NATURAL SELECTION IN ANTARCTIC LIMPETS

By R. J. BERRY* *and* P. J. RUDGE*

ABSTRACT. Antarctic shores are regularly scoured by ice and are bare of all but a few algae and lichens, limpets (*Patinigera polaris*), and an ephemeral diatom fauna. The ability of limpets to survive in these conditions implies a high degree of adaptation and hence the capability to respond to intense selection pressures. The study reported was an investigation of these putative forces of selection.

Samples of limpets were collected from the littoral zone in summer from 14 sites, ranging from Marguerite Bay (lat. 68°S.) to the Falkland Islands (lat. 51°S.) (where *P. polaris* is replaced by *P. aenea*). The variance of a shell character in young and old members of each sample was compared. In most comparisons the older specimens had a lower variance than the younger. In general, the greater the exposure of the shore from which collections were made to wave action, the greater the reduction in variance. There was no correlation between variance reduction and length of ice cover.

The coefficient of variability of Antarctic limpets is much greater than British littoral whelks but the variation seems to be used in the same way—as a means of adaptation in life to wave action. It seems probable that *P. polaris* escapes from sea ice by migrating into deeper water (as suggested by Walker (1972)) rather than adapting to it.

THE littoral zone of the Antarctic is inimical to living organisms. The main problem to colonizers is the recurring scouring ice, presenting a major physical problem to all but the most ephemeral animals and plants. Consequently, the shores are barren of the wide variety of life supported in temperate and sub-Antarctic regions (Knox, 1968), even though a rich and varied flora and fauna exists in sub-littoral regions (e.g. Price and Redfearn, 1968). It is true that there is a well-developed diatom flora on rocky shores (Delépine and Hureau, 1963) (and on the underside of fast ice (Bunt, 1964*a*, *b*)), but larger organisms are represented mainly by filamentous green algae (principally *Ulothrix australis* or *Urospora penicilliformis*), together with encrusting red algae, *Lithothamnion* and *Lithophyllum* species. Lichens and *Porphyra* may occur in the upper regions. The most obvious animal by far is the patelloid limpet *Patinigera* (*Patella*) *polaris* (Hombron and Jacquinot). In other words, the typical Antarctic shore is characterized merely by a thin algal growth and a variable concentration of limpets (e.g. Hedgepeth, 1969; Dayton and others, 1970; Gruzov and Pushkin, 1970; Propp, 1970; etc.).

The presence of animals the size of limpets (they range up to *c*. 6 cm. long and 2 cm. high) in such a biologically uninviting environment implies a degree of adaptation unnecessary in more benign climates, and hence the toleration of intense selective pressures too great for the other littoral forms found in profusion on nearby more clement shores (Knox, 1960, 1968; Kenny and Haysom, 1962; Bennett, 1971; Strange, 1972). This paper describes an investigation into these putative forces of selection. It follows a study on dog whelks (*Nucella lapillus* (L.)) in British waters (Berry and Crothers, 1968) in which it was shown that intensities of selection of up to 90 per cent were acting on populations on shores exposed to heavy wave action, whereas no selection was demonstrable in populations on sheltered shores. This work had been based in turn on an interpretation of Weldon (1901) that reduction in variance of a heritable character during the life of an organism is an indication of the operation of natural selection, and calculations by Haldane (1959) that the amount of variance reduction is a measure of the intensity of selection.

MATERIAL COLLECTED

The limpets studied were mainly of *Patinigera polaris*. This is a circum-polar species restricted to shores south of the Antarctic Convergence and occurring from the water's edge to depths of *c*. 60 m. (Powell, 1951). A benthic subspecies (*P. polaris concinna* Strebel) has been described at below 15 m. around South Georgia. Powell (1951) recognized eight species in the genus covering most of the Antarctic and sub-Antarctic including southern South America. The present study has been concerned with *P. polaris* from South Georgia, the South Orkney Islands, South Shetland Islands and the Antarctic Peninsula, but it also includes material of the very similar *P. aenea* (Martyn) from the Falkland Islands.

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* Royal Free Hospital School of Medicine, London, W.C.1.

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Collections were made of limpets at or just below the sea-level at 14 sites from the Falkland Islands (lat. 51°S.) to Stonington Island (lat. 68°S.). No limpets were found on the Puffball Islands in Marguerite Bay, about 64 km. south of Stonington Island, and in an area rarely free from ice. In all places, specimens were found both on exposed rock faces and in rock cracks and under boulders. Because of the irregular tidal movement, it was difficult to determine the upper limit of the species, but Hedgepeth (1969) noted that it occurs sparsely several feet above high-tide level on wave-swept rocks near Palmer station (lat. 64°S.). *P. polaris* occurs at higher densities in the sub-littoral than the littoral proper; Hedgepeth recorded densities of *c.* 200/m.^{2} at depths of 2–3 m. In general, the numbers at higher levels decreased with latitude south. For example, on Signy Island (lat. 60°S.) limpets occurred commonly to mid-tide level in mid-summer, whereas in Marguerite Bay (lat. 68°S.) there were few above low-water mark.

One of the main mechanisms by which limpets survive ice scouring in the winter is by seasonal migration into deeper water. Walker (1972) noted that the littoral density at Signy Island (South Orkney Islands) decreased in March–April when the air temperature was falling, wave action increasing and bird predation greater than earlier in the summer, although at a time before the formation of sea ice. At least some of this fall in numbers he attributed to increased mortality (more empty shells were found at that season than at other times), but he believed from biometrical and ecological evidence that many individuals migrated into deeper water. He observed no littoral limpets in the spring when the fast ice disappeared (although winter diving showed that there was some upward movement under the ice after the formation of fast ice). From a longitudinal study, Walker (1972) concluded that there are two discrete populations of *P. polaris* on Signy Island: a seasonally migrating one and one which remains submerged in the sub-littoral throughout the year. The present study concerns only specimens collected during the summer in the littoral (i.e. members of Walker's migrating group). This means that only the more environmentally stressed were sampled and that there should be no confusion with the non-migrating "race".

All the collections described in this paper were made by one of us (R.J.B.) during a cruise of R.R.S. *John Biscoe* in January–March 1969, with the exception of that from South Georgia which was made by a British Antarctic Survey party in 1970.

The sites from which limpets were collected were all rock-strewn shores. They were (Fig. 1):

1. *Stonington Island* (lat. 68°11′S., long. 67°00′W.). In front of the British station, from a shore facing slightly south of west into Marguerite Bay, sheltered on the south by Neny Island.
2. *Horseshoe Island* (lat. 67°51′S., long. 67°12′W.). On the south side of the small Sally Cove (*c.* 1·6 km. across), sheltered on the west by Horseshoe Island and north by Pourquoi Pas Island.
3. *Adelaide Island* (lat. 67°46′S., long. 68°54′W.). Near the southern tip of Adelaide Island, open to the Bellinghausen Sea to the west but protected by Avian Island 3·2 km. to the south.
4. *Argentine Islands* (lat. 65°15′S., long. 64°16′W.). From the west coast of Galindez Island, exposed to the open sea on all sides but the east.
5. *Foyn Harbour* (lat. 64°33′S., long. 62°01′W.). The collection was made on the west side of Nansen Island in Wilhelmina Bay in Gerlache Strait, protected from the open sea by Brabant Island to the north and Anvers Island to the west at a distance of under 8 km.
6. *Intercurrence Island* (lat. 63°55′S., long. 61°24′W.). From the east side of one of a small group of scattered islands in Palmer Archipelago south of Hoseason Island.

7 and 8. *Deception Island* (South Shetland Islands) (lat. 62°59′S., long. 60°34′W.). Two populations were sampled here:

Outside—from the south-west corner of Deception Island, which is the southernmost island of the South Shetland Islands group.

Inside lagoon—in the sheltered water of the crater lake of Deception Island, near Lighthouse Point. This was as far away from the open sea that limpets were found. (The previous year there had been a volcanic eruption, resulting in substantial thermal and chemical pollution of the lagoon.)

9. *Signy Island* (South Orkney Islands) (lat. 60°43′S., long. 45°36′W.). From a south-facing shore near the British station in the sheltered waters of Borge Bay, screened to the north by Coronation Island about 8 km. away.
10. *Bay of Isles, South Georgia* (lat. 54°02′S., long. 37°20′W.). The Bay of Isles faces east of north. The collection was made from a west-facing shore, with a maximum reach of wave action of less than 3·2 km. The whole bay is sheltered with much kelp.

The three Marguerite Bay sites (1–3) are subject to ice at the shoreline from April until January in most years; the Argentine Islands have an ice cover only slightly less; Foyn Harbour has ice from the end of May to October; Intercurrence Island may have open water throughout the year; the South Shetland and South Orkney Islands are iced from about mid-June to mid-November (Heap, 1963). Ice cover varies considerably from year to year;

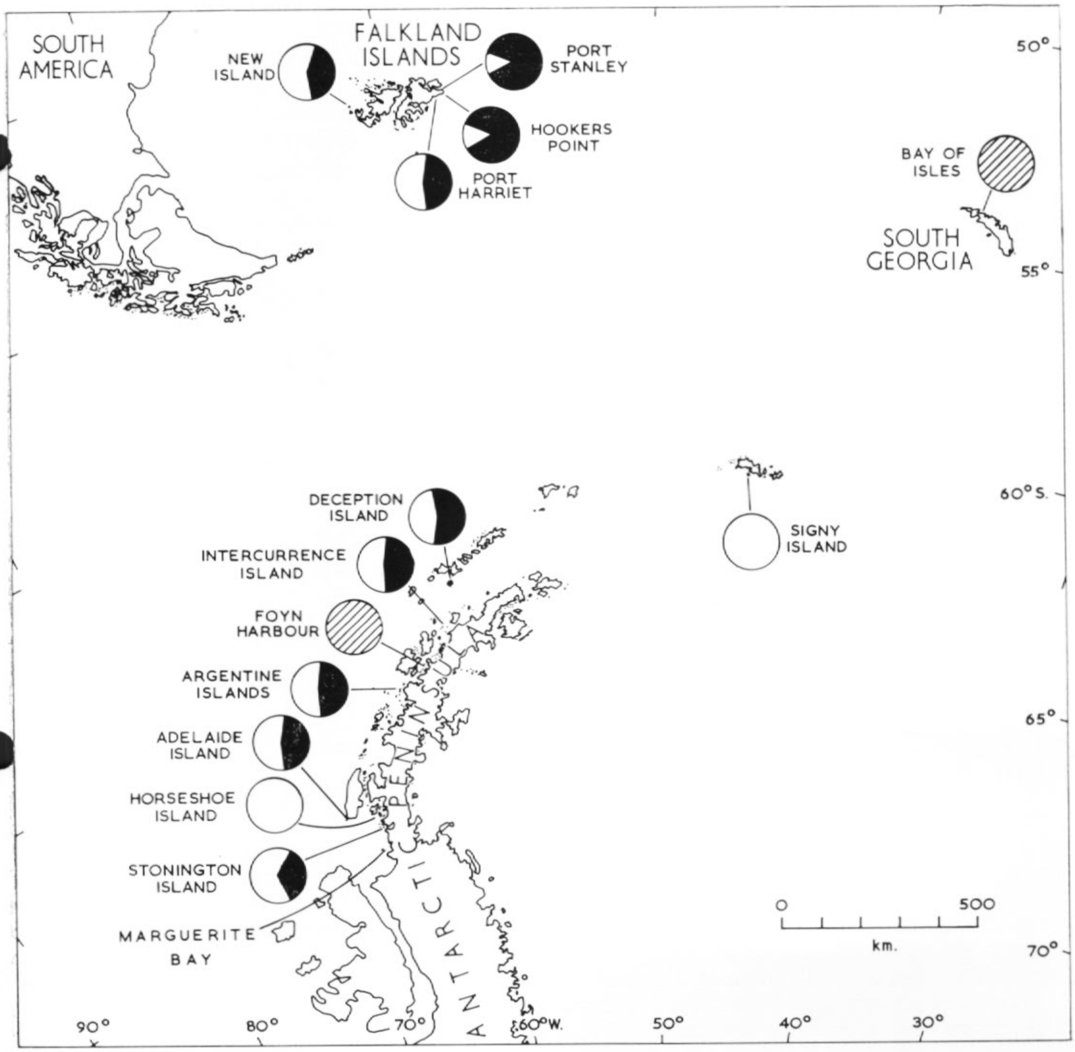

Fig. 1. Map showing sites from which limpet collections were made. The proportion of black in each circle represents the reduction in variance in old as compared with young members of the same sample. The cross-hatched circles are samples where the older group was more variable than the younger.

in the winter before the collections were made (1968) there was less sea ice than in the immediately preceding years.

In addition to the ten collections of *P. polaris*, four collections of *P. aenea* were made from the Falkland Islands. Three of these were from East Falkland in the vicinity of Port Stanley (lat. 51°42′S., long. 57°52′W.); the fourth was from New Island (lat. 51°43′S., long. 61°16′W.), which lies off the west coast of West Falkland:

11. *Port Stanley*. To the east of the town, opposite the entrance to the harbour.
12. *Hookers Point*. An exposed westerly facing promontory on the south-easterly coast of East Falkland.
13. *Port Harriet*. A more sheltered shore on the south side of Port Harriet point.
14. *New Island*. From the east (sheltered) coast, near the settlement. Nevertheless, this site was widely exposed to easterly waves.

No attempt was made to gather a random sample at each site. The design of experiment involved a comparison of young with old individuals. In practice, this meant special care to collect young (i.e. small) limpets. No colour or banding variants were found.

Methods

Limpets collected were fixed in alcohol, and four parameters that could be accurately and easily measured were determined on each specimen: maximum length, transverse diameter (i.e. width), height and weight (including soft parts) (Fig. 2). A fifth measurement (shell thickness at anterior end) was attempted but standards of consistency were not good and this was discontinued. All of the measurements were made by one of us (P.J.R.).

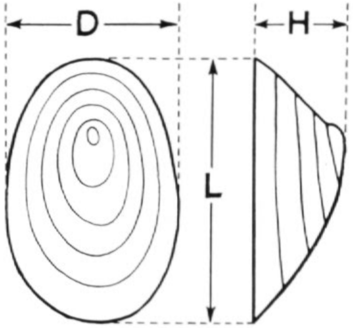

Fig. 2. Shell of *Patinigera polaris* showing the measurements made.

The study was designed along the lines and as an extension of the work of Berry and Crothers (1968, 1970) on the amount of variation in a littoral mollusc and its elimination at different stages of the life cycle in relation to environmental stress. This made it necessary to divide each of the limpet samples into groups of different age.

Following work on *Patella* spp. in Britain (Orton, 1928; Orton and others, 1956; personal communication from A. J. Southward), the limpets were aged by plotting frequency histograms of each sample against the four parameters measured. This is a similar but less sophisticated method to the one advocated by Harding (1949). Each sample was found to be composed of three unequal groups. In general, the length histograms gave the best separations. Uncertain specimens (i.e. individuals intermediate between two groups) were allotted to one of the three groups by their position in the other histograms. It was found that all specimens could be unequivocally assigned to one of the three classes by this method.

The three groups have been named I, II and III, representing the smallest, middle and largest size classes, respectively. It was assumed that these classes are also age classes, although there is no evidence whether they represent year groups or (more likely) juvenile, adult and post-mature (or sex-changed; Orton and others, 1956) categories. Notwithstanding, this is clearly an objective method of distinction which must be largely age related.

TABLE I. MEAN LENGTH (*L*), DIAMETER (*D*), HEIGHT (*H*) (mm.) AND WEIGHT (*W*) (g.) OF ANTARCTIC LIMPETS

	Age class I (*youngest*)					*Age class II*					*Age class III* (*oldest*)				
	N	*L*	*D*	*H*	*W*	*N*	*L*	*D*	*H*	*W*	*N*	*L*	*D*	*H*	*W*
Stonington Island	32	19·1±3·3	13·1±2·4	4·7±1·0	0·5±0·2	74	36·2±2·7	25·3±2·0	10·6±1·1	4·0±0·8	29	47·7±3·1	34·0±2·5	16·1±1·7	9·4±2·0
Horseshoe Island	39	19·1±2·1	13·0±1·5	5·4±0·7	0·5±0·2	114	29·7±2·5	20·6±1·8	9·1±1·1	2·0±0·5	19	42·8±2·7	30·9±2·4	14·4±1·4	6·2±1·6
Adelaide Island south	76	18·3±1·5	12·6±0·9	5·1±0·5	0·5±0·1	154	24·9±1·5	17·1±1·0	7·5±0·6	1·5±0·2	98	33·9±3·6	23·8±2·6	11·3±1·6	4·1±1·5
Argentine Islands	50	10·9±1·6	7·4±1·2	2·5±0·4	0·08±0·03	82	19·9±1·8	13·6±1·2	5·3±0·6	0·6±0·2	69	31·8±3·9	22·4±2·8	11·0±2·3	3·5±1·6
Foyn Harbour	58	12·8±1·0	8·7±0·7	3·3±0·3	0·1±0·03	95	17·1±0·6	11·7±0·4	5·0±0·3	0·4±0·07	59	23·1±2·5	16·2±2·0	7·7±1·0	1·2±0·4
Intercurrence Island	175	19·4±2·8	13·2±1·9	5·4±1·1	0·7±0·2	43	27·2±0·7	19·4±0·7	9·1±0·3	2·1±0·1	49	34·6±2·5	25·0±2·0	13·2±1·7	4·6±1·2
Deception Island:															
Outside	49	28·9±1·9	20·2±1·2	8·9±0·8	2·4±0·4	64	33·8±0·7	23·9±0·6	11·5±0·6	4·0±0·4	28	40·2±1·8	29·0±1·2	15·1±1·2	7·5±1·3
Inside lagoon	122	14·4±2·7	10·0±1·9	3·8±0·8	0·2±0·1	185	24·0±1·4	16·7±1·0	7·5±0·6	1·1±0·2	92	33·5±3·4	23·7±2·7	12·0±1·9	3·7±1·5
Signy Island	52	24·8±1·8	16·7±1·3	7·4±0·7	1·1±0·2	126	30·6±1·1	21·9±0·9	10·8±0·7	2·5±0·3	32	36·8±2·3	26·3±1·9	14·5±1·1	5·5±1·4
Bay of Isles, South Georgia	19	19·7±6·7	13·0±4·5	4·8±1·9	0·7±0·4	22	31·2±1·4	21·1±0·9	9·1±0·8	2·5±0·4	23	39·8±3·7	28·3±2·8	13·4±2·3	6·0±2·0
Falkland Islands:															
Port Stanley	82	16·6±3·9	11·8±2·7	4·3±1·0	0·3±0·1	82	31·4±2·2	22·8±1·7	10·2±1·0	2·4±0·5	36	48·1±5·2	35·3±3·7	19·0±2·4	9·4±3·2
Hookers Point	146	11·0±2·3	8·2±1·8	4·1±1·1	0·2±0·1	36	22·1±2·9	16·7±1·5	7·2±1·0	1·3±0·3	66	39·3±4·1	28·8±3·0	13·6±2·6	7·0±2·8
Port Harriet	166	12·6±1·6	9·3±1·2	4·6±0·8	0·2±0·09	21	18·0±1·4	13·4±0·9	6·8±1·1	0·7±0·1	41	33·6±5·1	25·0±4·0	11·3±2·7	4·0±2·1
New Island	121	9·5±2·2	6·7±1·4	2·8±0·7	0·07±0·05	62	17·1±1·1	11·9±0·8	4·2±0·4	0·3±0·09	195	34·5±5·1	26·0±4·3	9·6±2·6	3·3±2·6

RESULTS

The means and standard deviations of the four parameters measured are given in Table I for the three size groups of each sample. Since the object was to compare the variance of different age classes, it was desirable to find some character which had a similar mean in all populations and age classes. From a series of plots of one character against another, it seemed that the traits which were most use for this purpose were the ratios of length (L) over transverse diameter (D), and height (H) over the cube root of weight (W). However, the mean of the latter character tended to rise in most age classes within a population and was higher in the Falkland Islands samples than in *P. polaris* proper. Hence, only the ratio L/D was considered. This was determined for each specimen and the mean and variance for each age class was calculated (Table II). Omitting the Falkland Islands samples which may be presumed to be different, the average of the means decreases slightly from size classes I to III:

Size class I	$1\cdot465\pm0\cdot023$
Size class II	$1\cdot442\pm0\cdot022$
Size class III	$1\cdot404\pm0\cdot017$

It seemed reasonable to neglect these small differences. Within each size class, the mean values were homogeneous (χ^2_9 for heterogeneity $2\cdot56$, $3\cdot64$ and $2\cdot02$, respectively). Bartlett's test for variance heterogeneity showed considerable diversity (χ^2_9 for class I was $38\cdot1$, χ^2_{13} when the Falkland Islands samples were included was $212\cdot0$; for class II, the values were $36\cdot4$ and $201\cdot6$, respectively; and for class III, $77\cdot7$ and $122\cdot5$. At the 5 per cent probability level, χ^2_9 has a value of $16\cdot9$, and χ^2_{13} one of $22\cdot4$). The variance ratio (F) values and their formal "significance" are also given ($F_{\mathrm{I,II}}$, $F_{\mathrm{II,III}}$ and $F_{\mathrm{I,III}}$). In two cases (Foyn Harbour and Bay of Isles), there was a significant increase in variance between small and large groups; in all other samples there was either no significant change of variance (three samples) or a reduction (nine cases). Out of the 42 variance comparisons, 18 represented a change with a probability of chance occurrence of less than 5 per cent, and all but four of these showed a reduction of variance.

Finally, there have been a number of reports that the height (H) to length (L) ratio of shells varies with habitat (Russell, 1907, 1909; Orton, 1928, 1932; Moore, 1934). Walker (1972) concluded that the H/L ratio gave some measure (at least among the older individuals) of the intensity of wave action. Accordingly, the H/L values have been determined for all of the sub-samples (Table III).

DISCUSSION

The investigation began from the premise that the intensity of environmental stress on littoral organisms increased to an absolute limit where ice persists throughout the year; in other words, if one studies populations exposed to increasing environmental pressures, one is likely to encounter growing selective pressures. It was hoped to determine whether this led to increased developmental homoeostasis (i.e. a progressive reduction in stabilizing selection) or increased variation (i.e. selection for the mean or average becoming more pronounced). Tables I and II are arranged with the southernmost and notionally most stressed populations first, and thence populations subjected to decreasing ice exposure as duration of ice cover becomes less. Ice conditions vary considerably from year to year, but, if there is any correlation between ice cover and genetical effect, it should be apparent from the tables.

There is no obvious tendency for either increased variance southwards along the Antarctic Peninsula or for any increased selection. As expected, and as found in the comparable studies of Berry and Crothers (1968, 1970), the usual happening was a reduction of variance during life. A significant reduction took place in nine of the 14 populations; in two samples (Foyn Harbour and the Bay of Isles) there was apparently an increase of variance between young and old members of the population, whilst in three (Stonington, Horseshoe and Signy Islands) there was no significant change. Two of these last (Stonington and Horseshoe Islands) were the southernmost sampled and the most subject to ice scouring, but the next two populations, the Adelaide Island and Argentine Islands samples, had an overall halving of the variance, whereas the Foyn Harbour and the ice-free South Georgia samples both apparently increased their variance four-fold. The apparently anomalous situation of a putative inherited variant

TABLE II. MEANS AND STANDARD DEVIATIONS OF THE RATIO L/D IN ANTARCTIC LIMPET SAMPLES

	N	*Age class I (youngest)*	N	*Age class II*	N	*Age class III (oldest)*	$F_{\mathrm{I,\,II}}$	$F_{\mathrm{II,\,III}}$	$F_{\mathrm{I,\,III}}$
Stonington Island	32	1·456±0·042	74	1·430±0·043	29	1·402±0·034	−1·069	1·612	1·509
Horseshoe Island	39	1·469±0·041	114	1·143±0·040	19	1·385±0·051	1·050	−1·625	−1·548
Adelaide Island south	76	1·451±0·055	154	1·455±0·044	98	1·424±0·040	1·549*	1·219	1·888‡
Argentine Islands	50	1·472±0·056	82	1·457±0·047	69	1·421±0·041	1·424	1·341	1·910*
Foyn Harbour	58	1·466±0·037	95	1·457±0·056	59	1·423±0·068	−2·275‡	−1·468	−3·341‡
Intercurrence Island	175	1·470±0·049	43	1·404±0·042	49	1·382±0·035	1·393	1·373	1·913†
Deception Island									
Outside	49	1·430±0·048	64	1·412±0·030	28	1·388±0·034	2·618‡	−1·281	2·044*
Inside lagoon	122	1·439±0·064	185	1·439±0·039	92	1·418±0·041	2·647‡	−1·105	2·396‡
Signy Island	52	1·486±0·039	126	1·448±0·032	32	1·399±0·041	1·485	−1·642	−1·097
Bay of Isles, South Georgia	19	1·510±0·044	22	1·476±0·038	23	1·393±0·089	1·267	−5·300‡	−4·184‡
Falkland Islands:									
Port Stanley	82	1·402±0·077	82	1·378±0·033	36	1·360±0·036	5·387‡	−1·189	4·530‡
Hookers Point	146	1·336±0·095	36	1·325±0·105	66	1·365±0·031	−1·282	9·094‡	7·094‡
Port Harriet	166	1·352±0·088	21	1·325±0·084	41	1·344±0·046	1·038	1·831	1·901†
New Island	121	1·417±0·083	62	1·434±0·067	195	1·331±0·063	1·490	1·165	1·736‡

Negative values of the F ratio indicate where there has been an *increase* in variance from younger to older class.

* Corresponds to log F/standard error F of 1·96–2·57 ($P = 0·05$–$0·01$ per cent); † to 2·58–3·28 ($P = 0·01$–$0·001$ per cent); ‡ to 3·29 + ($P < 0·01$ per cent).

Table III. Means and standard deviations of the ratio H/L in Antarctic limpet samples

	Age class I (youngest)		*Age class II*		*Age class III (oldest)*	
	N		*N*		*N*	
Stonington Island	32	0·247±0·019	74	0·294±0·0281	29	0·339±0·031
Horseshoe Island	39	0·283±0·025	114	0·308±0·025	19	0·337±0·023
Adelaide Island south	76	0·279±0·026	154	0·303±0·028	98	0·335±0·030
Argentine Islands	50	0·235±0·018	82	0·269±0·028	69	0·344±0·047
Foyn Harbour	58	0·261±0·025	95	0·291±0·022	59	0·336±0·032
Intercurrence Island	175	0·279±0·031	43	0·334±0·017	49	0·381±0·031
Deception Island:						
Outside	49	0·310±0·020	64	0·340±0·020	28	0·376±0·026
Inside lagoon	122	0·263±0·023	185	0·316±0·020	92	0·358±0·030
Signy Island	52	0·300±0·018	126	0·353±0·024	32	0·395±0·022
Bay of Isles, South Georgia	19	0·242±0·017	22	0·293±0·024	23	0·335±0·038
Falkland Islands:						
Port Stanley	82	0·264±0·039	82	0·325±0·022	36	0·397±0·035
Hookers Point	146	0·380±0·070	36	0·333±0·068	66	0·345±0·043
Port Harriet	166	0·369±0·056	21	0·383±0·075	41	0·337±0·043
New Island	121	0·302±0·072	62	0·250±0·028	195	0·289±0·021

increasing during life is probably a sign of an ecologically unstable situation for the species, involving local extinction and re-colonization. Berry and Crothers (1970) found irregularities of this sort in estuarine populations of *N. lapillus*, close to the physiological limit of dog whelks.

It is necessary to look for factors other than simple physical stress due to ice action to account for differences between samples. The obvious environmental feature that can account for the results is amount of wave action—the same stress that affects variation in British littoral whelks. The five samples with a variance higher in the large than in the small class are the five which were collected in the most sheltered areas. Conversely, the greatest reduction between large and small was the exposed Hookers Point population from East Falkland. Indeed, all of the Falkland Islands samples showed a high degree of response to wave action in the "furious fifties"; the two Deception Island samples and the ones from Intercurrence Island, Argentine Islands and Adelaide Island (all except possibly the Deception Island lagoon one collected from wave-exposed shores) showed an approximate reduction in variance by one-half. Unfortunately, the data in Table III did not give any pattern which might help in the objective diagnosis of the amount of wave exposure. Nevertheless, the distinction between "clearly" sheltered and "clearly" wave-affected shores was so distinct that there seems no doubt that Antarctic limpets are responding to similar selection pressures as British whelks.

The excoriating effect of ice in the Antarctic littoral has already been described, and it has been recorded that limpets are the only reasonably large animals that occur there. The results presented here do not prove that this successful colonization is the consequence of behaviourally avoiding the environmental stress (i.e. by seasonal migration, as shown by Walker (1972)), but they support the conclusion that a substantial proportion of the genome (Murray and Clarke, 1968) is unaffected by the increasingly severe ice conditions experienced southwards along the Antarctic Peninsula.

Parsons (1971) has set out biochemical and genetical evidences for believing that heterosis may become more pronounced in extreme environments. Dunbar (1968, 1970), supported by Benninghoff (1970), has argued on ecological grounds that increased intraspecific diversity is likely to characterize polar flora and faunas, in contrast to the high degree of speciation found in tropical areas (Lowe-McConnell, 1969). This is certainly true of cold temperate regions (e.g. Kettlewell and others, 1969; Berry and Davis, 1970; Berry and Murphy, 1970), but too few genetical studies have been carried out on Antarctic organisms to permit any generalizations (e.g. Shaughnessy, 1969; Carrick and Ingham, 1970; but see Moore (1964, 1967)). The coefficient of variation of the limpets described in this study is of the order of 20–80 for the three ratios studied (L/D, H/L and $H/W^{\frac{1}{3}}$). This is an order higher than the coefficient of variation of British dog whelks, which is about five. Unfortunately, comparable data for temperate-region limpets do not seem to exist. It would be foolish to lay too much stress on this difference. However, it seems reasonable to assert that limpets in the Antarctic are probably more variable than a successful British littoral mollusc, and that much of this variation is likely to be genetical in origin. Stabilizing selection with an intensity of *c*. 50 per cent was detected as operating on one trait in many of the *P. polaris* populations studied (i.e. variance was reduced by a half); it is quite impossible to say how much selection is acting on other characters, nor to forecast from the evidence available how many of the causes of death involve a genetical component (cf. Berry and Jakobson, 1971).

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