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MARINE BENTHIC POPULATIONS IN ANTARCTICA: PATTERNS AND PROCESSES

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Sampling difficulties have meant that there have been more studies of population patterns than of processes in Antarctic benthos, but a number of generalizations can be made. Benthic marine invertebrates in Antarctica have species/abundance relationships similar to those found in temperate or tropical regions but, several striking examples of gigantism notwithstanding, most species are small. Diversity is generally high, particularly in comparison with the Arctic, although some taxa (for example molluscs) are low in diversity when compared with temperate or tropical faunas. Most species produce larger eggs than related non-polar species, and embryonic development is typically slow. Although the Southern Ocean contains fewer taxa reproducing by feeding pelagic larvae than elsewhere, such larvae are by no means absent. Somewhat paradoxically, these larvae are often released in winter. Post-juvenile growth rates are typically slow, and recruitment rates are slow and episodic. The low temperature slows many biological processes, but other factors are also involved. Ice is an important factor in many biological processes, and the recently described sub-decadal variability in the extent of winter sea-ice is likely to exert a profound influence on benthic ecological processes in Antarctica.

1. INTRODUCTION

It has long been traditional in ecology to draw a distinction between the study of pattern and process. These two complementary approaches provide different information, and require different techniques. In particular studies of ecological processes require time, and in Antarctica, where many ecological processes take place slowly, such studies are necessarily long-term. The particular difficulties of ecological research in Antarctica mean that most studies have been directed at understanding ecological patterns; studies of ecological processes have been less common, although a few generalizations can be made.

Aspects of the biology of Antarctic benthic organisms have been reviewed regularly during the past twenty years [*Hedgpeth*, 1971; *Dell*, 1972; *Clarke*, 1983; *White*, 1984; *Dayton*, 1990; *Arntz et al.*, 1994, in press]. In this review I shall therefore concentrate on selected features of particular interest to the Antarctic Peninsula area. Distributional patterns are discussed elsewhere [*Clarke*, this volume]; in this chapter I shall concentrate on species/abundance patterns and diversity. For ecological processes I shall discuss reproductive ecology, settlement, growth rate and the influences of temperature and sea-ice.

2. ECOLOGICAL PATTERNS

2.1. Ecological Patterns in Antarctic Benthos: Species Size and Abundance

The large-scale and small-scale distributional patterns of Antarctic benthos have been described elsewhere in this volume [*Clarke*, this volume]. Overall, the distribution of Antarctic benthos appears to be governed by substratum, depth, food supply and ice impact.

In general, distributional studies of Antarctic benthos have relied on remote sampling techniques which are essentially destructive (for example, grabs, dredges and bottom trawls). Trawls and dredges in particular suffer from the intense disadvantages of damaging many specimens, destroying any structure in the community (such as tiering or ecological associations) and mixing samples from many different habitats, thereby masking any heterogeneity in the distribution of different assemblages. In shallow waters these difficulties can be overcome by the use of SCUBA techniques, but safety considerations restrict both the depth and the amount of time available underwater and thereby limit the types of study that can be undertaken. Remote photographic techniques were used in deeper waters for some of the

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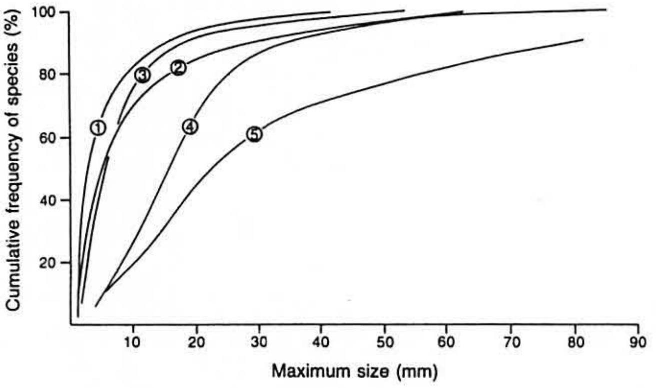

Fig. 1. Cumulative size/frequency spectra for prosobranch gastropods from a variety of polar sites and one tropical beach. The data are plotted as cumulative percentage frequency against maximum size of each species. 1: Shallow water prosobranchs from Signy Island (n = 31 species). 2: All prosobranchs collected at Signy Island (n = 51). 3: Prosobranch gastropods from Terre Adélie (n = 61, *Arnaud*, 1974). 4: Prosobranch gastropods from a tropical beach in Costa Rica (n = 72, from data in *Spight*, 1976). 5: Prosobranch gastropods from the Canadian Arctic (data compiled by *Arnaud* from *Macpherson*, 1971).

earliest studies of Antarctic benthos [*Bullivant & Dearborn*, 1967] but were then largely ignored. Recently, however, German biologists have made extensive use of modern photographic techniques in the Weddell Sea, and these new studies have demonstrated clearly the value of such techniques to marine ecology [*Barthel et al.*, 1991; *Gutt et al.*, 1991; *Gutt and Pipenburg*, 1991; *Ekau and Gutt*, 1991; *Gutt et al.*, 1994].

One of the primary considerations for any ecologist faced with making the choice of sampling gear is that of size selectivity. Photographic techniques are by their very nature limited to epifaunal macroinvertebrates above a certain size. Sampling techniques based on nets will also miss all organisms below a size set by the mesh of net being used, and the mesh size of sieves used for sorting will also influence the size distribution of organisms finally collected. These considerations are of particular relevance to Antarctic benthic communities, for although the small number of Antarctic taxa which are unusually large have long attracted attention [*Arnaud*, 1974] it is now recognized that many Southern Ocean benthic organisms are very small.

Brey and Clarke [1993] collated all the data on the population dynamics of Antarctic marine benthos available up to 1992. Comparison of the polar species with species from temperate and tropical waters indicated no significant difference in mean adult size. This result, however, reflects the tendency of ecologists to choose larger organisms for study rather than the actual size distribution of polar marine invertebrates. Antarctic bivalves and gastropods, for example, have long been known to typically be small [*Nicol*, 1964, 1966, 1978; *Arnaud*, 1974]. True size spectra can only be derived where communities have been sampled exhaustively and quantitatively. Unfortunately few such studies have been undertaken in Antarctica; two are summarized in Figure 1. The cumulative size/frequency spectra show that for at least some taxa, most Antarctic species are small. In the case of gastropods, for example, many Antarctic species are so small as to be missed by some conventional types of sampling or sorting gear. The curve for the Canadian Arctic prosobranchs is distinctly different; in direct contrast to the data for Signy Island, most species included in the data set were large. This may reflect a real difference in the assemblages between these two polar regions, possibly related to evolutionary and biogeographic history [*Dunton*, 1992]; alternatively it may be that the collections on which the curve is based suffered from a sampling bias against the smaller species. Given the extensive ecological differences between the northern and southern polar marine benthos [*Dayton*, 1990], this intriguing difference needs further investigation.

A second feature of importance in describing patterns in animal communities is the distribution of individuals amongst species. Typically species/abundance plots will exhibit a log-normal distribution, and the conventional graphical representation is that proposed by *Preston* [1962]. Construction of Preston plots requires careful attention to sampling techniques: the sampling must be quantitative to ensure all individuals are taken, cover the entire size range, and be sufficiently thorough to ensure that most of the rare species are sampled. Two samples where these criteria have been fulfilled at least approximately are shown in Figure 2. These two plots derive from very different types of sample, but both approximate to the expected conventional log-normal species/abundance distribution. The gastropod data were obtained by pooling a series of repeated monthly samples of obtained by suction sampling of standard sized quadrants (0.25 m^2) in an area of shallow water (2-12 m depth) with a mixed substratum. These data therefore represent a fully quantitative sample for all animals above about 2 mm in size. The Preston plot (Figure 2*a*) nevertheless indicates that these data are subject to sampling error (no data in octaves 3 to 5), and three species were represented by two or fewer individuals.

The amphipod data are from a semi-quantitative study which covered a range of different habitats using a variety of sampling techniques. The full collection was then analyzed by *Thurston* [1972]. The Preston plot (Figure 2*b*) indicates that some rare species were probably missed, and eight species were represented by three or fewer individuals.

Ecologists have long debated the significance of the shape of Preston species/abundance plots. A typical plot of logarithmically transformed data where a large number of individuals have been sampled often looks as though it would be well described by a normal distribution truncated to the left. This truncation (the so-called veil line) is inevitable because those species which are so rare that the expected number of

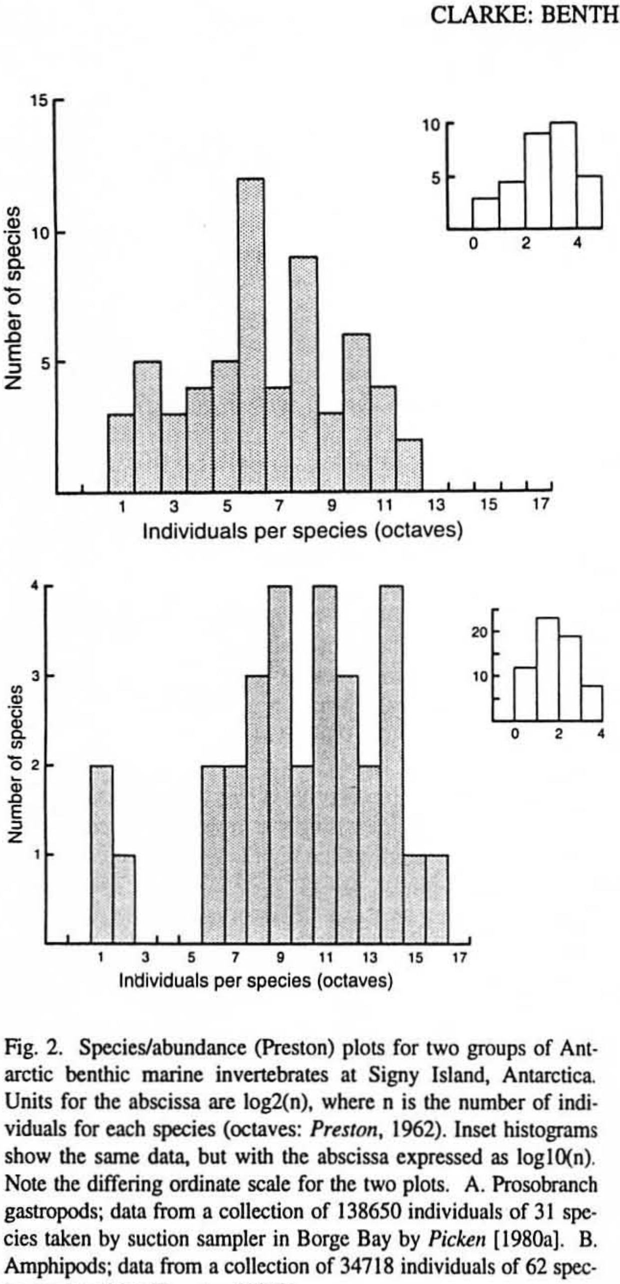

Fig. 2. Species/abundance (Preston) plots for two groups of Antarctic benthic marine invertebrates at Signy Island, Antarctica. Units for the abscissa are log2(n), where n is the number of individuals for each species (octaves: *Preston*, 1962). Inset histograms show the same data, but with the abscissa expressed as log10(n). Note the differing ordinate scale for the two plots. A. Prosobranch gastropods; data from a collection of 138650 individuals of 31 species taken by suction sampler in Borge Bay by *Picken* [1980a]. B. Amphipods; data from a collection of 34718 individuals of 62 species analysed by *Thurston* [1972].

individuals in the sample being plotted is less than one, would be unlikely to be recorded [*Pielou*, 1969]. The position of the veil line would be expected to move to the left as sample size increases [*Magurran*, 1988].

Transforming the data to log10 (n) smooths the distribution by reducing sampling error (Figure 2*a*, 2*b*, insets). This suggests that the gastropod data are well described by a log/normal distribution, although a veil line is clearly apparent, indicating that some very rare species were not sampled. The amphipod data are less well described by a log/normal distribution, exhibiting a distinct tail to the left (Figure 2*b*); this may reflect the semi-quantitative nature of the sampling [*Thurston*, 1972].

The underlying process (or processes) leading to the frequently (but by no means universally) observed log-normal distribution of species' abundances has remained elusive. Although some theoretical models have proved successful under some circumstances, no single model has been found to provide a general description of species/abundance data. In fact the log-normal distribution would be expected as a result of a large number of interacting influences, and hence its general applicability as a descriptor may simply be telling us that the abundance of species in the wild is dictated by many factors and not a single process.

Figure 2 shows the only species/abundance data for Antarctic marine benthos known to the author where a quantitative collection has been accompanied by a thorough taxonomic study. These data indicate that although many species are small, species/abundance distributions are not discernibly different from those found in marine habitats elsewhere [*Gray*, 1987; *Magurran*, 1988; *Gaston*, 1994].

2.2. *Diversity*

For many people, reference to the polar regions conjures pictures of a vast bleak wasteland populated by those few hardy species able to maintain a precarious existence in the face of extremely harsh physical conditions. Although to some extent this is true of the high polar deserts on land, it is certainly not true for the marine environment. Underwater, life is both rich in abundance and taxonomically diverse and although a fully developed hard substratum epifaunal assemblage in Antarctica may not quite rival a tropical reef in diversity it is nevertheless rich in species.

Although the study of Antarctic benthic communities has a long and distinguished history [*Dayton*, 1990] detailed studies of the Arctic fauna have lead to the impression that polar marine communities in general are typically lacking in diversity. The Arctic is indeed impoverished in its marine benthic fauna [*Curtis*, 1975]. This may be related in part to the high riverine sediment input and extreme disturbance, both physically by ice and biologically by marine mammal foraging activity [*Dayton*, 1990], but it is also a consequence of the relative youth of the Arctic marine system [*Dunton*, 1992]. Recently, *Vermeij* [1991] has shown convincingly from molluscan data that colonization of the Arctic basin is currently underway from the north Pacific.

The combination of a depauperate Arctic fauna, and the intensely rich shallow-water faunas of the Indo-West Pacific lead inevitably to a cline in species richness from tropics to poles in the northern hemisphere. This cline is not simply a function of the two end-points, however, for careful examination of several taxa have shown the existence of latitudinal clines in species richness in more temperate areas (for a particularly detailed example see the recent analysis of molluscan distribution along the Pacific seaboard of North America by *Roy et al.*, 1994).

It has long been known that the Southern Ocean supports a rich and diverse benthic fauna [*Dell*, 1972]. Recent work in the deep sea has suggested that broadscale patterns of diversity may differ between the northern and southern hemispheres [*Rex et al.*, 1993] and *Clarke* [1992] raised the question of whether there was any compelling evidence at all for a latitudinal diversity cline in non-calcareous marine taxa. Continuing taxonomic work has confirmed the richness of the Southern Ocean benthic marine fauna [*Poore and Wilson*, 1993; *Brey et al.*, 1994; *Arntz et al.*, in press] and at present there is no convincing evidence for a latitudinal diversity cline in marine shallow-water benthos in the southern hemisphere to match that in the northern hemisphere [*Clarke and Crame*, in press]. Such a cline may well exist, but at present there is no firm evidence either way.

The primary reasons for the striking differences between the diversity of shallow-water marine benthos in the Arctic and the Southern Ocean appear to be the very different tectonic and evolutionary histories of the two regions [*Clarke and Crame*, in press]. Whereas the Arctic basin is relatively young, the Southern Ocean has a long history of evolution *in situ* [*Lipps and Hickman*, 1982; *Clarke and Crame*, 1989, 1992]. There is no evidence that speciation proceeds any more slowly in the polar regions [*Crame and Clarke*, in press] and the frequent climatic cycles which have characterized the Cenozoic history of the high southern latitudes may actually have promoted speciation [*Crame*, 1993, 1995, in press].

Although the overall diversity of the Southern Ocean benthic marine fauna appears to be quite high [*Arntz et al.*, in press], the fauna comprises a mixture of species-poor (for example, gastropod and bivalve molluscs) and species-rich (for example, ascidians, polychaetes, sponges, bryozoans, amphipods and isopods) taxa [*Clarke and Crame*, in press]. Unfortunately, a critical appraisal of Southern Ocean (indeed, southern hemisphere) marine benthic diversity is hindered by the poor state of taxonomic knowledge of many groups [*Winston*, 1992] (Table 1).

An alternative approach to the problem of broad patterns in diversity is to look for geographical patterns in within-habitat diversity. *Thorson* [1957] could find no evidence of a latitudinal cline in the species-richness of shallow-water soft-bottom communities in the northern hemisphere, and this result has been confirmed by more recent analyses [*Kendall and Aschan*, 1993].

The only measurement of infaunal community diversity at an Antarctic site is that at Arthur Harbour, Anvers Island [*Richardson*, 1976; *Richardson and Hedgpeth*, 1977]. The diversity at this site, expressed both as Shannon-Wiener and Margalef indices, was fully comparable with a range of other, lower latitude, soft-bottom communities (mostly from the northern hemisphere). This comparison is confounded by the traditional difficulties for diversity studies of comparability of sampling and analytical protocols, and also the impact of the seasonality of recruitment on the evenness component of diversity statistics. Nevertheless there is as yet no evidence from anywhere of a latitudinal cline in the within-habitat (alpha) diversity of shallow-water soft-bottom communities [*Clarke and Crame*, in press]. Interestingly, there is evidence of such a cline in the deep sea [*Rex et al.*, 1993] but the reasons for this difference remain obscure.

It is not clear to what extent there may be a latitudinal cline in diversity *within* the Southern Ocean. Although sampling has been undertaken widely around Antarctica, this has mainly clarified the circumpolar nature of the distribution of many taxa and suggested a division into major biogeographic provinces [*Hedgpeth*, 1969; *Dell*, 1972; *Clarke*, this volume]. The only study which is sufficiently detailed to reveal a latitudinal cline within Antarctica is that of *Moe and DeLaca* [1976] on macroalgal distribution. This study revealed a statistically significant decline in species richness from Elephant Island (61°S) to Marguerite Bay (68°S). A broader-scale analysis of southern hemisphere marine algal distribution has confirmed this general pattern [*John et al.*, 1994], although recent work has increased the number of macroalgal species recorded at a number of sites (Signy Island: *Brouwer et al.*, 1995; King George Island: *Chung et al.*, 1994; *Klöser et al.*, 1994, Anvers Island: *Amsler et al.*, 1990).

Part of the cline in diversity along the Antarctic Peninsula will reflect the increasingly severe physical constraints limiting macroalgal growth at high latitudes (particularly ice scour), but it may also reflect the evolutionary and biogeographic history of Southern Ocean macroalgae in relation to elimination of the previous flora by extension of the ice-sheet and subsequent recolonization along the Antarctic Peninsula [*Clayton*, 1994]. Unfortunately we have no comparable data for any animal taxa, so it remains unclear whether this is a general result, or limited to macroalgae (or perhaps the shallow sub-tidal ecosystem).

3. ECOLOGICAL PROCESSES IN SOUTHERN OCEAN BENTHOS

3.1. Egg Size and Reproductive Effort

The life history of organisms is essentially cyclical (adult to egg to adult) and hence the choice of a starting point for description of reproductive ecology is somewhat arbitrary. In polar regions, however, the embryonic stages (eggs and larvae) show striking differences from warmer latitudes, and thus reproductive biology forms a logical point to initiate discussion.

It has been recognized since the pioneering work on Arctic and cold-temperate benthos by *Thorson* [1936, 1950] that there is a distinct tendency for polar marine invertebrates to produce a smaller number of larger eggs than related species from lower latitudes. Thorson's studies in Greenland concentrated on molluscs (gastropods and bivalves) and echinoderms, though he also examined polychaetes and crustaceans. In all cases he observed a wide range of egg sizes,

TABLE 1. A summary of marine benthic diversity in the Southern Ocean. Species richness data for the Southern Ocean are an amalgamation of data collated by *Arntz et al.* [in press] and *Clarke and Crame* [in press]; estimates of the percentage of Antarctic species known are from *Winston* [1992] and estimates of total taxon diversity are from *Minelli* [1993].

Taxon	Estimated number of Southern Ocean species known	Estimated percentage of Southern Ocean species known	Estimated number of species in the world
PORIFERA	>300	50	6000
CNIDARIA			
Octocorallia	33	50	
Scleractinia	37	90	
Actiniaria	31	95	
BRACHIOPODA	16		335
BRYOZOA	>350	40-50	5000
PRIAPULIDA	3		9
MOLLUSCA	~870		130000[b]
Gastropoda	604[a]		
Bivalvia	166[a]		
SIPUNCULIDA	~15		320
POLYCHAETA	562		12000
PYCNOGONIDA	>150		1000
CRUSTACEA			
Decapoda	4		10000
Amphipoda	520		8600
Cirrepedia	37		1220
Isopoda	346		10000
ECHINODERMATA			6700
Asteroidea	104		
Crinoidea	27		
Echinoidea	25	80	
Ophiuroidea	87	70	
Holothuroidea	103	80	
TUNICATA			3000
Ascidia	>130	95	

[a] Data for number of species below 50°S, so includes some Subantarctic taxa.

[b] Other estimates are 50000 and 75000 [*Minelli*, 1993].

indicating in turn a range of reproductive strategies in the species present in Greenland. Based on a relationship between egg size and development mode proposed by *Mortensen* [1921, 1936], Thorson concluded that most east Greenland echinoderms and prosobranch gastropods reproduced without a pelagic larval phase. Thorson also established, however, that some bivalves did reproduce *via* a pelagic larva, and that the appearance of these larvae in the plankton was distinctly seasonal.

Although it was Thorson's work in east Greenland which first established the tendency for polar marine invertebrates to avoid a pelagic larval phase, earlier work in the Southern Ocean had already demonstrated that Antarctic echinoderms contained a high proportion of species which brooded their eggs (for a succinct summary of the history of these ideas see *Pearse and Bosch*, 1994). *Mileikovsky* [1971] undertook a re-evaluation of the available data and, basing his argument around prosobranch gastropods, established a clear lati-

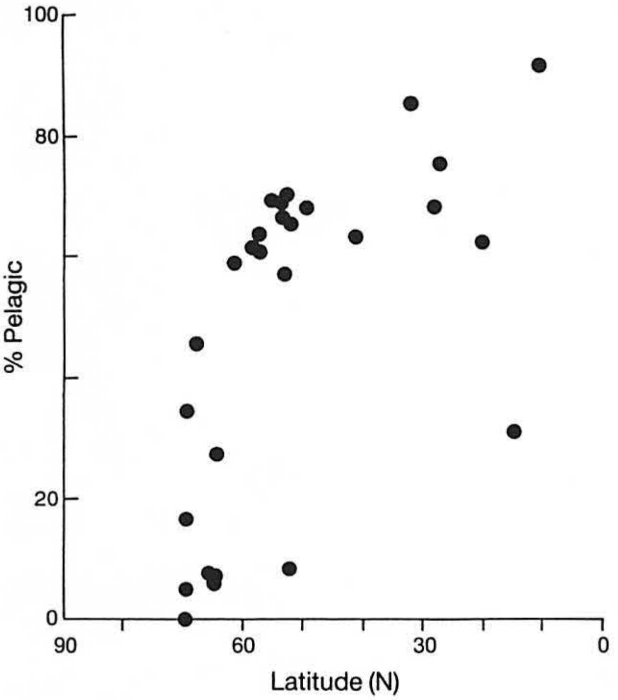

Fig. 3. 'Thorson's rule' exemplified by a clear latitudinal cline in the proportion of prosobranch gastropod species reproducing *via* a pelagic larval stage. Redrawn from *Mileikovsky* [1971].

tudinal cline in the proportion of species reproducing via a pelagic larva from, almost all species in the tropics, to virtually none in the polar regions. *Mileikovsky* termed this cline 'Thorson's Rule' and although the original term was concerned primarily with larval development, it has now broadened through use to include a suite of (not necessarily related) reproductive features including a large egg size, the avoidance of a pelagic larva, and brooding.

A cline in the proportion of species reproducing *via* a pelagic larva is shown most clearly by prosobranch gastropods (Figure 3). *Thorson* [1950] explained this pattern on the basis that the very slow rates of development resulting from the low seawater temperatures and the associated very brief summer period of food availability would not allow the larvae to reach metamorphosis before starvation. Work on echinoderms by Pearse and colleagues at McMurdo Sound and subsequently at Palmer Station has, however, shown clearly that explanations for patterns of larval development in polar regions based simply on the seasonality of food availability are unlikely to be correct [*Bosch and Pearse*, 1990; *Pearse and Bosch*, 1994].

This comprehensive study of development in Antarctic echinoderms has shown clearly that many species reproduce by pelagic larvae but that most of these larvae are lecithotrophic (and hence do not feed in the plankton). Whereas polar gastropods exhibit a switch from pelagic-feeding larvae to direct development, polar echinoderms switch from feeding to non-feeding larvae (Table 2). *Pearse and Bosch* [1994] propose that this switch has evolved not in response to patterns of food availability (as argued by *Thorson*, 1936 and *Clarke*, 1983), but in response to the oceanographic regime which developed followed the opening of Drake Passage. The Antarctic circumpolar current would tend to sweep long-lived pelagic larvae into areas with few suitable sites for settlement (deep water), and comparison with other areas dominated by similar current regimes (for example, southern Australia and New Zealand) reveals a similar high incidence of non-pelagic development [*Pearse and Bosch*, 1994]. In this context it is intriguing that many demersal fish in the Southern Ocean have retained a pelagic larval stage [*North and White*, 1987].

The resurrection, and refinement, by *Pearse and Bosch* [1994] of the original hypothesis relating the high incidence of non-pelagic development to the impact of the oceanographic current regime on dispersal is provocative. It is also important in highlighting two factors often ignored in ecological discussion: the physical environment and phylogenetic history. Ecologists are now recognizing the extent to which the oceanographic environment controls the spatial distribution of larvae, and hence the distribution and abundance of adults (for a recent short review see *Grosberg and Levitan*, 1992). There is also a growing recognition of the influence of phylogeny on ecology, and in the case of reproductive strategies it is important to distinguish between the evolution of non-pelagic development from ancestors with pelagic development, and selection for species showing non-pelagic development in a clade which already possessed this trait (as may well be the case for isopods, amphipods and ctenocidarid echinoids in Antarctica: *Fell*, 1976; *Brandt*, 1992).

Although the predominance in the Southern Ocean of species without a pelagic feeding larva is now well established, there are nonetheless many species which do produce such larvae and, rather intriguingly, they are often very common [*Clarke*, 1992]. A recent two-year systematic study of the presence of marine invertebrate larvae in the plankton at Signy Island has revealed a wide range of larvae, including echinoderms, molluscs, crustaceans, polychaetes and nemerteans (D.P. Stanwell-Smith, personal communication, 1995). In some cases the appearance of larvae was distinctly seasonal (for example, most echinoderm larvae appeared in winter), whereas in others larvae appeared to be present all-year round at low densities (for example, nemertean pilidia). Some of these larvae are clearly planktotrophic and it is therefore of interest that simultaneous measurements of water column chlorophyll showed that whereas the larger diatoms and colonial forms exhibited the classical short summer bloom, nanoflagellates showed an extended bloom with significant concentrations remaining in the water column during winter [*Clarke and Leakey*, in press].

In crustacean groups which brood their eggs (amphipods,

TABLE 2. Mode of larval development in echinoderms from two polar and one temperate location. Table compiled from data in *Pearse* [1994], incorporating original data from *Thorson* [1936]. Data are number of species at that location utilizing a given mode of larval development, with percentage of total species in parentheses.

Site	Number of species reproducing by		
	Pelagic feeding larva	Pelagic non-feeding larva	Protected development
TEMPERATE			
Monterey Bay, CA	18 (50%)	8 (22%)	10 (28%)
POLAR			
N.E. Greenland	4 (17%)	16 (70%)	3 (13%)
McMurdo Sound	5 (23%)	11 (50%)	6 (27%)

caridean decapods and isopods) egg size has shown to be larger in Southern Ocean species compared with related species from lower latitudes [*Bone*, 1972; *Bregazzi*, 1972; *Clarke*, 1979]. In caridean shrimps the larger egg size is accompanied by a reduced overall brood mass [Table 3; *Clarke*, 1979]. This might suggest an overall reduction in reproductive investment, but model calculations indicate that this is not the case [*Clarke*, 1987]. Indeed data for the Arctic deep-water caridean *Pandalus borealis* suggest that the balance between a reduced annual investment in eggs and the lower basal (maintenance) metabolism characteristic of high latitude marine invertebrates result in an overall lifetime reproductive effort similar to shorter-lived warmer water species [*Clarke*, 1987]. Unfortunately there are too few data to test whether this might be a general result.

Recent data have shown that there are also clines in egg size *within* Southern Ocean crustaceans [*Wägele*, 1987; *Clarke and Gore*, 1992; *Gorny et al.*, 1992]. Chemical analyses have shown that the larger eggs produced by populations at higher latitudes represent an increased investment per embryo [*Clarke*, 1993a], and comparison between individual females within a population has revealed subtle but significant trade-offs between egg size and fecundity [*Clarke*, 1993b].

The presence in the nearshore Southern Ocean fauna of a number of common species with pelagic feeding larvae and the clines in egg size within Antarctica shown by some species suggest that there are more factors influencing reproductive biology than just dispersal. Reproductive ecology, particularly in relation to population structure as shown by modern molecular techniques (an almost untouched field in Antarctic marine biology to date) is clearly a research area in need of urgent work.

3.2. Recruitment

There have been relatively few studies of recruitment in the nearshore Antarctic marine environment. *Rauschert* [19-

TABLE 3. Egg size (dry mass, mg) and reproductive output (RO: mass newly spawned eggs/mass female) in polar and temperate caridean decapods (shrimps). Data from *Clarke* [1979, 1987, 1993a], presented as mean and standard deviation with number of individuals analyzed in parentheses. ND: no data. All data are for newly spawned eggs.

Species	Egg dry mass (mg)[a]	RO	Climatic Zone
PANDALIDAE			
Pandalus borealis	0.88 ± 0.08 (10)	0.177 ± 0.024 (95)	Polar
Pandalus montagui	0.021[b]	0.242 ± 0.056 (39)	Temperate
HIPPOLYTIDAE			
Chorismus antarcticus	1.01 ± 0.07 (119)	0.171 ± 0.018 (28)	Polar
Lebbeus polaris	2.88 ± 0.23 (5)	0.131 ± 0.034 (12)	Polar
Eualus gamardii	0.15 ± 0.04 (99)	ND	Polar
CRANGONIDAE			
Crangon crangon	0.0059[b]	0.165 ± 0.033 (68)	Temperate
Notocrangon antarcticus	0.80 ± 0.05 (34)	0.118 ± 0.014 (23)	Polar
Sabinea septemcarinata	0.63 ± 0.07 (16)	0.136 ± 0.060 (29)	Polar

[a] Note that egg mass varies from site to site; representative data are provided for a single site.

[b] Mean egg mass derived from a single sample of eggs pooled from 20 individuals.

TABLE 4. Colonization of settlement plates over a 20 month period at Signy Island, South Orkney Islands, maritime Antarctic. Plates were deployed at three depths, and the total coverage by all taxa combined assessed by image analysis. Coverage of the top surface, bottom surface and sides was assessed separately. Data are presented as mean coverage (% total area), with maximum value in parentheses; from *Barnes* [in press].

Depth (m)	n[a]	Coverage (% total area)		
		Upper surface	Lower surface	Sides
6	5	0.72 (1.77)	1.25 (2.69)	0.71 (1.34)
12	4	0.19 (0.23)	2.41 (4.60)	1.09 (1.30)
25	4	6.54 (11.62)	4.71 (8.63)	7.49 (12.30)

[a] Five plates were deployed at each depth, but some plates were destroyed by ice impact before recovery.

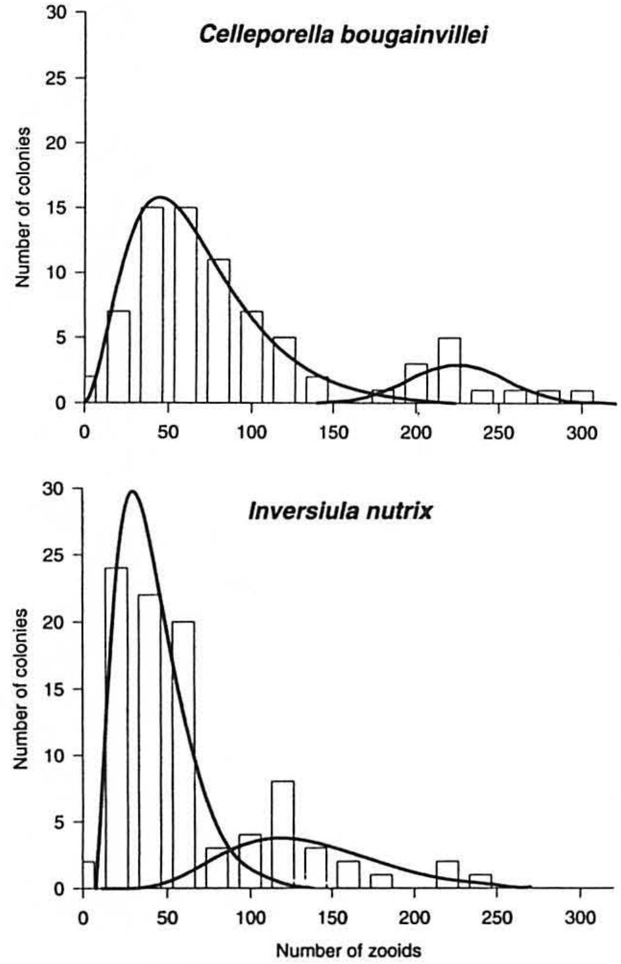

Fig. 4. Frequency histograms, with fitted models, of colony size (number of zooids) of the two most abundant bryozoan species colonizing perspex settlement panels deployed at 25 m in Borge Bay, Signy Island. The models were fitted using the software package MIX, and suggest two settlement events of dissimilar magnitude; the absence of significant numbers of empty ancestrulae of zooids indicated that post-settlement mortality was not the explanation for the difference in recruitment between years (reproduced, with permission, from *Barnes*, in press).

91] deployed settlement plates at King George Island and noted that those plates which survived ice damage were heavily colonized after three years. In contrast, artificial substrata deployed at McMurdo Sound showed virtually no colonization after five years, but then inspection after a further four years revealed a dense recruitment of a typical hard substratum fouling community [*Dayton*, 1989]. With only two such long-term studies having been undertaken it is difficult to know whether the results represent a true difference between recruitment dynamics in the high Antarctic (McMurdo Sound) and maritime Antarctic (King George Island), or simply fortuitous timing in relation to infrequent recruitment events.

A recent study of recruitment to perspex settlement panels deployed at Signy Island (in the maritime Antarctic) for 20 months revealed very low levels of recruitment (Table 4). At 6 m the plates were colonized only by calcareous algae and spirorbid polychaetes and two plates were destroyed by ice impact. No algae were present on plates deployed at 12 m, where the colonizing fauna comprised spirorbids, one cyclostome and two cheilostome bryozoans. At 25 m the dominant colonizers were again spirorbid polychaetes and bryozoans (two cyclostome and 15 cheilostome species). Three species, *Celleporella bougainvillei*, *Celleporella antarctica* and *Inversiula nutrix* together comprised between 55% and 80% of all bryozoan colonies, and size-frequency histograms suggested that there had been two settlement events during the 20 month deployment (Figure 4). Mortality following settlement (for example, caused by predation) can be detected from the presence of empty ancestrulae or zooids. In this case no significant mortality could be detected and so it would appear that the earlier settlement event was smaller than the later one.

The most striking feature of these results is the very low rate of colonization (by over an order of magnitude) compared with settlement plates immersed in tropical or temperate latitudes [*Barnes*, in press]. This has important ecological consequences both in terms of the dynamics of recovery from ice impact in the shallow water marine ecosystem, and also for recovery from human impact. The

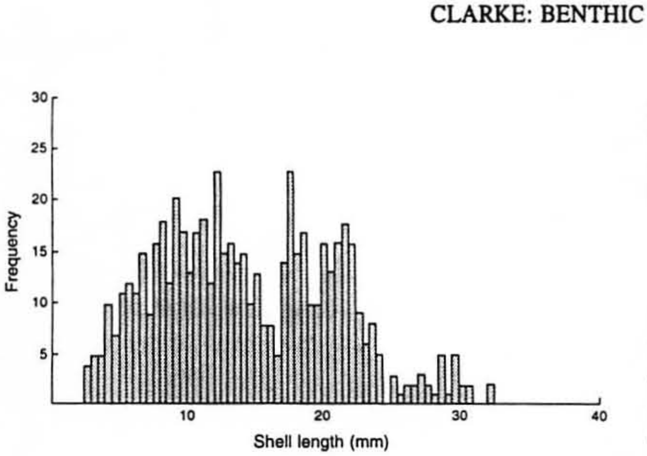

Fig. 5. Size/frequency histogram for sample of 592 individuals of the infaunal nuculanid bivalve *Yoldia eightsi* collected by suction sampler (cut-off size 2 mm) at Borge Bay, Signy Island, December 1989, illustrating the relative lack of younger animals.

intriguing question, to which we have as yet no answer, is whether this background level of very low recruitment to hard substrata is interspersed with intermittent years of very heavy recruitment [*Dayton*, 1989].

3.3. Juvenile Survival

We know very little about either recruitment to soft-bottom communities in Antarctica, or about the subsequent survival of juveniles. Several published size-frequency histograms lack the expected large size class(es) of juvenile forms. This could be the result either of episodic recruitment events, or of the sampling techniques being used having missed the smaller juvenile stages (Figure 5).

3.4. Growth Rate

It was quickly established by the early autoecological studies of Antarctic benthos that most species grew slowly, or very slowly, and tended to have long life-spans [reviewed by *Arnaud*, 1974; *Everson*, 1977; *Clarke*, 1980, 1983].

There are, however, a number of interesting exceptions to this general rule. These include the sponges *Mycale acerata* and *Homaxinella balfourensis* in McMurdo Sound [*Dayton et al.*, 1974; *Dayton*, 1989] and the ascidians *Ascidia challengeri, Cnemidocarpa verrucosa* and *Molgula pedunculata* at King George Island [*Rauschert*, 1991] all of which have been shown to grow rapidly in comparison with other Antarctic marine invertebrates. A relatively fast growth rate was also determined for the Antarctic limpet, *Nacella concinna* by a mark/recapture study at Palmer Station (Figure 6) and a similarly fast growth rate has recently been noted in the same species at Signy Island [*Clarke and Prothero-Thomas*, unpublished data].

Brey and Clarke [1993] collated all available data on the production and biomass of Antarctic benthic marine invertebrates and showed that the production/biomass (P/B) ratio of polar species was significantly lower than that of temperate or tropical species. These data were subsequently expanded and analysed further, expressing overall growth performance as the generalized measure ϕ:

$$\phi = [\log(K) + (0.667 \times \log(M_\infty))]$$

where K and M_∞ are the two parameters of the von Bertalanffy growth function [see *Arntz et al.*, 1994, for further details]. Comparison of data for 28 Antarctic benthic populations with 141 data sets for non-Antarctic sites showed clearly that the growth index was significantly lower ($P < 0.002$) in the Antarctic populations (Figure 7). Tabulated biomass, production and P/B data are given in *Brey and Clarke* [1993] and *Arntz et al.* [1994].

Most studies of growth in Antarctic benthic marine invertebrates have, for obvious practical reasons, tended to concentrate on the larger and more common species; since most polar marine invertebrates are small (Figure 1), there is a possible bias to these results. Important studies of small species have included those of the prosobranch *Laevilacunaria antarctica* [*Picken*, 1979], and the two philobryid bivalves *Lissarca miliaris* [*Richardson*, 1979] and *Lissarca notorcadensis* [*Brey and Hain*, 1992].

We do not yet fully understand why the growth rates of most polar benthic marine invertebrates are so slow. Where detailed studies have been undertaken these have usually indicated a strongly seasonal pattern of growth; examples include the caridean shrimp *Chorismus antarcticus* [*Clarke and Lakhani*, 1979], the philobryid bivalve *Lissarca miliaris* [*Richardson*, 1979], the prosobranch *Laevilacunaria antarctica* [*Picken*, 1979] and serolid isopods [*Luxmoore*, 1982]. This seasonality of growth is clearly related to the overall

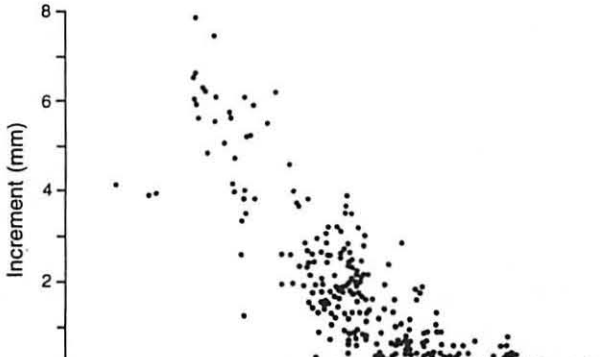

Fig. 6. Growth rate in the Antarctic limpet, *Nacella concinna*, as determined by a mark/recapture experiment. The data have been taken from *Shabica* [1976] and plotted to show the annual increment in shell length as a function of length at initial measurement (both in mm). Note that this measure of growth declines with adult size, but that growth can be quite fast in smaller limpets.

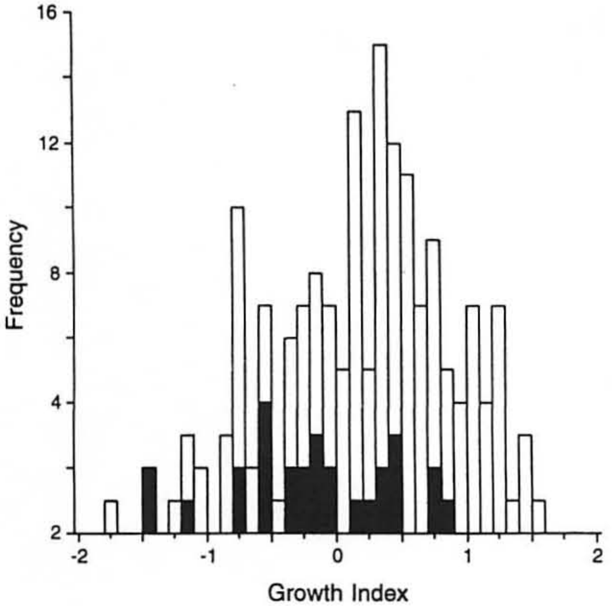

Fig. 7. A comparison of an index of overall growth performance (derived from the generalized von Bertalanffy growth equation) in 28 Antarctic (black bars) and 141 non-Antarctic (open bars) of benthic marine invertebrates. The index is significantly lower in the Antarctic populations (Mann-Whitney test, $P<0.002$). Redrawn, with permission, from *Arntz et al.* [1994].

seasonality of the system [*Clarke*, 1988] and indicates that these organisms probably suffer a seasonal resource limitation which forces them to cease growth in winter. *Brand* [1976] has documented a clear seasonal variation in the feeding activity of two specialist amphipod predators, the large amphipod, *Bovallia gigantea*, and the polychaete, *Harmathoe spinosa*, at Palmer Station. The occurrence of amphipod remains in the guts of two generalist feeders, the echinoid, *Sterechinus neumayeri*, and the polychaete, *Amphitrite kerguelensis*, was markedly less seasonal.

The extent to which the overall slow growth is also related to temperature limitation is not known [*Clarke*, 1991], although a detailed analysis of data for the growth rate of larval polar, temperate and tropical fish indicated a clear link between temperature and growth rate [*Clarke and North*, 1991].

Recent studies of the seasonality of feeding in a number of shallow-water Antarctic bryozoans have shown that many species cease feeding for only a very short period in winter; indeed the massive calcareous species *Arachnopusia inchoata* feeds continuously throughout the year [*Barnes and Clarke*, 1994]. This long period of feeding appears to be coupled with a reduced seasonality of growth [*Barnes*, 1995] suggesting that it is indeed resource limitation which causes the reduction of growth rate in winter. A general study of the seasonality of feeding in polar suspension feeders [*Barnes and Clarke*, 1995] suggested that those taxa which take larger particles (such as large diatoms or colonial forms) exhibited a much longer period of starvation than those taxa believed to take smaller cells such as nanoflagellates. In this context it is intriguing that almost all of the Antarctic benthic marine invertebrates which have been shown to grow relatively fast are suspension feeders.

The relationship between feeding and energetics in polar marine benthos clearly needs further clarification, particularly in relation to temperature adaptation in growth.

4. ENVIRONMENTAL FACTORS INFLUENCING ECOLOGICAL PROCESSES IN THE SOUTHERN OCEAN MARINE BENTHOS

The etymology of the term 'ecology' highlights the recognition that biological processes can only be understood in terms of the physical environment in which they operate. Of particular importance is the relationship between biological processes and the scales of temporal and spatial variability in the environment. This is a growing area in marine ecology, and I will touch on three subjects here: temperature, sea-ice and habitat heterogeneity.

4.1. Temperature

Although it is widely recognized that the Southern Ocean is cold, seawater temperature varies seasonally and also from place to place. In general habitats close to the Antarctic continent are very cold (often below -1.8°C), and show almost no seasonal variability; a typical example is McMurdo Sound where the seawater temperature varied by less than 0.2 K in one year of observations [*Littlepage*, 1965].

Further north in the maritime Antarctic at Signy Island, South Orkney Islands seawater temperature varies seasonally from <-1.8°C in winter to a summer maximum which is usually somewhere between +0.3°C and +1.7°C (Figure 8).

Three features of the long-term record shown in Figure 8 are of interest. The first is that the seasonal variation in temperature is small, and hence is unlikely to drive seasonal changes in biology. In temperate regions, the annual variation in seawater temperature is greater, often by an order of magnitude, than in polar regions. Seasonal changes of 10-15 K are large enough to have significant thermodynamic effects on the physiology of marine invertebrates and fish, and evidence for seasonal temperature regulation of physiology is widespread in temperate regions. In polar regions, however, seasonal variation is so low that physiological processes would have to be unduly thermally sensitive for temperature variation to be the forcing variable. For example, a physiological processes which doubled its rate in summer at Signy would suggest a Q_{10} of >15, and a similar doubling of rate in summer at McMurdo would imply a $Q_{10} > 10^{15}$. These are both biologically unrealistic values, and they indicate that the forcing variable for seasonal variation in biological processes in polar regions is not temperature;

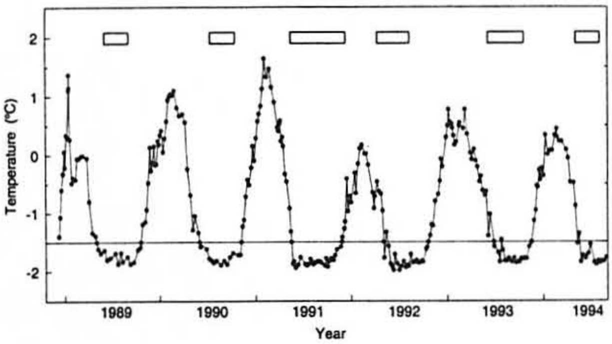

Fig. 8. Seasonal and interannual variability in seawater temperature. Data are from 10 m depth at a nearshore oceanographic station in Borge Bay, Signy Island. The line shown at -1.5°C marks an arbitrary threshold for integrating summer thermal environment. Note that the summer maximum temperature varies significantly from year to year, and is related to the duration of fast-ice (shown by the open bars) in the previous winter. Reproduced, with permission, from *Clarke and Leakey* [in press].

rather it is likely to be seasonal resource limitation.

One physiological process which does, however, show extreme temperature sensitivity, particularly at the lowest temperatures, is embryonic development. For many polar marine organisms the rate of egg and/or larval development becomes very slow indeed at temperatures below about -1.5°C [*Ross et al.*, 1988; *Clarke*, 1992].

The second feature of interest is the overall low temperature. Since, all else being equal, a low temperature slows down the rate of physiological reactions, polar organisms will need to have evolved some mechanism(s) of compensating for the effect of this low temperature. This is an area of active investigation, though most studies are concerned with fish (*Clarke* [1983, 1991] provides reviews of this subject).

One of the most striking physiological correlations with temperature is that of basal (or maintenance) metabolic rate: polar marine invertebrates exhibit a much lower resting metabolism than temperate or tropical species [*Clarke*, 1991, where original citations are provided]. The reduced metabolic rate in polar species has important consequences for overwintering energy requirements [*Clarke and Peck*, 1991], but also has subtle implications for overall energy budgeting, including reproductive investment [*Clarke*, 1987]. Of current interest is the extent to which the energetic benefits to be gained from a low resting metabolism are offset by a concomitant reduction in overall maximum metabolic rate.

The third feature of interest which emerges from the five year temperature record in Figure 8 is interannual variability. There are significant differences between years in the maximum summer temperature reached, and the overall integrated thermal environment (degree-days above -1.5°C). This variability is linked to variability in ice dynamics and is part of a wider-scale process (see next section).

4.2. Long-term Temperature Change

Although the high Southern latitudes are currently very cold, and thereby contribute to a strong latitudinal temperature gradient from tropics to poles, this has not always been the case. The Southern Ocean fauna that we see today has evolved *in situ* over a long period, during which time it has been subject to variations in glacial extent, the fragmentation of Gondwana, massive changes in oceanographic circulation and an overall decline in temperature of perhaps 15-20 K during the past 55 million years [*Lipps and Hickman*, 1982; *Clarke and Crame*, 1989, 1992].

The marine invertebrates and fish living today are thus the descendants of ancestors who lived in much warmer waters. Current evidence, however, indicates that the present fauna is highly stenothermal [*Somero and DeVries*, 1967; *Somero*, 1991]. It is not clear whether this stenothermal physiology is an inevitable consequence of adaptation to a low temperature or may have been selected for on energetic grounds [*Clarke*, 1991, 1993]. Neither is it clear the extent to which it may represent an evolutionary blind alley, limiting the ability of polar marine organisms and fish to respond to continued temperature change [*Somero*, 1986].

4.3. Sea-ice

The impact of sea-ice on polar marine ecosystems is all-pervasive, but there are five key areas where the ecological effects of sea-ice are of particular importance to benthic populations:

- o Ice-scour in the intertidal and shallow sub-littoral
- o The impact of iceberg grounding in deeper waters
- o The effect of winter sea-ice in influencing water column productivity, and hence food availability for benthos
- o The rafting of debris into deeper water where drop-stones may provide isolated patches of hard-substratum habitat
- o Sub-decadal variability in ice dynamics

Ice-scour and the effect of anchor-ice in structuring shallow-water benthic communities has been dealt with elsewhere in this volume [*Clarke*, this volume].

The rafting of land-derived material by ice is a complex process which can have a variety of impacts on benthic populations. Where glacial outflow is substantial, then a high rate of deposition of unsorted rock flour and moraine debris can limit benthic communities to those species tolerant of high rates of disturbance [*Dayton*, 1990]. In deeper water, ice-rafting can introduce isolated islands of hard substratum (drop-stones) into areas otherwise dominated by soft sediments. Colonization of such habitats thus represents a challenge somewhat akin to that of the more ephemeral vent communities. This is an area which has received relatively little attention from polar biologists, primarily because of sampling difficulties.

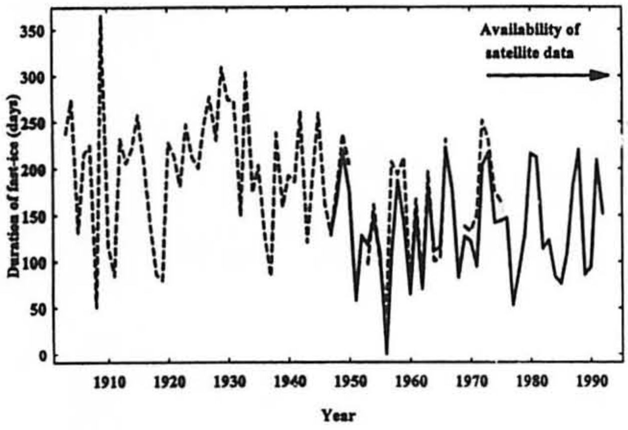

Fig. 9. The duration of winter fast-ice at Signy Island (solid line) and at Laurie Island, 40 km due east (broken line). The shaft of the arrow shows the period for which satellite sea-ice data are available. The key features of these long-term data sets and the overall decline in the average duration of winter fast-ice in the South Orkney Islands in the 1940s and 1950s, and the strong 7-9 year cyclicity apparent from the mid-1960s to 1990. From *Murphy et al.* [1995].

Sea-ice is of intense significance to the patterns of energy flow in polar marine ecosystems. It stabilizes the water column, thereby allowing much of the suspended particulate material to sink to the seabed where it is utilized by both macrofauna and the microbial flora. The resultant high water clarity can lead to very high rates of primary production in the early spring, in both the water column and, in shallow waters, in benthic algae [*Gilbert*, 1991]. In more oceanic waters the stabilization of the water column may lead to ice-edge blooms [*Smith and Sakshaug*, 1990] though it is now clear that such blooms are by no means a universal feature of a retreating ice-edge. Where such blooms do occur, however, they can result in a significant flux of phytoplankton material to the seabed [*Honjo*, 1990]. Sea-ice also influences the biology of the pelagic zone by providing feeding and habitat for zooplankton [*Ross et al.*, this volume].

4.4. Sea-ice Dynamics in the Southern Ocean

Analysis of a long-term fast-ice record from the South Orkney Islands has revealed a number of features of ecological interest [*Murphy et al.*, 1995]. Although there has been an overall decrease in the duration of winter fast-ice at the South Orkney Islands, this has not been a simple linear decline but is the result of a reduction in fast-ice duration in the 1940s and 1950s. There was also a period of clear subdecadal cyclicity from the mid-1960s to 1990 (Figure 9). Comparison with satellite microwave data showed that variability in fast-ice duration at the South Orkney Islands reflects the larger-scale ice dynamics in the Weddell Sea, and that this in turn reflects the precession of anomalies in circumpolar ice extent around the Antarctic continent. This precession has a period of approximately 7-9 years and suggests that a sub-decadal variability is likely to affect many ecological processes in the Southern Ocean [*Murphy et al.*, 1995].

At present there are almost no long-term data sets to examine for such sub-decadal variability, although the temperature record at Signy Island (Figure 8) reveals a significant correlation between summer seawater temperature and ice duration in the previous winter [*Murphy et al.*, 1995]. The only benthic ecological data available which suggests the impact of this variability are those of *Dayton* [1989], which indicate a possible sub-decadal variability in recruitment to settlement panels in McMurdo Sound, itself possibly related to oceanographic variability. In the pelagic realm there are preliminary indications that variability in ice dynamics may influence year-class (recruitment) strength in Antarctic krill, *Euphausia superba* [*Ross and Quetin*, 1991] and variability at higher trophic levels [*Testa et al.*, 1991; *Fraser et al.*, 1992]. Nevertheless the ecological impact of the seasonal ice-cover in polar regions is sufficiently important and all-pervasive that it is safe to assume that the recently described long-term variability will carry through to ecological processes.

The dynamics of sea-ice and its impact on marine ecology is an important area of polar marine biology, which needs increased attention in both benthic and pelagic realms.

4.5. Habitat Heterogeneity

Whereas the discussion of temperature and sea-ice concerns primarily variability in time, habitat heterogeneity concerns variability in space. It has long been recognized that an increased diversity of habitats is related in some way to an increased diversity of the associated flora and fauna, and for example it is likely that the overall low diversity of the Southern Ocean fish fauna is related to the low habitat diversity. The almost complete absence in the Southern Ocean of habitats traditionally rich in fish species, such as estuaries or tidal flats, has resulted in a low overall fish diversity although individual habitats may be as species-rich as comparable habitats elsewhere [*Eastman*, 1993].

There are few data for marine invertebrates, although *Picken* [1979] has suggested that the contagious (overdispersed) distribution of prosobranch gastropods in shallow-water habitats is related to the contagious distribution of their macroalgal habitat. Further work in this area is needed, particularly to elucidate the extent to which differences in habitat heterogeneity may help explain the marked differences in diversity between the two polar regions.

On a larger spatial scale, patterns of habitat heterogeneity are important in influencing population dynamics through the creation of fragmented population structure (metapopulations) and the resultant impact on dispersal and recruitment dynamics in populations dominated by species with low-dispersal larval or juvenile stages. At present we know very little of the population structure of most benthic marine invertebrates, although the very different dispersal dynamics in water means that direct comparison with metapopulation dynamics in terrestrial habitats may be misleading.

5. CONCLUSIONS

Although there is a long history of both descriptive and ecological work on Southern Ocean benthos [*Hedgpeth*, 1971; *Dell*, 1972; *White*, 1984; *Dayton*, 1990; *Arntz et al.*, 1994, in press], there remain many gaps in our knowledge and understanding. Taxa are generally well described but we have few thorough analyses of communities or assemblages. Many taxa appear to be circumpolar in distribution but our biogeographic understanding is based on relatively few and scattered data. The role of historical processes in producing many of the patterns we see in Antarctica today is better understood than in many other areas, but we need to utilize modern molecular techniques to distinguish the impact of history and the physical environment in, for example, determining patterns of distribution in the Antarctic Peninsula area.

Ecological studies are generally limited, for reasons of logistics, to the austral summer. It is becoming clear, however, that winter is an important time in the ecology of many species, and further year-round studies are badly needed. Biological work in the Southern Ocean has also revealed the importance of long-term data sets both for understanding the biology itself and for relating this to variability in the physical environment. Key areas for future work are thus year-round studies, the use of modern molecular techniques, the further development of remote techniques such as photography, and (perhaps most important of all), continued uninterrupted work to build long-term data.

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