

Review

Benthic Organisms and Environmental Variability in Antarctica: Responses to Seasonal, Decadal and Long-term Change

Andrew Clarke

*British Antarctic Survey, NERC, High Cross, Madingley Road
Cambridge CB3 0ET, UK*

Abstract: Marine organisms in Antarctica live in an environment which exhibits variability in physical processes over a wide range of temporal scales, from seconds to millennia. This time scale tends to be correlated with the spatial scale over which a given process operates, though this relationship is influenced by biology. The way organisms respond to variability in the physical environment depends on the time-scale of that variability in relation to life-span. Short-term variations are perceived largely as noise and probably have little direct impact on ecology. Of much greater importance to organisms in Antarctica are seasonal and decadal variations. Although seasonality has long been recognised as a key feature of polar environments, the realization that decadal scale variability is important is relatively recent. Long-term change has always been a feature of polar environments and may be a key factor in the evolution of the communities we see today.

Key words: Antarctica, benthos, climate change, El Niño, life-history, seasonality, variability.

1. Introduction

Marine organisms live in a fluid medium which is always in motion. Only the larger nekton can exhibit behaviour which is independent of this motion. Whereas plankton are transported by the medium which supports and surrounds them, benthic organisms are typically either fixed (sessile) or slow moving. For many benthos, water movement is essential to bring food and oxygen, and to remove waste products. It is also important in the successful fertilisation of zygotes, and dispersal of embryos or larvae.

The relationship between physical and biological processes in the sea is both subtle and complex (Vogel 1981; Mann and Lazier 1991). Fundamental to this relationship are the length scales over which the various physical processes of importance to organisms operate (Denman 1994). Typical ocean basins are 10^7 m wide or more, and this is the geographic scale of whole marine communities in the pelagic or abyssal benthic realm. The Coriolis and gravitational forces define the Rossby internal deformation

scale, which varies with latitude and governs the width of oceanic currents, coastal upwelling regions or the radius of oceanic eddies. Also important is the very much smaller scale at which viscosity balance the inertial forces of turbulent eddies (the viscous or Kolmogoroff length). This scale is of enormous significance to marine organisms because it marks an important change in locomotion and feeding mechanisms. For larger animals (typically 1 cm or above) nutrients and waste products are moved rapidly by turbulent diffusion, unaffected by viscosity. Small organisms must depend on molecular diffusion for this transfer, and this is significantly affected by viscosity (and hence by temperature).

For turbulent physical processes, length scales are linked intimately with time scales, and to a first approximation these two scales are directly proportional. Thus on a global scale the thermohaline circulation takes on the order of 10^4 years to complete one circuit (Mann and Lazier 1991), whereas major gyres take up to 10 years and mesoscale eddies and gyres have lifetimes of weeks or months. For physical processes in the ocean energy flows broadly from larger to smaller scales, until the energy of

*Corresponding author. E-mail : andrew.clark@bas.ac.uk

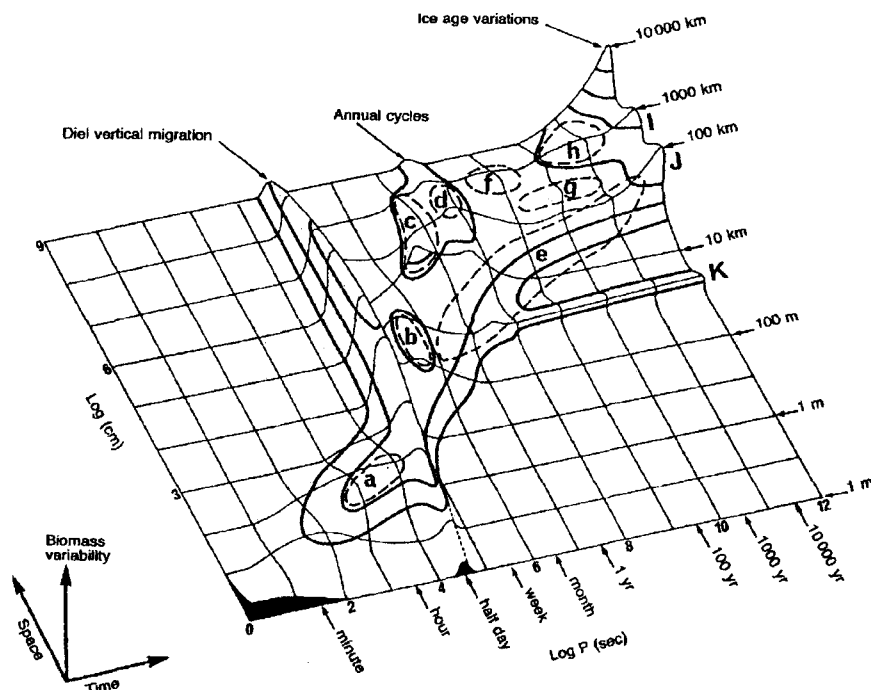


Fig. 1. A conceptual framework for the variability in time and space of zooplankton biomass, illustrating the strong correlation between biomass and the hydrodynamics of turbulence in the oceans (from Haury *et al.* 1978). Although the pattern is dominated by the correlation between spatial and temperature scales, it also illustrates how biological process can modify this pattern (for example, through vertical migration or life-history).

the smallest eddies is eventually dissipated into heat by molecular viscosity (Denmann 1994).

In contrast, energy in biological systems tends to flow predominantly from smaller scales (primarily production by phytoplankton and the microbial community) to larger (herbivores to nekton and ultimately the largest top predators). Biological processes such as vertical migration and life-history also add complexity to the time-length scale proportionality of purely physical processes in the sea (Fig. 1). The original diagram (Haury *et al.* 1978) was developed for planktonic systems. Although some elements could be criticised (for example the scale of diel vertical migration for an individual zooplankton is probably only hundreds of metres) the basic concept is equally valid for benthic communities. Murphy *et al.* (1988) have developed this conceptual framework with particular reference to polar environments, where physical and biological processes of a range of scales are modified significantly by the presence of sea-ice.

Although physical processes in the sea exhibit variability over a vast range of spatial and temporal scales, some scales are of greater biological relevance than others (Table 1). In this paper I will concentrate on four scales of

Table 1. A summary of temporal variability in the coastal Antarctic marine ecosystem.

Frequency (sec^{-1})	Process
Microscale processes	(Time scale up to 1 sec)
$>10^1$	Molecular diffusion
10^0	Eddy turbulency; surface waves
Mesoscale processes	(Time scale seconds to hours)
10^{-2}	Internal waves
10^{-5}	Tides; diurnal variations; storm surges
Synoptic scale processes	(Time scale weeks)
10^{-6}	Frontal currents; meanders; Rossby turbulence
Seasonal processes	(Time scale 1 year)
10^{-7} - 10^{-8}	Seasonal warming; convective overturn; stratification
Sub-decadal processes	(Time scale 1-10 years)
10^{-8}	El Niño Southern Oscillation; Antarctic circumpolar wave
Very long time-scale processes	(Time-scale hundreds to millions of years)
10^{-10} and below	Climate change; Milankovitch cycles; glacial cycles)

temporal variability, and examine their importance to coastal benthic communities in Antarctica. These time-

scales are short-term (minutes to hours), seasonal, sub-decadal and evolutionary.

Typical coastal (continental shelf) environments differ in important aspects from the open ocean. While they are subject to the same seasonal cycles of warming by the sun as the pelagic realm, in coastal regions the mixed layer can extend to the seabed and this may change significantly the dynamics of nutrient availability. Furthermore coastal environments are generally subject to strong tidal mixing, and are influenced by freshwater run-off and upwelling under the influence of off shore winds. Antarctic coastal regions differ from those elsewhere in that there is effectively no riverine input, although meltwater processes from glacier fronts and ice shelves can be of great importance. In addition the influence of solar radiation and wind is modulated significantly by surface ice. The continental shelf around Antarctic is also exceptionally deep (typically 500 m but in some areas extending to 1000 m or more); in consequence much of the Antarctic coastal benthos is below the mixed layer and in some aspects of their physiology and ecology are more akin to deep-sea benthos than other continental shelf communities.

Short-term variability

Microscale processes of particular importance to marine organisms are molecular diffusion and eddy turbulence. The boundary layer which surrounds the external surface of all organisms means that exchange of nutrients and waste products is dominated by diffusion processes. The transition from turbulent flow to the realm where molecular motion predominates and flow becomes laminar depends on shear rate and viscosity. The ratio between these two is expressed as the Reynolds number (R_c), a dimensionless number of enormous significance in marine ecology. The critical value of R_c in seawater lies between 500 and 2000, with flow being laminar below R_c and turbulent above it (Vogel 1981). In the realm of low Reynolds numbers inertia is irrelevant and transport of nutrients and gases is by molecular diffusion. Over very small distances, such as around a typical bacterium or small flagellate cell, molecular diffusion is relatively fast and these cells are unlikely to become nutrient limited (Fogg 1991).

Both viscosity and molecular diffusion are affected by temperature (Clarke 1983, in press) but the extent to which this affects the ecology of polar organisms themselves, there is also an important boundary layer is shown by the various mechanisms used by organisms to penetrate into the water column. These include stalked or other extend growth forms in sessile benthos, or selecting substrata

(including other organisms) which extend away from the surface in motile filter feeders such as isopods and crinoids (Gutt and Schickan 1998). The prevalence of these adaptations in the Antarctic benthos may reflect the influence of temperature on the physical variables determining boundary layer, and the role of bulk flow or eddy turbulence in modifying this.

Antarctic coastal environments are similar to those elsewhere in the importance of physical processes such as

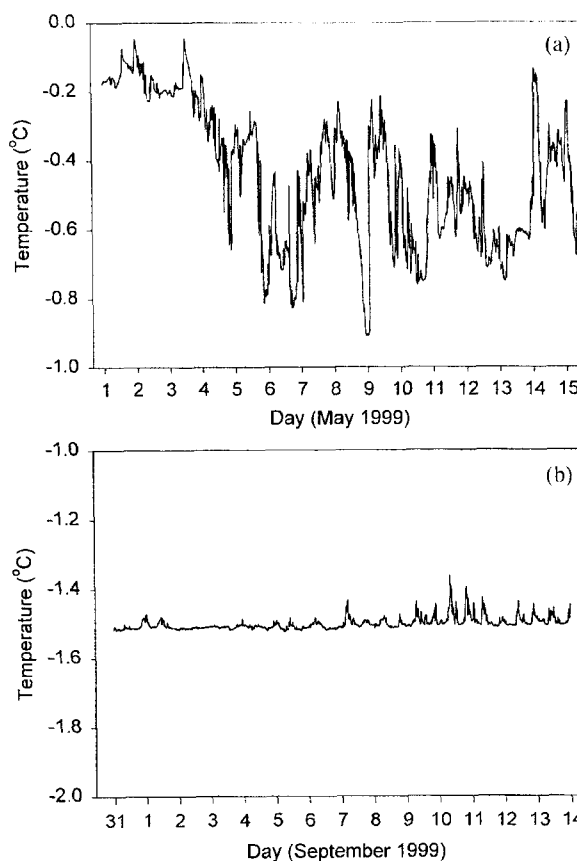


Fig. 2. High resolution temperature records from 20 m depth at Cheshire Island, Rothera Point, northern Marguerite Bay (67°34'S). Data were collected with a temperature recorder with a resolution of -0.001°C and a recording interval of 600 seconds. The signal is thus dominated by internal waves and tidal flow, with eddy turbulence below the temporal resolution of the record and hence filtered out. (a) May 1999. Open water period, showing high variability, (b) September 1999. A record when fast-ice was present showing greatly reduced variability the dominant signal is tidal. The temperature scale for the two plots is the same (range 1°C).

tidal currents and internal waves, while they also differ in some features such as freshwater input from meltwater rather than rivers, and the difference in the Rossby scale, there are also ecologically highly significant differences in small-scale processes between open water (summer) and ice-covered (winter) periods.

High resolution temperature records have shown that under winter sea-ice, short-term variability is greatly reduced (Fig. 2). These data suggest that in winter processes which would replenish local depletion of nutrients around sessile benthos are greatly reduced in intensity. Sessile benthic organisms are thus likely to be subject to severe local reduction in food availability when fast-ice is present.

The characteristic time-scale of short term variations in nutrient concentration, food availability or temperature is less than the life-span of polar organisms (even in the microbial community, where minimum reported doubling times are typically of the order of 1-2 days: Smith and Sakshang 1990). This variability will generally be perceived as environmental noise, with some form of average or intermediate value being the ecologically relevant driver.

Seasonality

The marked seasonality of polar marine ecosystems compared with those at lower latitudes has long been

recognised as a major ecological factor (Clarke 1988). The seasonal variations in temperature in the Antarctic coastal marine environment is small compared with that in temperate regions (where the annual range in temperature is typically 15 °C and may reach 20 °C). The seasonal range in Antarctica also varies geographically, with a greater seasonal variation in the lower latitude maritime Antarctic compared with some high latitude areas (Fig. 3).

The overall small range of temperature change will affect the physiology and ecology of benthic organisms, but this effect is small compared with that of the seasonal variation in food availability (Clarke 1988; Brockington and Clarke, under review). The seasonal variation in photoperiod, exacerbated by the influence of sea-ice, leads to a highly seasonal pattern of primary production (Fig. 4).

Two features of this seasonality are important ecologically. The first is the long winter period for which the biomass of large cells is very low, and the second is that in winter the biomass of nanoplankton exceeds that of microplankton (Fig. 4). Suspension feeders which take larger cells (for example *Cucumarian holothurians*) thus have a feeding period of at most six months, and there is a long winter period of starvation (Barnes and Clarke 1995). In contrast, taxa which feed on nanoplankton can feed for

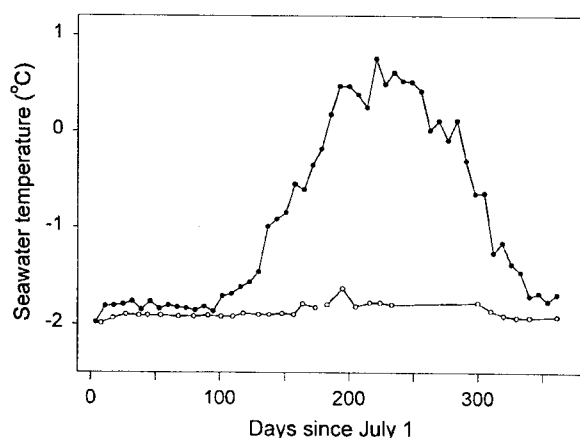


Fig. 3. Seasonal variation in seawater temperature at two Antarctic coastal locations. Filled circles: Signy Island, 60°43'S, 15 m depth; data are for 1989 to 1995, pooled by week (from Clarke and Leakey 1996). Open circles: McMurdo Sound, 77°51'S; data are individual measurements for 25 m depth over the period Jan. 2 to Dec. 31, 1961 (from Littlepage 1965). Note the break in the date: this is because the data were collected over a full calendar year but have been plotted here to emphasize the seasonal rise during the austral summer.

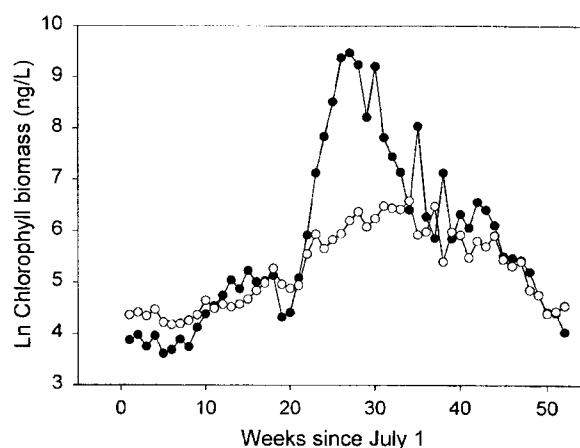


Fig. 4. Seasonal variation in the standing crop biomass (mg m^{-3}) of chlorophyll in two size fractions. Open circles: cells retained by a 20 μm filter (typically large individual diatoms, chain-forming and globular taxa). Closed circles: cells $<20 \mu\text{m}$ but retained by a 2 μm filter (nanoplankton; typically smaller individual diatoms and flagellates). Data from Signy Island, 1989 to 1994 pooled by week. Note the logarithmic scale, and the vertical offset for clarity. From Clarke and Leakey (1996).

much longer and some bryozoan taxa may even feed year-round (Barnes and Clarke 1994, 1995). This implies that even though bulk-flow and turbulent processes are greatly reduced in winter (see previous section), sufficient movement does take place to prevent complete local depletion of resources. Some taxa may also be able to reduce the problem of local depletion of resources by active pumping of seawater (bivalves, ascidians), movement of the feeding apparatus (bryozoans, crinoids, polychaetes) or even changing the orientation of the whole body (brachiopods).

The impact of seasonal variations in phytoplankton will be greatest in suspension feeders. This seasonality does, however, propagate through the food-web and is a feature of the Antarctic coastal marine ecosystem as a whole. Typically, growth is constrained to summer and although complete maturation of an oocyte takes over a year in many species, the bulk of vitellogenesis is dependent upon summer feeding (Clarke 1988). The duration and timing of the summer feeding period vary within the Southern Ocean, with summers tending to be shorter and later at high latitudes. This will lead to spatial variations in ecology with, for example, growth rates in many taxa being slower at high latitudes locations (Brey and Clarke 1993).

Decadal variability

Although the importance of environmental seasonality in polar marine ecology has long been recognised, the recognition that interannual variability on a roughly decadal scale is also important is much more recent. The first indication that decadal-scale shifts in oceanographic processes might influence the population dynamics of Antarctic benthic organisms came from observations of sponge communities in McMurdo Sound (Dayton 1989). At about the same time biological oceanographers were beginning to appreciate that interannual variability in open-ocean and marginal ice zone primary production was likely to have significant ecosystem consequences in the Southern Ocean (El-Sayed 1988; Smith *et al.* 1988).

A major difficulty in understanding the ecological consequences of temporal variability on this scale is the almost complete lack of suitable long-term environmental data sets for the Southern Ocean. Satellite remote-sensing only extends back to 1973, a period which would cover only about two cycles of any process exhibiting decadal variability. Meteorological data does extend back to the early 20th century at some sites on the Antarctic Peninsula, but the longest environmental data set for any site in Antarctica is a composite of the duration and

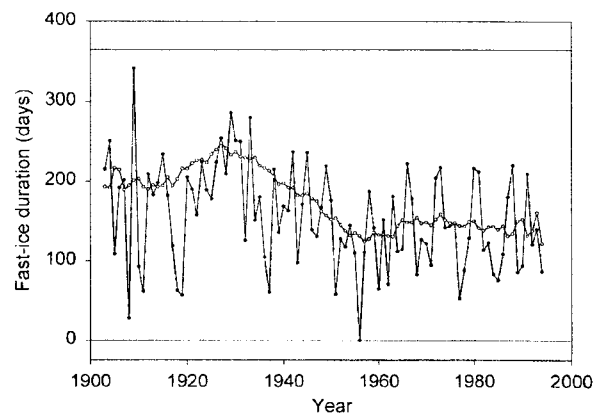


Fig. 5. The duration of winter fast-ice in the South Orkney Islands, 1904 to 1999. This is a composite data set combining data for Orcadas Station, Laurie Island (1904 to 1973) and Signy Island (1947 to 1999). Filled circles show the raw data, and the line shows a tapered fifteen-year running mean. From Murphy *et al.* (1995), with permission.

timing of winter fast-ice in the South Orkney Islands (Murphy *et al.* 1995).

The duration of winter fast-ice in the South Orkney Islands is highly variable, ranging from 342 days (1909) to 0 days (1956). The latter was a year of widespread poor winter sea-ice throughout the Antarctic Peninsula. Time-series analysis indicated three different periods of behaviour. From 1904 to 1930 winter fast-ice duration varied apparently chaotically around a mean of 182 days. From about 1930 to the mid-1950s fast-ice duration remained highly variable but there was a secular decrease in mean duration of about 24 days per decade. From the mid-1950s to the present day the mean duration from the mid 1960s to the late 1980s, with a period of 7-8 years (Fig. 5).

The duration of winter fast-ice in the South Orkney Islands reflects regional patterns of ice dynamics in the Weddell Sea. The cyclicity observed between 1970 and 1991 is thus an expression of dynamics on a broader spatial scale, and satellite data revealed a regular precession of ice anomalies around Antarctic (Murphy *et al.* 1995). This is a large-scale coupled ice/ocean/atmosphere system and the dynamical behaviours has become known as the Antarctic Circumpolar Wave (White and Peterson 1996).

Dayton (1989) was the first to draw attention to the possible connection between variability in the Antarctic coastal marine ecosystem and the El Niño Southern Oscillation (ENSO). Murphy *et al.* (1995) were able to demonstrate a statistical correlation between fast-ice and

seawater temperature anomalies at Signy Island and ENSO. It is now recognised that ENSO plays a significant, if not always over-riding, role in the dynamical behaviour of the Southern Ocean.

Although it is acknowledged that the now widely observed decadal-scale variability in the Southern Ocean must have significant ecological consequences, data on these are lacking. Records of seawater temperature and chlorophyll biomass at Signy Island show marked interannual variability (Clarke *et al.* 1988; Murphy *et al.* 1995; Clarke and Leakey 1996) but as yet there are few other data for other sites in Antarctica (although observations undertaken as part of the international EASIZ, Ecology of the Antarctic Sea Ice Zone, programme will increase our knowledge here).

It is likely that interannual variability in seawater temperature will influence processes such as embryonic or larval development which in some Antarctic species are very sensitive to temperature (Bosch *et al.* 1987; Stanwell-Smith and Peck 1998). Variability in primary production is also likely to influence ecological processes such as growth and reproduction. The literature contains many anecdotal observations of interannual variability in settlement or recruitment of Southern Ocean benthic invertebrates but as yet no study has been able to link these with

variability in the physical or biotic environment.

Studies of benthic marine invertebrates which record a history of individual growth in their skeleton have revealed that interannual variability in growth rate is widespread. The only study to date where this variability has been linked to the environments is that of Barnes (1995) who showed that interannual variability in the growth rate of the bryozoan *Cellarinella watersi* was correlated tightly to the duration of the bloom of nanophytoplankton of which it feeds (Fig. 6).

The slow growth rates and extended life-spans of many Southern Ocean benthic marine invertebrates mean that individual organisms will experience significant decadal-scale interannual variability within their life-span. More data on the effect of this variability on growth, reproductive output and recruitment will be essential to improve our understanding of the population dynamics of Southern Ocean benthic marine invertebrates.

Long-term environment change

From the point of view of an ecologist, long-term environmental change can be regarded as that with a temporal scale longer than the life-span an individual organisms. For Southern Ocean marine invertebrates, some of which probably reach ages in excess of 100 years (Dayton *et al.* 1984), this means environmental change on time scales $> 10^2$ - 10^3 years.

For the Southern Ocean the best source of data documenting environmental variability on these scales come from ice cores and sediment cores, and both indicate significant variability (Leventer *et al.* 1996; Peel *et al.* 1996; Kirby *et al.* 1998; Domack and Mayerski 1999; Petit *et al.* 1999). It is likely that this variability will have ecological impact through factors such as primary production, but as yet we have no firm data.

On longer time scales the most impact variability is that associated with Milankovitch cyclity (Clarke and Crame 1989, 1992). It is likely that in Antarctica these changes in received solar energy have driven significant changes in ice volume, resulting in periodic advance and retreat of ice over the continental shelves (summarised recently by Anderson 1999). The poor Cenozoic fossil record of the Antarctic marine fauna means that we have no direct record of the biological consequences of these changes. We can, however, make inferences from the contemporary fauna.

The Southern Ocean benthic marine fauna is generally rich and diverse (Arntz *et al.* 1997) indicating that the cycles of advance and retreat of continental ice may have

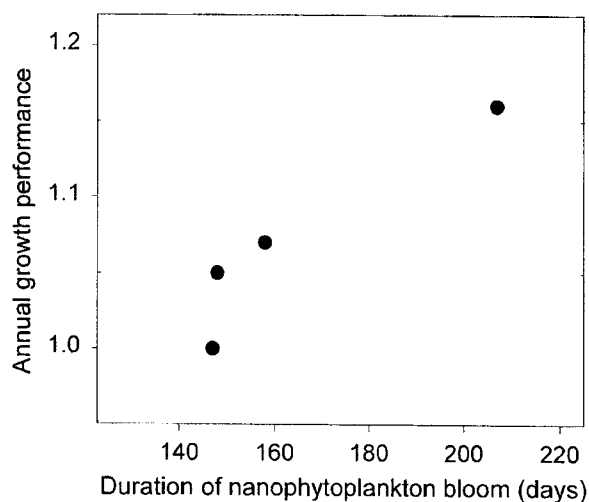


Fig. 6. Relationship between annual growth in the bryozoan *Cellarinella watersi* and the duration of the nanophytoplankton bloom at Signy Island, South Orkney Islands, 1988 to 1991. Growth data were derived from a fitted logarithmic growth model, and the bloom was defined as the period when nanophytoplankton chlorophyll biomass exceed 10 ng m^{-3} . From Barnes (1995), with permission.

promoted speciation in some taxa through repeated isolation and allopatric speciation (Clarke and Crame 1989; 1992), a process termed the climatic diversity pump by Valentine (1968). Compared with continental shelf faunas elsewhere, many benthic taxa in Antarctic have a broader bathymetric range extending into deep water (Brey *et al.* 1996). This suggests that these taxa were forced into the deeper water of the continental slope during periods of glacial maxima.

The fossil record indicates that the Eocene marine fauna of Antarctica was different from that of today. In particular the fish fauna was strikingly different (Eastman 1993) and there was a more diverse decapod crustacean fauna than we see today (Clarke and Crame 1989). The climate and the seawater temperature of Antarctica cooled significantly during the later Cenozoic, with significant continental glaciation probably dating from the rapid cooling at around 35-30 Ma BP (Anderson 1999). It is certain that the cooling and onset of glaciation were important events in the evolution of the Southern Ocean marine fauna, but the absence of a fossil record at critical times makes interpretation difficult.

The modern fauna is characterised by the relative lack of decapods, and the radiation of a single suborder of teleost fishes, the notothenioids (Eastman 1993). This radiation exhibits some characteristics of a species flock, and it is likely that the key innovation underpinning this radiation was the evolution of the antifreeze glycoprotein (Eastman and Clarke 1998).

Long-term environmental variation has thus been important in shaping the modern fauna. Although it is tempting to speculate on the potential impact of the current climate change, both regional and global, on the benthic marine fauna of Antarctica, our current knowledge of both patterns and processes is too fragmentary to permit informed discussion. A key area for future research will be to determine the role of Milankovitch and shorter-term variability on the evolution of the benthic fauna.

Acknowledgements

I thank Dr. Hosung Chung and the organisers of the 7th International Symposium on Antarctic Science for the invitation to give this paper, and for supporting my attendance. My research is supported by the British Antarctic Survey (NERC), I thank Eugene Murphy for many enlightening discussions on the nature and role of environmental variability in Antarctic ecology. This paper is a contribution to the SCAR EASIZ (Ecology of the

Antarctic Sea Ice Zone) programme.

Reference

- Anderson, J.B. 1999. *Antarctic Marine Geology*. Cambridge University Press. 289 p.
- Arntz, W.E., J. Gutt, and M. Klages. 1997. Antarctic marine biodiversity: an overview. p. 3-14. In: *Antarctic Communities: Species, Structure and Survival*, eds. by B. Battaglia, J. Valencia, and D.W.H. Walton. Cambridge University press.
- Barnes, D.K.A. 1995. Seasonal and annual growth in erect species of Antarctic bryozoans. *J. Exp. Mar. Biol. Ecol.*, 188, 181-198.
- Barnes, D.K.A. and A. Clarke. 1994. Seasonal variation in the feeding activity of four species of Antarctic bryozoan in relation to environmental factors. *J. Exp. Mar. Biol. Ecol.*, 181, 117-131.
- Barnes, D.K.A. and A. Clarke. 1995. Seasonality of feeding activity in Antarctic suspension feeders. *Polar Biol.*, 15, 335-340.
- Bosch, I., K.A. Beauchamp, M.E. Steele, and J.S. Pearse. 1987. Development, metamorphosis and seasonal abundance of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayen*. *Biol. Bull.*, 173, 126-135.
- Brey, T. and A. Clarke. 1993. Population dynamics of benthic marine invertebrates in Antarctic and Subantarctic environments: are there unique adaptations? *Antarct. Sci.*, 5, 253-266.
- Brey, T., C. Dahm, M. Gorny, M. Klages, M. Stiller, and W.E. Arntz. 1996. Do Antarctic benthic invertebrates show an extended level of eurybathy? *Antarct. Sci.*, 8, 3-6.
- Brockington, S. and A. Clarke. The relative importance of temperature and food to the metabolism of a marine invertebrate. *J. Exp. Mar. Biol. Ecol.* (under review).
- Clarke, A. 1983. Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanogr. Mar. Biol. Ann. Rev.*, 21, 341-453.
- Clarke, A. 1988. Seasonality in the Antarctic marine ecosystem. *Comp. Biochem. Physiol.*, 90B, 461-473.
- Clarke, A. Evolution at low temperature. In: *Evolution on Planet Earth: The Impact of the Physical Environment*, eds. by A. Lister and L.J. Rothschild. Academic Press. (In press).
- Clarke, A. and J.A. Crame. 1989. The origin of the Southern Ocean marine fauna. p. 253-268. In: *Origins and Evolution of the Antarctic Biota*, ed. by J.A. Crame. The Geological Society, London.
- Clarke, A. and J.A. Crame. 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. *Phil. Trans. Roy. Soc. Lond. B.*, 338, 299-309.
- Clarke, A. and R.J.G. Leakey. 1996. The seasonal cycle of phytoplankton, macronutrients and the microbial community in a nearshore Antarctic marine ecosystem. *Limnol. Oceanogr.*, 49, 1281-1294.

- Clarke, A., L.J. Holmes, and M.G. White. 1988. The annual cycle of temperature, chlorophyll and major nutrients of Signy Island, South Orkney Islands, 1969-1982. *Bull. Br. Antarct. Surv.*, 80, 65-86.
- Dayton, P.K. 1989. Interdecadal variation on an Antarctic sponge and its predators from oceanographic climate shifts. *Science*, 254, 1484-1486.
- Dayton, P.K., G.L. Kooyman, and J.P. Barry. 1984. Benthic life under thick ice. *Antart. J. US*, 19, 128.
- Denman, K.L. 1994. Scale-determining biological-physical interactions in oceanic food webs. p. 377-402. In: *Aquatic Ecology. Scale, Pattern and Process*, eds. by P.S. Giller, A.G. Hildrew, and D.G. Raffaelli. Blackwell Scientific Publications, Oxford.
- Domack, E.W. and P.A. Mayerski. 1999. Bi-polar ocean linkages: evidence from late- Holocene Antarctic marine and Greenland ice-core records. *Holocene*, 9, 247-257.
- Eastman, J.T. 1993. *Antarctic Fish Biology. Evolution in a Unique Environment*. Academic Press, San Diego. 322 p.
- Eastman, J.T. and A. Clarke. 1998. A comparison of adaptive radiations of Antarctic fish with those of non-Antarctic fish. p. 3-26. In: *Fishes of Antarctica, A Biological Overview*, eds. by G. di Prisco, E. Pisauo, and A. Clarke. Springer-Verlag, Berlin.
- El-Sayed, S.Z. 1998. Seasonal and interannual variabilities in Antarctic phytoplankton with reference to krill distribution. p. 107-119. In: *Antarctic Ocean and Resources Variability*, ed. by D. Sahrhage. Springer-Verlag, Berlin.
- Fogg, G.E. 1991. The phytoplanktonic ways of life. *New Phytol.*, 118, 191-232.
- Gutt, J. and T. Schichkan. 1998. Epibiotic relationships in the Antarctic benthos. *Antart. Sci.*, 10, 398-405.
- Haury, L.R., J.A. McGowan, and P.H. Loiebe. 1978. Patterns and processes in the time- space scales of plankton distributions. p. 277-328. In: *Spatial Pattern in Plankton Communities*, ed. by J.H. Steele. Plenum Press, New York.
- Kirby, M.E., E.W. Domack, and C.E. McClennan. 1998. Magnetic stratigraphy and sedimentology of Holocene glacial marine deposits in the Palmer Deep, Bellingshausen Sea, Antarctica: implications for climate change? *Mar. Geol.*, 152, 247-259.
- Leventer, A., E.W. Domack, S.E. Ishman, S. Brachfeld, C.E. McClennan, and P. Manley. 1996. Productivity cycles of 200-300 years in the Antarctic Peninsular region: understanding linkages among the sun, atmosphere, oceans, sea-ice and biota. *Bull. Geol. Soc. Amer.*, 108, 1626-1644.
- Littlepage, J.L. 1965. Oceanographic investigations in McMurdo Sound, Antarctica. *Antart. Res. Ser.*, 5, 1-37.
- Mann, K.H. and J.R.N. Lazier. 1991. *Dynamics of Marine Ecosystems. Biological-physical Interactions in the Oceans*. Blackwell Scientific Publications, Boston. 466 p.
- Murphy, E.J., D.J. Morris, J.L. Watkins, and J. Priddle. 1988. Scales of interaction between Antarctic krill and the environment. p. 120-130. In: *Antarctic Ocean and Resources Variability*, ed. by D. Sahrhage. Springer-Verlag, Berlin.
- Murphy, E.J., A. Clarke, C. Symon, and J. Priddle. 1995. Temporal variation in Antarctic sea-ice: analysis of a long-term fast-ice record from the South Orkney Islands. *Deep-sea Res.*, 42, 1045-1062.
- Peel, D.A., R. Mulvaney, E.C. Pasteur, and C. Chenery. 1996. Climate changes in the Atlantic sector of Antarctica over the past 500 years from ice-core and other evidence. p. 243-262. In: *Climatic Variations and Foraging Mechanisms of the Last 2000 Years. NATO ASI Series 41*, eds. by P.D. Jones, R.S. Bradley, and J. Jouzel. Springer-Verlag, Berlin.
- Petit, J.R., J. Jouzel, D. Raynaud, N.I. Barkov, J.M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygne, M. Delmotte, V.M. Kotlyakov, M. Lagrand, V.Y. Lipenkov, C. Lorius, L. Pepin, C. Ritz, E. Saltzman, and M. Stievenand. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, 399, 236-429.
- Smith, W.O. and E. Sakshang. 1990. Polar phytoplankton. p. 477-525. In: *Polar Oceanography, Part B: Chemistry, Biology and Geology*, ed. by W.O. Smith. Academic Press, New York.
- Smith, W.O., Keene N.K., and J.C. Comiso. 1988. p. 131-139. In: *Antarctic Ocean and Resources Variability*, ed. by D. Sahrhage. Springer-Verlag, Berlin.
- Stanwell-Smith, D. and L.S. Peck. 1998. Temperature and embryonic development in relation to spawning and field occurrence of larvae of three Antarctic echinoderms. *Biol. Bull.*, 194, 44-52.
- Valentine, J.W. 1968. Climatic regulation of species diversification and extinction. *Bull. Ecol. Soc. Amer.*, 79, 273-276.
- Vogel, S. 1981. *Life Moving Fluids. The Physical Biology of Flow*. Princeton University Press, New Jersey. 352 p.
- White, W.B. and R.G. Peterson. 1996. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature*, 380, 699-702.

Received Oct. 9, 2001

Accepted Dec 17, 2001