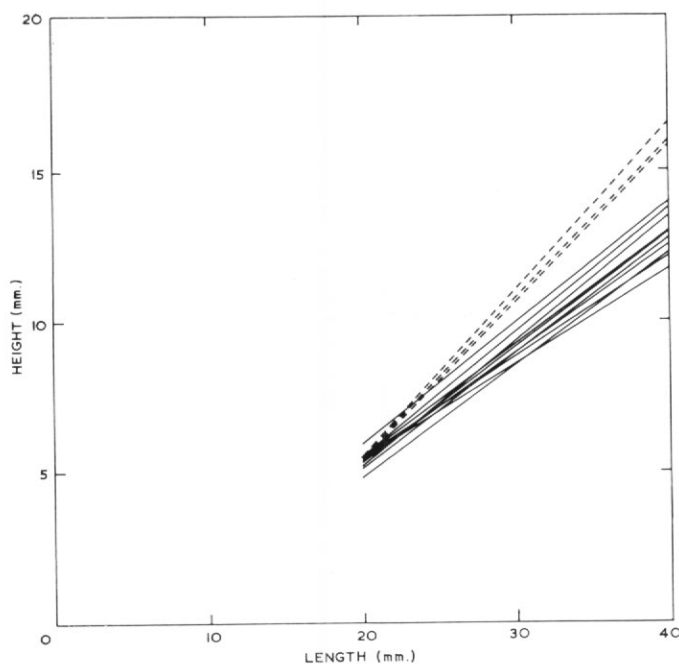


Fig. 7. Diagram illustrating the differences in gradient between the height/length regression lines of the littoral samples (broken lines) and the deep sub-littoral samples (continuous lines).

TABLE III. RESULTS OF REGRESSION ANALYSES OF HEIGHT TO LENGTH OF LIMPETS 20 mm. IN LENGTH AND OVER. SHALLOW SUB-LITTORAL SUB-SAMPLES WITH EPIBIOTA (+) AND WITHOUT EPIBIOTA (-)

Month collected	Depth (m.)	Number in sample (n)	Mean length (mm.)	Equation of regression line $a = y - bx$ (y, height; and x, length of shell)	Correlation coefficient
March	4	156	30.4	$-1.9 = y - 0.36x$	0.81
	<2	(+) 39	25.8	$-2.3 = y - 0.38x$	0.89
	<2	(-) 50	24.6	$-3.7 = y - 0.46x$	0.94
	Littoral	194	26.4	$-4.9 = y - 0.52x$	0.95
April	7-11	73	28.1	$-2.5 = y - 0.38x$	0.82
	<2		No sample		
Littoral		113	26.5	$-5.5 = y - 0.55x$	0.91
May	4-11	204	27.4	$-1.1 = y - 0.33x$	0.90
	<2	(+) 23	24.4	$-2.2 = y - 0.38x$	0.91
	<2	(-) 118	25.1	$-5.3 = y - 0.53x$	0.90
June	4-11	140	29.1	$-2.3 = y - 0.38x$	0.86
	<2	(+) 15	24.3	$-2.6 = y - 0.39x$	0.87
	<2	(-) 132	25.4	$-4.2 = y - 0.49x$	0.90
July	7-11	94	28.6	$-0.7 = y - 0.31x$	0.85
	<2	(+) 6	26.1	$-3.3 = y - 0.44x$	0.89
	<2	(-) 111	25.4	$-5.4 = y - 0.54x$	0.93
August	4-15	151	27.5	$-3.0 = y - 0.41x$	0.92
	<2	(+) 93	23.8	$-2.6 = y - 0.37x$	0.88
	<2	(-) 145	24.3	$-5.4 = y - 0.51x$	0.88
September	11-16	76	28.3	$-2.1 = y - 0.40x$	0.87
	<2		No sample		
October	9	135	23.6	$-1.9 = y - 0.37x$	0.94
	<2		No sample		
Littoral		112	26.9	$-5.0 = y - 0.52x$	0.91
November	7-11	63	26.3	$-2.6 = y - 0.37x$	0.88
December	11	180	28.6	$-2.7 = y - 0.41x$	0.93
TOTAL	≥ 4	1,272	27.9	$-2.3 = y - 0.38x$	0.89
TOTAL	Littoral	419	26.5	$-5.0 = y - 0.53x$	0.93

P (D.F. = $n-2$) = <0.001 in all cases except the following:

The July shallow sub-littoral sub-sample with epibiota where $P = <0.02 > 0.01$.

then compared with the slope for the total number of limpets from the deep sub-littoral zone (slope 0.38; range of samples 0.31-0.41), and found to be significantly different (Table IV, a). Thus, the limpet samples from the two habitats differed in shell shape.

Epibiota

Smith and Newell (1955), in a study of *Littorina littorea* (L.) in England, used evidence from the epibiotic barnacle *Elminius modestus* Darwin to discover the direction and extent of individual and group movements of the winkles. At Signy Island, it was noticed that limpets in the sub-littoral zone in summer were much more often marked by epibiotic organisms than those in the littoral zone, and the degree of cover appeared to be related to the extent of cover of the substrate. The epibiotic organisms, which are the coralline algae *Lithothamnion* and *Lithophyllum* and various species of spirorbid polychaete (unidentified), are not found in the littoral zone except in some low-level pools. In the sub-littoral zone coralline algae almost

TABLE IV. TABLE OF *F* TESTS COMPARING THE SLOPES OF THE REGRESSION LINES FOR SHELL HEIGHT/LENGTH.
 FOR DETAILS OF REGRESSION LINES SEE TABLE III.

SHALLOW SUB-LITTORAL SUB-SAMPLES WITH EPIBIOTA (+) AND WITHOUT EPIBIOTA (-)

Calculation (see text)	Months collected	Depth (m.)	<i>F</i> test for slopes	Degrees of freedom	Probability
a	March to December	Total littoral and total ≥ 4	159.04	1 : 1687	<0.01
b	March (+) and (-)	<2	3.85	1 : 85	>0.05
	April (+) and (-)	<2	No sample	No sample	—
	May (+) and (-)	<2	6.67	1 : 137	<0.05
	June (+) and (-)	<2	1.22	1 : 143	>0.05
	July (+) and (-)	<2	0	1 : 113	>0.05
	August (+) and (-)	<2	14.29	1 : 234	<0.01

completely cover the rocks. In the present study epibiota were simply recorded as present or absent on *P. polaris*, and the degree of cover was not assessed. Limpets from the littoral and deep sub-littoral zones were divided into length groups and the percentages of shells bearing epibiota in each group were plotted (Fig. 8). The data show that littoral limpets differ considerably from those from the deep sub-littoral zone in the average incidence of epibiota.

The monthly differences in epibiota incidence in the littoral and deep sub-littoral samples are shown graphically in Fig. 9. In constructing these graphs, data from animals less than 20 mm. long were discarded (see above). The three littoral samples show little variation. This curve is interrupted between April and October because no limpets were found in the littoral zone in winter until August, and then the few that had moved up were not collected because of ice conditions. It is probable that the variation in epibiotic cover in samples from the deep sub-littoral zone was related to patchiness in the cover of the substrate. Because of ice and weather conditions, these samples were collected from widely differing depths (Table III) and localities in Borge Bay.

The evidence presented above indicated that there are two main groups of limpets. In summer one group lives in the littoral zone and the other inhabits the sub-littoral zone; it

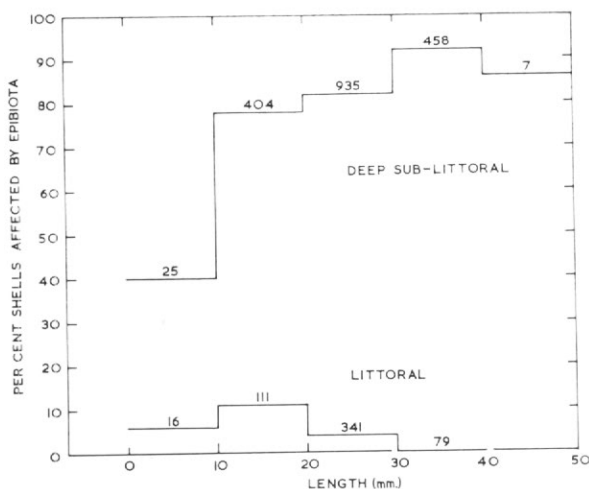


Fig. 8. Diagrams showing the percentage of shells in each size group bearing epibiota in the deep sub-littoral and littoral samples. The number of limpets in each group is indicated (all months combined).

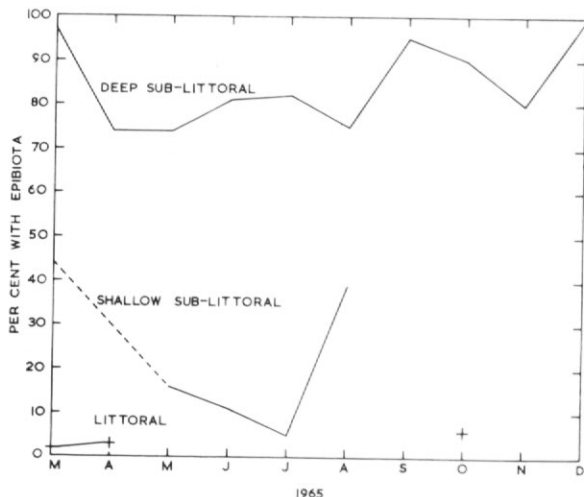


Fig. 9. Graphs showing the monthly percentages of shells (≥ 20 mm. long) bearing epibiota from the three sampling levels. Deep sub-littoral ≥ 4 m. depth; shallow sub-littoral ≤ 2 m. The discontinuity in the littoral samples is due to the absence of limpets in the littoral zone in winter.

seems likely that the morphological and epibiotic differences between the groups are related to exposure to air, breaking waves, or both of these factors.

Evidence from the shallow sub-littoral samples

If a downward movement of limpets from the littoral to the sub-littoral zone occurred in the autumn of 1965, it should have been possible to recognize these limpets in the sub-littoral zone during winter. The incidence of epibiotic organisms was therefore examined for evidence of a downward movement. However, Fig. 9 shows that data from epibiotic cover are not completely reliable in indicating the habitat of a limpet; not all limpets from the deep sub-littoral zone were affected, nor were all those from the littoral zone without epibiota. Evidence from shell shape was therefore also considered, the samples being subdivided according to whether or not they bore epibiota, after which shell-shape regression lines were calculated for each sub-sample. Differences in slope were then tested for significance.

The curve for the percentage of limpets bearing epibiota in each sample from the shallow sub-littoral zone (Fig. 9) is intermediate between the littoral and deep sub-littoral samples. In March, 44 per cent of the sample bore epibiota on their shells; in April weather conditions prohibited collecting in the shallow sub-littoral zone; in the May, June and July samples there was an increase in the proportion of limpets *without* epibiota, suggesting a downward movement from the littoral to the sub-littoral zone. The collection of these later samples coincided with the decrease in limpet numbers in the littoral zone. The July/August shallow sub-littoral samples showed an increase from 5 to 39 per cent of limpets bearing epibiota which coincided with the beginning of upward movement into the littoral zone (Fig. 5).

The shallow sub-littoral samples were subdivided into limpets with and without epibiota, and height/length regressions were calculated for each sub-sample (Table III). *F* tests were carried out comparing limpets with and without epibiota in each monthly sample. The results are shown in Table IV, b.

The comparatively low regression coefficient (0.46) of the March sub-sample without epibiota was found not to be significantly different from the coefficient of those with epibiota (0.38). This sample therefore gives no indication that a downward movement had begun and evidence from transect data (Fig. 5) shows that the littoral zone was well populated in March. No sample was collected in April, but the May shallow sub-littoral sample provides evidence for downward movement of limpets. The regression line for those animals without epibiota has a slope 0.53, which is similar to the slopes for the littoral samples, and significantly

different from the slope for the May sub-sample with epibiota (0.38). This evidence suggests that after March limpets had moved down from the littoral zone to join limpets that permanently inhabited the sub-littoral zone.

In both June and July the differences in slope (0.1 in each case) between the regressions for limpet sub-samples with and without epibiota are not significant (Table IV, b). However, the small sizes of both the June and July sub-samples (Table III) of limpets with epibiota probably account for the lack of significance. The August sample showed an increase in the proportion of limpets with epibiota, and the slope of the regression for these (0.37) is significantly lower than that for those without epibiota (0.51). This increase in the proportion of limpets with flatter shells and epibiota coincided with, and may be correlated with, the start of a movement from deeper water into the littoral zone (Fig. 5).

Conclusions

Two main points arise from the analysis of shell data. First, the evidence from epibiota organisms supported by the shell-shape data suggests that at Signy Island there are two main groups of *Patinigera polaris*. In winter they are both found in the sub-littoral zone but in spring one group moves into the littoral zone. Little mixing seems to occur between the two groups in summer.

Secondly, an analysis of the data on epibiotic cover and shell shape of the samples collected from the shallow (0-2 m. depth) sub-littoral zone provides evidence for downward movement in autumn, because limpets with littoral characteristics were found in these samples.

INFLUENCE OF ENVIRONMENTAL FACTORS ON LIMPET MOVEMENTS

No data for the abundance and distribution of limpets in the sub-littoral zone are available for 1964, so that no comparison with 1965 is possible in respect of limpet movements below L.W.S. Only variations in the littoral populations can be compared. In both 1964 and 1965 (Fig. 10), a drop in air temperature coincided with the autumn movement into the sub-littoral zone. The mean air temperatures for March and April were $+0.2^{\circ}$ and -5.0° C, respectively in 1964, and they were $+1.8^{\circ}$ and -0.8° C in 1965. In May and June 1965 they were -1.1° and -3.9° C. Exposed limpets were absent from the littoral zone about a month later in 1965, and thus the movements of limpets between the littoral and sub-littoral zones could be related to air temperature (Fig. 10). The subsequent upward movement of limpets from L.W.S. to low water at neap tides during the formation of fast ice (Table II), and the movements of limpets at Factory Cove in September 1965 (Fig. 10) both imply that low air temperatures may prevent occupation of levels above low water. At Factory Cove, the fast ice provided thermal insulation and crushing at low tide could be avoided because of crevices between the boulders. On the other hand, at Mooring Point re-colonization of the littoral zone was hindered by the lack of crevices in the substrate (Figs. 5 and 10).

Observations in the field and laboratory indicated that the formation of a film of ice on the rocks affected the movements of limpets. This occurs at air temperatures of below about -2° C, a conclusion which is supported by data from areas where the fast ice broke up early in the spring of 1965. Three such ice-free localities were examined in four visits (Table II). The results of these investigations together with data from two transect counts are presented in Table V. The abundance of limpets is represented using the notation introduced by Crisp and Southward (1958) as follows:

Abundant	over 50/m. ² .
Common	10 to 50/m. ² .
Frequent	1 to 10/m. ² .
Occasional	less than 1/m. ² .
Rare	only a few found in 30 min. search.

Three points arise from these data. First, the visits to Gourlay Peninsula and Foca Point were after cold spells, and limpet density and maximum distance from L.W.S. were inconsiderable; these areas were not covered by fast ice. Secondly, cold spells also preceded the transect counts at Factory Cove, but there were many limpets in the littoral zone at this transect. This shore, however, was insulated by fast ice (though a trench was cut in the ice for the

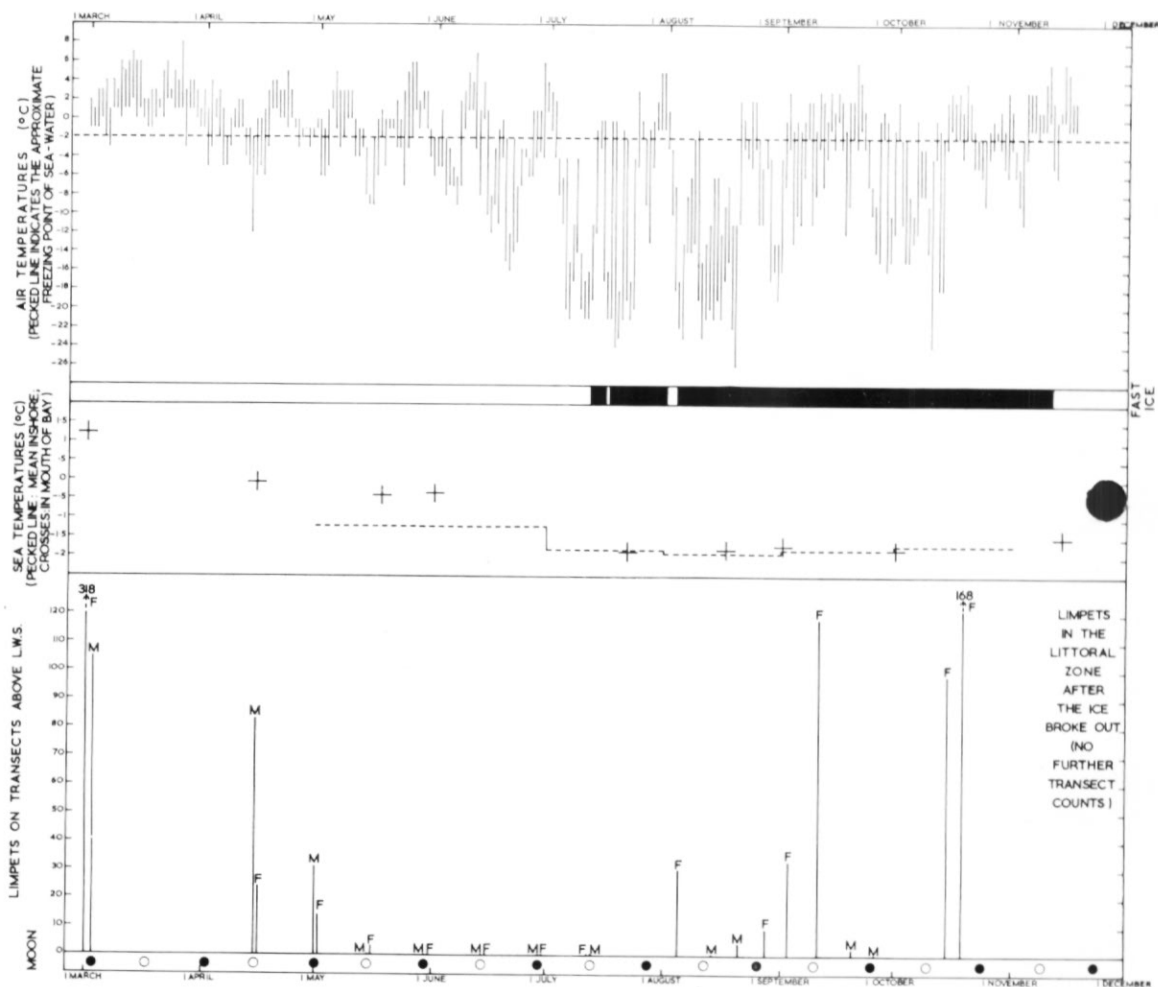


Fig. 10. Diagram showing the daily variation in air temperature, measurements of sea temperature, the duration of fast ice, the phases of the moon, and the numbers of limpets in the littoral zone at the Factory Cove (F) and Mooring Point (M) transects during winter 1965.

count on 15 October and may account for the slight downward movement at this transect between 11 September and 15 October). Thirdly, observations in the littoral zone near Drying Point showed considerable numbers of limpets. Since this shore had been free of fast ice, temperatures had generally been above the freezing point of the sea. It appears that, as at Factory Cove, limpets moved into the littoral zone under the fast ice; after this ice broke out on 6 November, no ice film formed in the littoral zone, and the limpets remained above L.W.S.

Although limpets moved into the littoral zone under fast ice in 1965, no such movement was recorded in 1964. When the fast ice broke up in Factory Cove in October 1964 no limpets were seen in the littoral zone. However, the ice foot extended much farther down the shore in 1964 (personal communication from P. Redfearn) and this would have limited re-colonization.

It is therefore suggested that an important proximate factor (Baker, 1938) influencing the downward movement of limpets is related to air temperature, and may be the formation of a film of ice on the rocks. Experimental confirmation is required. When the littoral zone is insulated by fast ice, the film either disappears or is prevented from forming. Under these

TABLE V. RELATIVE ABUNDANCE OF LIMPETS EXPOSED TO AIR IN THE LITTORAL ZONE OF VARIOUS LOCALITIES IN SPRING 1965
 (FOR EXPLANATION SEE TEXT)

<i>Date</i>	<i>Locality</i>	<i>Average abundance of limpets</i>	<i>Furthest distance (m.) from L.W.S. of limpets exposed to air at low tide</i>	<i>Previous air temperatures (°C)</i>	<i>Fast ice</i>	<i>Moon</i>
11 September	Factory Cove	Common (34/m. ²)	7	-11 to +3 Previous week	Present	Full moon 10 September
15 October	Factory Cove	Common (33/m. ²)	6	-24 to +2 Previous week	Present	Last quarter 17 October
23 and 26 October	Gourlay Peninsula	Frequent (greater numbers in pools)	0·1	-9 to -1 21-24 October	Absent	New moon 24 October
28-31 October	Foca Point	Rare	0·6	-9 to +1 Previous week	Absent	First quarter 1 November
4 November	Gourlay Peninsula	Occasional	0·2	-11 to -2 1-3 November	Absent	First quarter 1 November
9 November	Near Drying Point	Common	6	-2 to +4 5-9 November	Absent (since 6 November)	Full moon 9 November

conditions, limpets can re-colonize the littoral zone in spite of air temperatures below the freezing point of the sea. Upward movement is prevented, however, if the ice foot covers the littoral zone, or if the substrate does not allow adequate protection from the fast ice at low tide. No relationship was found between seasonal limpet movements and any other environmental variables (Tables I and II; Fig. 5), though more work would clarify this point and might show whether or not an underlying endogenous rhythm was involved.

TOLERANCE OF LOW AIR TEMPERATURES

On 13 April 1965, the remains of many dead limpets were found in the littoral zone. Although predatory birds were present, this limpet mortality was coincident with a sudden drop in air temperature to -12°C (Fig. 10) and the mortality may have been due to this. In late February and March 1965, an experiment was carried out to discover what to extent *Patinigera polaris* is adapted to withstand cold. For each temperature to which tolerance was investigated, limpets (over 20 mm. long) from the littoral zone were shaken dry and placed in a polythene container in an adjustable deep freeze. Animals were taken out at intervals and placed in fresh sea-water at about 1°C . Many had ice crystals in their tissues after treatment but many of these survived. After thawing, some animals reacted only to tactile stimulation and failed to recover in an open container suspended in the sea overnight. In this study these moribund animals were considered as dead. The results are shown in Table VI where temperatures are ambient air temperatures not limpet body temperatures. As a control, it may be stated that 21 limpets kept at -5° to -8°C showed 100 per cent survival after 510 min. in the deep freeze.

TABLE VI. SURVIVAL RATES OBTAINED FROM FREEZING LIMPETS FOR DIFFERENT LENGTHS OF TIME AT FOUR DIFFERENT TEMPERATURES IN FEBRUARY AND MARCH 1965

Temperature ($^{\circ}\text{C}$)	Time (min.)	Alive	Moribund/dead	Per cent survival
-20	60	16	0	100
	90	13	17	43
	135	3	25	11
	150	1	24	4
	165	0	23	0
-15	120	13	2	87
	150	10	8	56
	195	3	14	18
	225	2	17	11
	255	0	27	0
-12	240	15	1	94
	270	15	2	88
	300	8	13	38
	330	0	12	0
-9	270	16	0	100
	300	14	6	70
	405	10	9	53
	435	7	14	33
	465	1	14	7
	495	0	21	0

The results show that at an air temperature of -12°C death may occur after 4 hr. Total mortality was obtained after $5\frac{1}{2}$ hr., less than the time for which limpets at M.T.L. may be exposed. Kanwisher (1966) found that tolerance in *Littorina littorea* varied with season, and such variation may occur in *P. polaris*. However, if there was a similar tolerance of freezing on 13 April 1965 as in the experiment, the remains of limpets found in the lower littoral zone on that day could have been the result of mortality due to freezing.

Before fast ice forms at Signy Island, air temperatures may fall to -20°C , and it is suggested that the survival value of downward movement is that it enables *P. polaris* to avoid such low air temperatures. Low air temperature is thus an ultimate factor (Baker, 1938), resulting in downward movement in autumn. The importance of low air temperature does not preclude an additional ultimate effect on limpet distribution due to variation in food availability.

DISCUSSION

The immediate effects of freezing temperatures on littoral species in the Northern Hemisphere have been described by Smidt (1944), Stephenson and Stephenson (1954) and Kanwisher (1966). Their results can be summarized as follows. Cold has a direct effect on the physiology and behaviour of the organisms. It also has indirect actions, both involving effects on associated species such as predators and food organisms, and also producing the physical action due to ice.

Adaptations to polar and sub-polar littoral environments have been investigated for many northern species, and in the littoral zone in high latitudes molluscs have evolved a tolerance of freezing not shared by sub-littoral species (Kanwisher, 1955, 1959, 1966; Williams, 1967). Other studies concerned with the effect of low temperatures on molluscs include those of Crisp (1964), Kristensen (1957), Williams (1966), Batchelder (1915), Newcombe (1935), Petersen (1962), Willcox (1905), Lewis (1969) and Kinne (1970). In general it appears that littoral species show a correlation between cold tolerance and vertical distribution, geographical range, mobility and micro-habitat (Lewis, 1969).

Patinigera polaris shows characteristics typical of littoral molluscs of high altitudes. It is adapted to its environment in that it withstands certain low air temperatures and avoids the severe effects of the winter climate by movement into the sub-littoral zone. In spring there is a return upward movement into the littoral zone.

The greater proportion of limpets never appears to leave the sub-littoral zone (Fig. 5), and it is possible that these differ genotypically from those that move into the littoral zone. However, it is not known whether limpets occupy the littoral zone in summer because they happen to be near low water when conditions are favourable, or whether only certain individuals show upward movement, irrespective of their winter depth. Direct morphological or physical evidence of a consistent genotypic difference between the two populations is lacking. There is considerable variation in shell structure both between summer littoral and sub-littoral limpets, and also within the sub-littoral population, but these differences could be phenotypic. Shells of *P.p. concinna*, which is found in the sub-littoral zone at South Georgia, showed a shell shape (height/length) regression slope of 0.23, considerably lower than the deep sub-littoral sample with the least slope collected at Signy Island (0.31; Table III). Thus it does not appear that the summer sub-littoral limpets are members of this sub-species.

It might be considered that only limpets of certain age groups move into the littoral zone. Growth rates are unknown but limpets of similar sizes were found at all levels, except spat, which were found just below L.W.S. Also most of the large (and presumably old) limpets taken from the littoral zone were unaffected by epibiotic organisms, which leave an almost permanent trace, and so had probably always moved into the littoral zone in summer. Thus limpets of differing age groups do not differ consistently in respect of seasonal movements.

Possible proximate factors correlated with upward movement to the littoral zone have not been investigated. Jones (1946) and Southward (1956) found that *Patella* quickly re-invades areas rendered bare of limpets. A similar situation probably confronts *Patinigera* during favourable conditions in the spring at Signy Island. However, the last two transect counts at Factory Cove (Fig. 5) show that there was a build-up of limpets below L.W.S. in October. Also, there was a reduction in the upper sub-littoral zone in early winter (May and June). If this represents the general situation, conditions in the littoral zone are not the only factors influencing seasonal movements of *Patinigera polaris*. Food may be a significant factor. In spring 1964, soon after the break-up of the fast ice, green slime algae (unidentified) were observed near L.W.S. (and also continually submerged in an artificial pool placed in the littoral zone). At the same time limpets began to move and there was then a reduction in slime algae in the lower littoral zone. It is thus possible that *P. polaris* may follow the lower limit of the

algae up the littoral zone (see Petersen, 1962). However, limpets at Signy Island were found at all levels below M.T.L. in summer and were not concentrated at the edge of the green algal band, and secondly algal material was not detected in the littoral zone when limpets began to move up under fast ice in August 1965.

Conditions in the littoral zone are severe and are subject to sudden drops in air temperature. Is occupation of this zone of evolutionary advantage to those limpets that move up, or do these animals represent a "surplus" dispersing in response to population density to an unfavourable habitat as a form of population regulation (Wynne-Edwards, 1962; Jenkins and others, 1963; Lack, 1966)? *P. polaris* shows some adaptations to littoral conditions. It survives freezing to some extent, although it is by no means completely adapted to low air temperatures. The species also shows behavioural adaptations to the Antarctic environment in that it moves down in autumn and only settles on vertical surfaces (except in pools) in the littoral zone. This latter adaptation allows protection from ice floes which scrape the upper surfaces of littoral rocks. This may be an indication that a large enough proportion of the littoral population survives and breeds, for these adaptations to have evolved. More data, especially with respect to breeding and mortality, are required before it can definitely be shown whether upward movement has any survival value.

P. polaris is a dominant animal in shallow water around Signy Island. There is little competition from other species, which reflects the instability of the physical environment (Dayton and others, 1970), and it appears that there is a lack of predation (except, by gulls and sheath bills; see Appendix A). Adaptations to harsh environmental conditions are also an important factor in the success of the species.

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REFERENCES

- ARMSTRONG, T. and B. ROBERTS. 1956. Illustrated ice glossary. *Polar Rec.*, **8**, No. 52, 4-12.
- BAKER, J. R. 1938. The evolution of breeding seasons. (In DE BEER, G., ed. *Evolution, essays presented to E. S. Goodrich*. Oxford, Clarendon Press, 161-77.)
- BATCHELDER, C. H. 1915. Migration of *Ilyanassa obsoleta*, *Litorina litorea* and *Litorina rudis*. *Nautilus*, **29**, No. 4, 43-46.
- CHARLES, G. H. 1966. Sense organs (less cephalopods). (In WILBUR, K. M. and C. M. YONGE, ed. *Physiology of Mollusca, II*. New York and London, Academic Press, 455-521.)
- CRISP, D. J. 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *J. Anim. Ecol.*, **33**, No. 1, 165-210.
- . and A. J. SOUTHWARD. 1958. The distribution of intertidal organisms along the coast of the English Channel. *J. mar. biol. Ass. U.K.*, **37**, No. 1, 157-208.
- DALL, W. H. 1905. Notes on some preoccupied names of mollusks (*Patinigera*). *Nautilus*, **18**, No. 10, 113.
- DAYTON, P. K., ROBILLIARD, G. A. and R. J. PAINE. 1970. Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. (In HOLDGATE, M. W., ed. *Antarctic ecology*. London, Academic Press, 244-58.)
- DELL, R. K. 1964. Marine Mollusca from Macquarie and Heard Islands. *Rec. Dom. Mus., Wellington*, **4**, No. 20, 267-301.

- EVERSON, I. 1970. The population dynamics and energy budget of *Notothenia neglecta* Nybelin at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 23, 25–50.
- FISCHER, A. G. 1961. Latitudinal variations in organic diversity. *Am. Scient.*, **49**, No. 1, 50–74.
- HARDY, A. C. 1967. *Great waters*. London, Collins.
- HOLDGATE, M. W. 1964. Terrestrial ecology in the maritime Antarctic. (In CARRICK, R., HOLDGATE, M. and J. PRÉVOST, ed. *Biologie antarctique*. Paris, Hermann, 181–94.)
- HOMBRON, J. B. and G. A. JACQUINOT, 1841. Suite de la description de quelques mollusques provenant de la campagne de l'*Astrolabe* et de la *Zélée*. *Annls Sci. nat.*, Sér. 2, **16**, 190–92.
- JENKINS, D., WATSON, A. and G. R. MILLER. 1963. Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.), in north-east Scotland. *J. Anim. Ecol.*, **32**, No. 2, 317–76.
- JONES, N. S. 1946. Browsing of *Patella*. *Nature, Lond.*, **158**, No. 3980, 557–58.
- JONES, N. V. 1963. The sheathbill, *Chionis alba* (Gmelin), at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 2, 53–71.
- KANWISHER, J. W. 1955. Freezing in intertidal animals. *Biol. Bull. mar. biol. Lab., Woods Hole*, **109**, No. 1, 56–63.
- . 1959. Histology and metabolism of frozen intertidal animals. *Biol. Bull. mar. biol. Lab., Woods Hole*, **116**, No. 2, 258–64.
- . 1966. Freezing in intertidal animals. (In MERYMAN, H. T., ed. *Cryobiology*. New York and London, Academic Press, 487–94.)
- KINNE, O., ed. 1970. *Marine ecology. Vol. I. Pt. 1*. London, Wiley-Interscience.
- KNOX, G. A. 1960. Littoral ecology and biogeography of the southern oceans. *Proc. R. Soc., Ser. B*, **152**, No. 949, 577–624.
- KRISTENSEN, I. 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. *Archs néerl. Zool.*, **12**, No. 3, 351–453.
- LACK, D. 1966. *Population studies of birds*. Oxford, Clarendon Press.
- LEWIS, A. H. 1969. *The cold tolerance of intertidal animals*. M.Sc. thesis, University of Wales, 33 pp. [Unpublished.]
- MADSEN, H. 1936. Investigations on the shore fauna of East Greenland, with a survey of other Arctic regions. *Meddr Grønland*, **100**, No. 8, 1–79.
- MATTHEWS, D. H. and D. H. MALING. 1967. The geology of the South Orkney Islands: I. Signy Island. *Falkland Islands Dependencies Survey Scientific Reports*, No. 25, 32 pp.
- MOORE, H. B. 1934. The relation of shell growth to environment in *Patella vulgata*. *Proc. malac. Soc. Lond.*, **21**, No. 3, 217–22.
- MORTON, J. E. 1958. *Molluscs*. London, Hutchinson.
- NEWCOMBE, C. L. 1935. Certain environmental factors of a sand beach in the St. Andrews region, New Brunswick, with a preliminary designation of the intertidal communities. *J. Ecol.*, **23**, No. 2, 334–55.
- ORTON, J. H. 1928. Observations on *Patella vulgata*. Part II: Rate of growth of shell. *J. mar. biol. Ass. U.K.*, **15**, No. 2, 863–74.
- . 1932. Studies on the relation between organism and environment. *Proc. Trans. Lpool biol. Soc.*, **46**, No. 1, 1–16.
- PETERSEN, G. H. 1962. The distribution of *Balanus balanoides* (L.) and *Littorina saxatilis* Olivi, var. *groenlandica* Mencke, in northern West Greenland with remarks on some causative factors. *Meddr Grønland*, **159**, No. 9, 1–42.
- POWELL, A. W. B. 1951. Antarctic and subantarctic Mollusca: Pelecypoda and Gastropoda. 'Discovery' Rep., **26**, 47–196.
- . 1960. Antarctic and subantarctic Mollusca. *Rec. Auckland Inst. Mus.*, **5**, Nos. 3–4, 117–93.
- . 1965. Mollusca of Antarctic and subantarctic seas. (In OYE, P. VAN and J. VAN MIEGHEM, ed. *Biogeography and ecology in Antarctica. Monographiae biol.*, **15**, 333–80.)
- PRICE, J. H. and P. REDFEARN. 1968. The marine ecology of Signy Island, South Orkney Islands. (In *Symposium on Antarctic oceanography. Santiago, Chile, 13–16 September 1966*. Cambridge, Scott Polar Research Institute, 163–64.)
- RUSSELL, E. S. 1907. Environmental studies on the limpet. *Proc. zool. Soc. Lond.*, **77**, Pt. 2, 856–70.
- . 1909. The growth of the shell of *Patella vulgata* L. *Proc. zool. Soc. Lond.*, **79**, Pt. 1, 235–53.
- SMIDT, E. L. B. 1944. The effects of ice winters on marine littoral faunas. *Folia geogr. dan.*, **2**, No. 3, 1–36.
- SMITH, J. E. and G. E. NEWELL. 1955. The dynamics of the zonation of the common periwinkle (*Littorina littorea* (L.)) on a stony beach. *J. Anim. Ecol.*, **24**, No. 1, 35–56.
- SOUTHWARD, A. J. 1956. The population balance between limpets and seaweeds on wave-beaten rocky shores. *Rep. mar. biol. Stn Port Erin*, No. 68, 20–29.
- STEPHENSON, T. A. and A. STEPHENSON. 1954. Life between tidemarks in North America: III. Nova Scotia and Prince Edward Island. *J. Ecol.*, **42**, No. 1, 14–70.
- STREBEL, H. 1908. Die Gastropoden. *Wiss. Ergebn. schwed. Südpolarexped.*, Bd. 6, Lief. 1, 112 pp.
- THORPE, W. H. 1956. *Learning and instinct in animals*. Cambridge, Cambridge University Press.
- THORSON, G. 1944. The zoology of East Greenland. Marine Gastropoda Prosobranchia. *Meddr Grønland*, **121**, No. 13, 1–181.
- WILLCOX, M. A. 1905. Biology of *Acmaea testudinalis* Muller. *Am. Nat.*, **39**, No. 461, 325–33.
- WILLIAMS, R. J. 1966. Studies on the freezing resistance of intertidal molluscs. *Cryobiology*, **2**, No. 6, 299–300.
- . 1967. Cryoprotective agents in intertidal molluscs. *Cryobiology*, **3**, No. 5, 370.
- WYNNE-EDWARDS, V. C. 1962. *Animal dispersion in relation to social behaviour*. Edinburgh, Oliver and Boyd.

APPENDIX A

PREDATION

Predation in the littoral zone

Common predators of limpets in the littoral zone are the Dominican gull (*Larus dominicanus* Lichtenstein) and the sheathbill (*Chionis alba* (Gmelin)). Gulls obtain limpets by knocking them off the rocks and consuming them whole; the shells are regurgitated later. At the largest gull colony on Signy Island there are very large numbers of empty shells, and scattered over the island smaller groups may be found. Sheathbills prey on limpets especially during spring and autumn (Jones, 1963). The bird prises them from the rocks with its bill and removes the flesh from the shell by vigorous shaking or by holding the shell on the ground with the foot and pecking out the contents. Both of these birds, especially the gulls, take many limpets, but it is not known whether they have a significant effect on the littoral population.

Predation in the sub-littoral zone

Three species which prey on limpets in the sub-littoral zone are the fish *Notothenia neglecta* Nybelin, the starfish *Cryptasterias turqueti* (Koehler) and the prosobranch *Trophon cinguliferus* Martens and Pfeffer. The stomach contents of *Notothenia* have occasionally been found to contain limpet shells (personal communication from I. Everson), but it is not known how it obtains limpets or how it deals with the empty shells. *Cryptasterias* has been observed preying on limpets in an aquarium, and predation by *Trophon* has also occurred in the laboratory. The whelk first mounts the shell of a living limpet and tries to insert its proboscis under the rim of the shell and into the soft parts. After the proboscis has been inserted the limpet may release itself from the rock, in which case, if the whelk can remain on the shell, the limpet is easily consumed. Neither of these two invertebrate predators was found to be common (in Factory Cove), or appeared to take much advantage of the considerable numbers of limpets on the sub-littoral rocks. Data comparing the effects of predation in the littoral and sub-littoral zones are not available.

Avoiding reaction to invertebrate predators

Many molluscs exhibit escape reactions to predators (Charles, 1966) and *Patinigera polaris* exhibits such reactions on contact with the invertebrate predators mentioned above. An active limpet carries out searching movements with the head and mantle tentacles and, if these contact a predator, they are withdrawn quickly. In the aquarium this was seen to happen up to three times in succession. The limpet then swings its shell away from the predator and crawls away. After contacting prospective prey, *Cryptasterias* may pursue it, but no such pursuit by *Trophon* was observed. The whelk moves with its head well inside its shell and can approach a limpet quite closely because the avoiding reaction does not appear to be elicited by the predator's shell. The avoiding reaction was not elicited by other invertebrates in the aquarium.

APPENDIX B

FOOD

Patellid limpets are usually littoral herbivores (Morton, 1958), unselectively browsing on algae attached to the substrate. The broad vertical distribution of *Patinigera polaris* includes many different species of algae, and so gut contents and faeces of limpets were investigated to discover whether *P. polaris* was also unselective. The preparations were examined for algae by J. H. Price (Table VII) and it appears from the results that *P. polaris* is an unselective grazer. However, many common algae at Signy Island (e.g. *Desmarestia* species) were not found, so a more detailed investigation is required before a definite conclusion can be reached. Non-algal material included hydroid tissue, wood fragments and rock particles.

TABLE VII. GUT AND FAECES CONTENTS OF *Patinigera polaris*

I. Littoral zone

- Ulothrix* and *Urospora*
- Diatoms (free-living and colonial)
- Unicellular green alga (? pleurococcoid)
- Lone spore

II. Sub-littoral zone

- Diatoms
- Filamentous green alga (not *Ulothrix* or *Urospora*)
- Early stage of red algal cushion-forming spore
- Rasped surface of red alga
- Lithothamnion* and *Lithophyllum*
- Phyllogigas*
- Brown algal spores
- Green algal spores

APPENDIX C

HOMING BEHAVIOUR

Homing in limpets is a well-known phenomenon (reviewed by Thorpe (1956) and Morton (1958)). Limpets which exhibit this behaviour return to the same spot after feeding excursions. Here the shell may fit the substrate, rendering the animal less vulnerable to desiccation and bird predation. This aspect of the behaviour of limpets in the littoral zone at Signy Island was investigated in the summer of 1964-65. Initially, limpets were marked with paint so that their movements could be followed, but the animals seemed to react to this treatment, and also the paint blistered off. Photographic records were therefore used. Three rocks near M.T.L. were photographed regularly and the limpets present were counted and their positions noted. The results are presented in Table VIII. From these observations it appears that at Signy Island individual limpets do not return to the same spot between feeding excursions.

TABLE VIII. NUMBERS OF LIMPETS ON THE THREE ROCKS PHOTOGRAPHED AT LOW TIDE IN JANUARY AND FEBRUARY 1965

Date	January	18	19	20	21	22				
Rock 1		13	12	13	15	—				
Rock 2		23	26	22	13	—				
Rock 3		—	3	8	8	5				
During neap tides photography ceased but it was continued on 29 January.										
Date	January	29	30	31	February		1	2	3	5
Rock 1		2	1	1			0	1	0	0
Rock 2		4	3	0			3	4	1	4
Rock 3		10	10	8			—	7	9	—