PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1977 **279**, 55-66
doi: 10.1098/rstb.1977.0071

Phil. Trans. R. Soc. Lond. B. **279**, 55–66 (1977) [55]
Printed in Great Britain

Antarctic marine secondary production and the phenomenon of cold adaptation

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For several years marine biologists of British Antarctic Survey have been studying the nearshore communities at Signy Island and South Georgia. Most of these studies have been continued throughout the year so that variations in production in both the long and short term have been investigated.

In this paper changes in the rate of growth of selected crustacean, molluscan and fish species are considered throughout their life histories. Variations in growth rates are considered in relation to temperature, food availability and mode of life and comparisons are made with species from outside antarctic waters.

INTRODUCTION

Following the initial descriptions made of the Antarctic ecosystem (by, for example, Hart 1942; Knox 1970) attempts have been made to quantify both the biomass and production rates of the various components. In his review of the Antarctic ecosystem Holdgate (1967), by gross extrapolation of the very limited information available, was able to quantify biomass, and in some cases production, within very broad limits. The figures presented in that paper have been relied upon heavily in subsequent ecosystem studies and also used as a basis for more detailed studies of selected components (see, for example, White & Robbins 1972; Hardy 1972). In recent years some of the dominant species of the nearshore marine environment at both Signy Island and South Georgia have been made the subject of intensive ecological studies by a variety of people and their results form the basis for this contribution.

The shallow water marine environment of the Antarctic zone is characterized by low temperature with only small seasonal variation which decreases with increasing latitude (figure 1). In spite of this near constant environmental temperature there is nevertheless a very marked seasonal cycle of pelagic primary production (discussed in detail by Fogg in this Symposium). As a result, consumers of phytoplankton will themselves be expected to have considerable biochemical compensation, as for example in their lipid stores (Sargent & Lee 1975; Clarke, in prep.) as well as a discontinuous growth pattern such as is present in *Tryphosella kergueleni* Amphipoda (Bregazzi 1972). Many species which feed preferentially on phytoplankton will, however, utilize detritus if necessary (Mauchline & Fisher 1969; Ponomoreva 1963). Seasonal restrictions on feeding are only of a minor nature at the predator/scavenger level of the food chain. The isopod *Glyptonotus antarcticus* feeds throughout the year (White 1970, 1974) as does the fish *Notothenia neglecta* at Signy Island (figure 2). Although the examples are few compared to the total fauna they do show that the full range, from limited seasonal feeding to continuous year round feeding, is present in the Antarctic nearshore environment.

The fate of the food taken in may for convenience be compartmentalized in the following manner (figure 3).

The standard metabolism of polar organisms has been of particular interest since Scholander, Flagg, Walthers & Irving (1953) compared a wide variety of organisms from widely differing

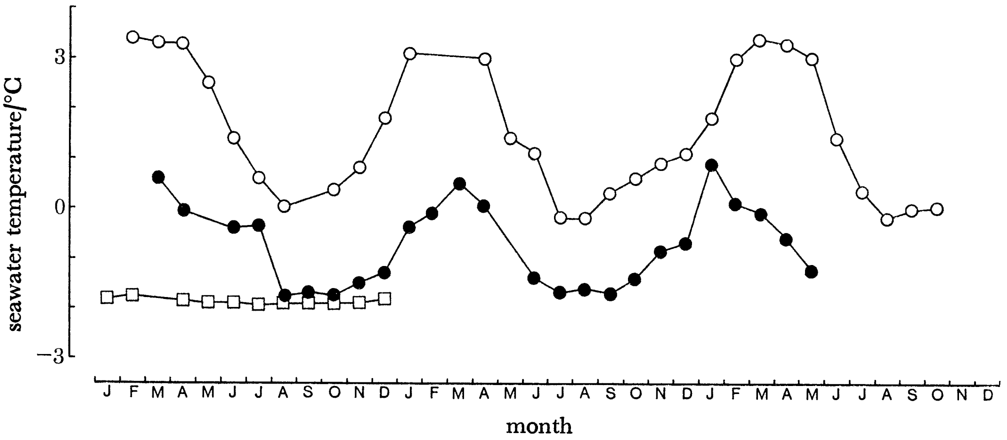

FIGURE 1. Seasonal variation in seawater temperature at three different Antarctic localities. ○—○, South Georgia: King Edward Cove, 54° 17′ S, 10–15 m depth, 1972–4 (Clarke and Lakhani, in press). ●—●, Signy Island: Borge Bay, 60° 43′ S, 30 m depth (Everson, 1970*b*). □—□, McMurdo South, Antarctica, 77° 51′ S, mean (3–275 m depth) (Littlepage 1965).

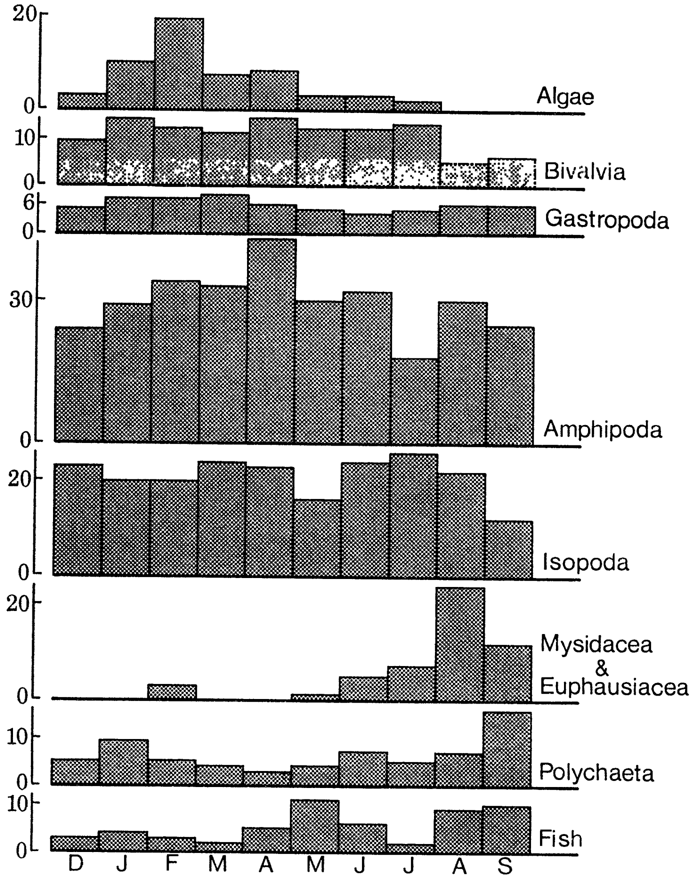

FIGURE 2. Diet of *Notothenia neglecta* throughout the year at Borge Bay, Signy Island, expressed as a percentage of all stomachs examined containing stated food item.

habitats and concluded that Arctic organisms at their environmental temperatures had an appreciably higher rate of standard metabolism than temperate or tropical species would have at polar temperatures. This elevation of metabolic rate is generally referred to as metabolic cold adaptation. In their paper, Scholander *et al.* (1953) give no reason for the existence of cold adaptation but merely draw attention to its existence and argue that cold adaptation is the result of an as yet unidentified selective advantage.

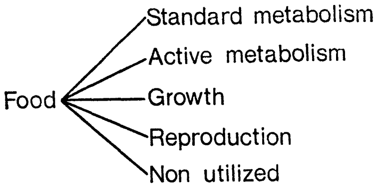

FIGURE 3. Subdivision of the major processes in the animal body requiring energy.

It can be seen from figure 3 that a relative increase in standard metabolism must, in the long term, be compensated for elsewhere. The compensation does not appear to be made by reduction in the formation of reproductive products since large yolky eggs are normal for fish (Marshall 1953; Everson 1970*a*) and prolonged brooding of young is common in Amphipoda (Bregazzi 1972). Although formation of yolk has been shown to take more than one year in *Notothenia neglecta* and *Odontaster validens* (Everson 1970*a*; Pearse 1965) since spawning is annual the total energy laid down is not reduced.

Of the other factors active metabolism and the non-assimilated fraction of the food have not been investigated sufficiently for Antarctic organisms and will therefore not be considered further. The remaining factor, growth, will be considered in relation to locality and standard metabolism.

GROWTH

Although direct comparison of size at a given age will often give an indication of the relative pattern of growth, this is not always reliable for comparing growth rates. A wide variety of equations have been used to describe growth in animals (see Beverton & Holt 1957; Paloheimo & Dickie 1965). However, none of these equations adequately describes growth in sufficient species to allow overall comparisons. Since production is concerned with rate of increase in size the simple relation:

$$\log_e \frac{\text{length at time } (t+1)}{\text{length at time } (t)} \tag{1}$$

has been used here, with length considered relative to the size at the start of the period under consideration rather than age. Although it would be better to use mass as an indication of size there are not sufficient published records of mass at known age to give reasonable comparisons.

Bivalve Mollusca

In figure 4 length at known age for a variety of Antarctic species are shown. These range from the relatively fast growing *Adamussium colbecki* and *Laternula elliptica* to the very slow growing species *Kidderia bicolor* and *Lissarca miliaris*. The last two species grow at a slower rate than *Venus striatula*, a temperate species that is included for comparison. Slow growth, an expected consequence of cold adaptation, is therefore present. It is not, however, universal since half of the species are growing more rapidly than the temperate *Venus striatula*. To make a more realistic comparison the Antarctic scallop *Adamussium colbecki* has been compared with scallops from warmer waters (figure 5). During the early stages the growth rate is similar to that for *Placopecten* but this rate is not maintained as the animals get larger. Thus although *Adamussium* grows quickly for an Antarctic species its growth rate is in general slower than comparable temperate species.

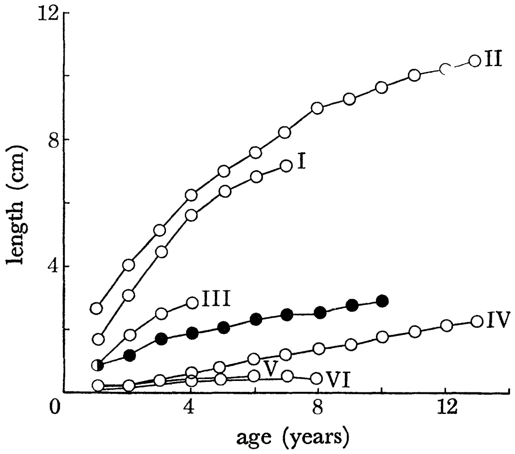

FIGURE 4. Growth in six species of Antarctic bivalve (○) compared with *Venus striatula* from Millport (●, Ansell 1961). I, *Adamussium* (Ralph & Maxwell, unpublished data); II, *Laternula* (Ralph & Maxwell, unpublished data); III, *Gaimardia* (Ralph & Maxwell, unpublished data); IV, *Yoldia* (Rabarts 1971); V, *Kidderia* (Ralph & Everson 1972); VI, *Lissarca* (Richardson, in preparation).

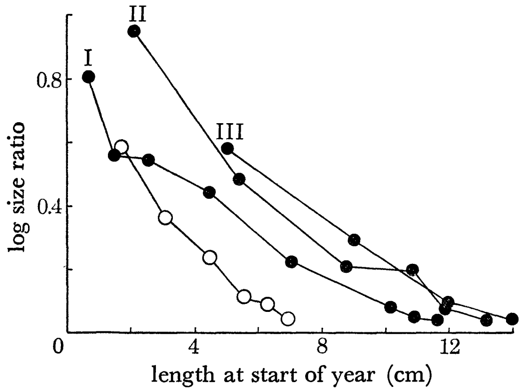

FIGURE 5. Comparison of the growth rate of *Adamussium* (○, Ralph & Maxwell, unpublished data) with those of *Placopecten* (I, Stevenson & Dickie 1954), *Pecten* from Port Erin (II, Baird 1966) and *Pecten* from Holyhead (III, Baird 1966), all as ●.

A natural consequence of a fast growth rate is that those species growing rapidly will tend to attain a large size and therefore be more conspicuous (assuming equal life spans). In comparison with those of temperate waters the majority of bivalve Mollusca in nearshore Antarctic waters are small, thus adding further weight to the conclusion that with relatively few exceptions growth tends to be slow.

Crustacea

In a recent study of the decapod crustacean *Chorismus antarcticus* Clarke & Lakhani (in press) showed that growth in this species was appreciably slower than in any of the other species they examined (figure 6). However, Decapoda are not nearly as abundant in Antarctic waters as they are in temperate waters and it could be argued that *Chorismus* is not a typical example of the crustacean fauna. Of the other crustacean groups, Amphipoda and Isopoda are the two which are most conspicuous and abundant in the nearshore environment. There are published results for growth in three species of Antarctic amphipod: *Bovallia gigantea* (Thurston 1970; Bone 1972), *Cheirimedon femoratus* and *Tryphosella kergueleni* (Bregazzi 1972). Unfortunately direct comparison of growth of Antarctic and temperate species is not valid because of the very great difference in life span between the two groups. This is summarized in figure 7 which is derived from data presented by Bregazzi (1972). The fact that the time taken to grow from hatching to sexual maturity is very much longer in the Antarctic species (30 months as opposed to 7 months; calculated from Bregazzi 1972, Table VI) implies that the rate of growth is also very slow.

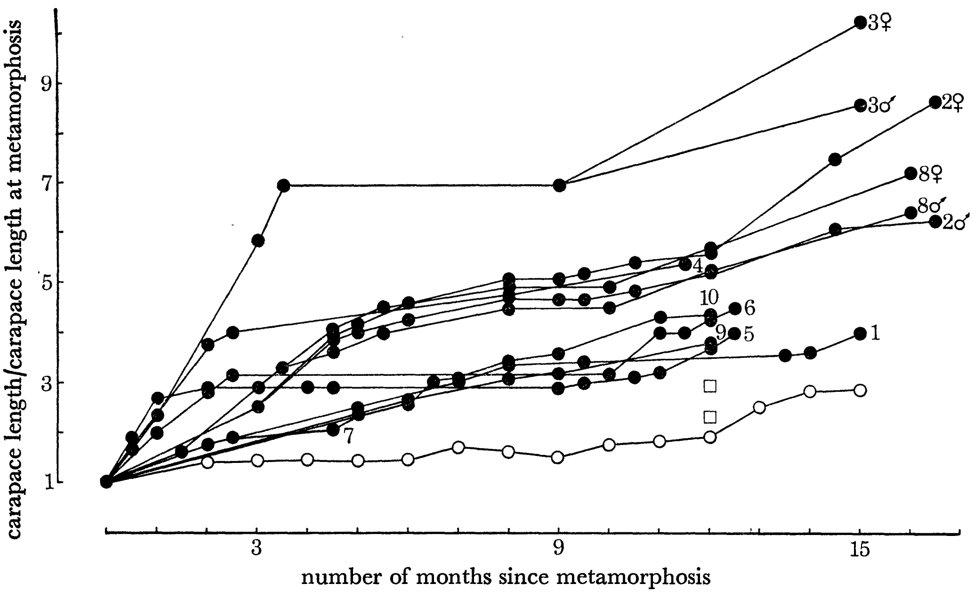

Figure 6. Comparison of the growth rate of the Antarctic prawn *Chorismus antarcticus* (○) with other temperate water carideans (●) and also *Pandalus borealis* from the Arctic (□). Data from Clarke & Lakhani, in press. 1, *Crangon allmanni*; 2, *Spirontocaris lilljeborgii*; 3, *Palaemon serratus*; 4, 5, *Palaemon elegans*; 6, *Palaemon squilla*; 7, *Pandalus montagui*; 8, *Pandalus bonnieri*; 9, 10, *Pandalus borealis* from temperate waters.

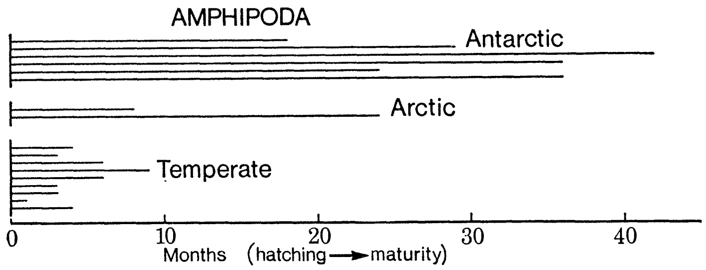

Figure 7. Diagrammatic representation of growth in Amphipoda showing time taken to achieve sexual maturity (derived from data presented by Bregazzi 1972).

The only information available for isopods relates to *Glyptonotus antarcticus* which although attaining large ultimate size (up to 20 cm length) does so over a period of several years (White 1970). This species has been considered as growing ‘relatively rapidly’ (White 1974) but this conclusion is not confirmed by comparison of the size ratio (equation (1)) with the amphipod species considered above. Assuming a 100-day intermoult period (White 1970), the result for *Glyptonotus antarcticus* falls between those for *Bovallia* and *Cheirimedon.*

An interesting relation may also be demonstrated between growth rate and environmental temperature. In figure 8 the growth rate is plotted against the maximum environmental temperature for a number of species. Since growth tends to occur in the warmest summer months the figures are based on the first half year of free living existence and the maximum temperature during that period. The results are interesting for two reasons, firstly because they show the general trend that would intuitively be expected of a slower growth rate of lower temperature, and secondly that *Euphausia superba*, the Antarctic krill, has a much faster growth rate than any of the other Antarctic species. Apart from obvious anatomical differences between the species the most obvious difference between krill and the other crustaceans studied is that the former is totally planktonic. The implications of this are discussed later in relation to metabolism.

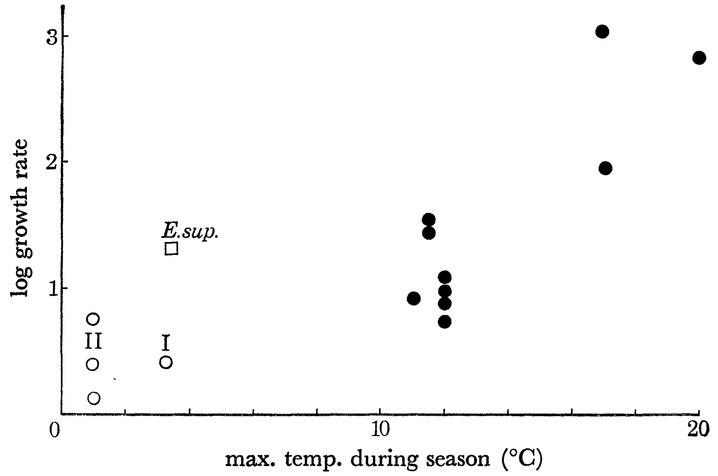

FIGURE 8. Relation between growth rate and maximum environmental temperature during the growth season for selected crustaceans. ●, temperature water Caridea (data derived from information used in preparing figure 6). ○, *Chorismus antarcticus* at South Georgia (Clarke & Lakhani 1977) and three species of Antarctic amphipod (Bone 1972; Bregazzi 1972; Thurston 1970). □, *E. sup.*, *Euphausia superba* (Marr 1962).

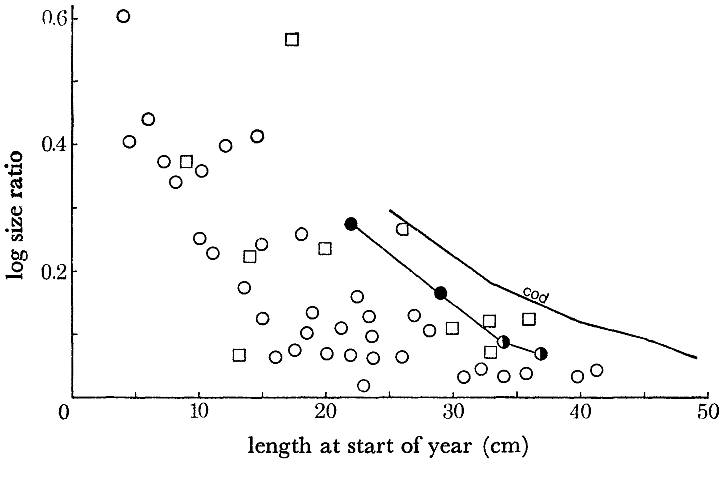

FIGURE 9. Comparison of the growth rates of a variety of Antarctic fish (○, Everson (1970*b*); Hureau (1970) but excluding data for *Notothenia rossii*) with those of Arctic char (□, Grainger 1953), yellowtail flounder (●, Scott 1954) and cod (solid line, May, Pinhorn, Wells & Fleming 1965).

Fish

Because of the relative ease with which age may be determined for fish a far wider range of species have been studied than from any other group of Antarctic marine organisms. These results (with the exception of those for *Notothenia rossii*) are shown in figure 9, from which it is clear that growth rate tends to be slower in Antarctic fish compared with temperate fish. The results for arctic char (*Salvelinus alpinus*), a species whose metabolism has received particular attention, show it to have a growth rate similar to that of the Antarctic fish.

For the first few years of its life *Notothenia rossii* lives demersally in the shallow coastal areas of subantarctic islands. When about five years old the fish move offshore and live pelagically, feeding on krill (*Euphausia superba*) (Olsen 1954). This change in mode of life is accompanied by a very sharp change in growth rate to a level comparable with that of the cod (*Gadus morhua*) (figure 10).

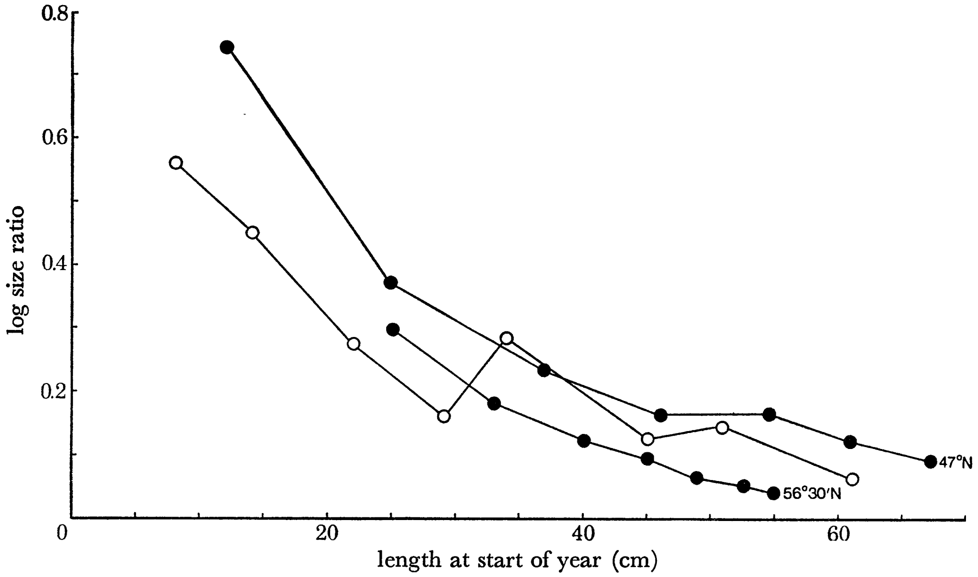

FIGURE 10. Comparison of growth rate of *Notothenia rossii* (○, data from Olsen 1954) with that of cod (●, May *et al.* 1965).

RESPIRATION

In the same way that there are problems in comparing growth between species and groups there are difficulties in comparing respiration rates. It is often not clear how estimates of standard metabolism relate to the actual situation because of unquantifiable but easily-seen stress factors such as insufficient acclimation period or the wrong type of respirometer. In addition the great difference in size range between species even within groups means that valid comparisons are not possible. As far as possible, therefore, comparison has been made below only between experimental animals falling within the same size range and between results that clearly indicate the animals were at rest.

Fish

In his paper discussing cold adaptation Holeton (1974) presents results for oxygen consumption by 12 Arctic fish (*Boreagadus saida*, five species of cottid, three species of zoarcid, two species of liparid and *Salvelinus alpinus*), all of which are lower than those of cold adapted Antarctic fish (results of Wohlschalg 1964). Holeton (1974) considers that the elevated metabolic rates reported by Wohlschalg (1960, 1964) are purely a result of experimental technique. In support of this opinion he mentions several recent papers which contain results that, although not directly comparable because of size difference, nevertheless indicate a standard metabolic rate that is not cold adapted.

The situation based on direct measurement of oxygen uptake rate by Antarctic fish is therefore not clear, although the suggestion that cold adaptation is not present is very strong. Holeton's results for arctic fish clearly indicate that the phenomenon is not present in any of the species he has studied. Growth in one of these (arctic char *Salvelinus alpinus*) has been shown to be similar to that of Antarctic fish (figure 9); this point is discussed later.

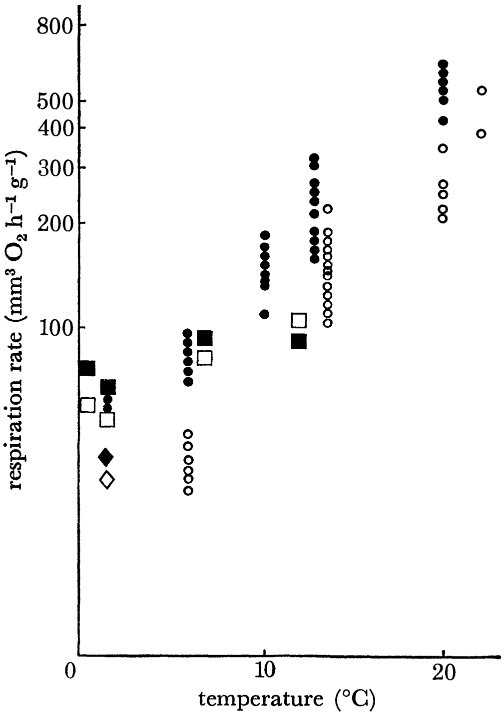

FIGURE 11. Comparison of the respiration rates of two Antarctic Caridea with that of *Crangon crangon*. ●, 100 mg wet *Crangon crangon* data from Hagerman 1970; ○, 200 mg wet *C. crangon* data from Hagerman 1970; ■, 100 mg wet *Chorismus antarcticus* (Maxwell, unpublished data); □, 200 mg wet *C. antarcticus* (Maxwell, unpublished data); ◆, 100 mg wet *Notocrangon antarcticus* (Maxwell, unpublished data); ◇, 200 mg wet *N. antarcticus* (Maxwell, unpublished data).

Crustacea

In his study of the respiration of the Antarctic isopod *Glyptonotus antarcticus*, White (1974) showed clearly that at Signy Island this species is not cold adapted. White's values are appreciably lower than those of Belman (1976) for the same species at McMurdo Sound, although since the latter was using closed chambers it is very likely that the experimental animals had not settled to a genuine standard metabolic rate at the time of the determination. (Belman (1976) also has a difference interpretation of the definition of cold adaptation from that given by Scholander *et al.* 1953.)

Respiration in the other major crustacean group, the Amphipoda, has been studied by several workers (Armitage 1962; Rakusa-Suszczewski & Klekowski 1973; Klekowski, Opalinski & Rakusa-Suszczewski 1973) and a tendency for this group to have elevated metabolic rates is indicated. However, the results for *Orchomonella chilensis* (Armitage 1962) and for *Paramorea walkeri* (Rakusa-Suszczewski & Klekowski 1973) were both obtained using closed respirometers that allowed no time for the animal to become acclimated to the respirometer. It is interesting that the results of Klekowski *et al.* (1973) using a constant pressure respirometer are significantly lower than those of Rakusa-Suszczewski & Klekowski for the same species. This difference is attributed to seasonal variation, although it is more likely to be associated with the technique employed.

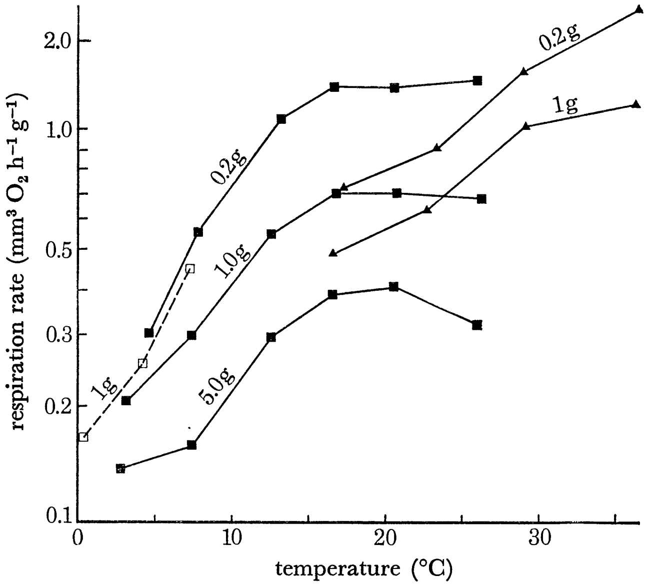

FIGURE 12. Comparison of the respiration rates of bivalve molluscs. ■, *Mytilus edulis* and ▲, *Brachidontes demissus* (Read 1962). □, *Gaimardia trapesina* (Ralph & Maxwell, in press).

At South Georgia a study of the two decapod crustaceans *Chorismus antarcticus* and *Notocrangon antarcticus* has indicated quite clearly that these two species do not exhibit cold adapted metabolism (Ralph & Maxwell, unpublished data) (figure 11). However, as has already been mentioned, this particular group is poorly represented in the Antarctic and should not therefore be considered typical.

The only other group to have been studied is the Antarctic krill *Euphausia superba* which was considered to show cold adapted metabolism (McWhinnie 1964). However, since these experiments were performed in a Warburg respirometer the experimental animals are likely to have been under considerable stress.

Bivalve mollusca

Results are available for one species from this group, *Gaimardia trapensina* (Ralph & Maxwell 1977) which occurs commonly on kelp (*Macrocystis pyrifera*) at South Georgia. From figure 12 it can be clearly seen that the oxygen uptake rate falls well within that for the temperate species measured at the same temperature, indicating that there is no cold adaptation.

Discussion

Having briefly considered growth and standard metabolism in a variety of polar marine species the following features are apparent:

(1) With few exceptions growth is slow.

(2) Rates of standard metabolism in most cases are similar to those expected from extrapolation of results from temperate species to polar temperatures.

Intuitively it is to be expected that as a direct result of temperature, growth in polar habitats will be slow. If the phenomenon of cold adaptation is present, then because of the necessity of channelling additional energy to metabolism, one would expect an even greater reduction in growth rate than would be caused by temperature alone. Cold adaptation is therefore likely to be revealed by consideration of the relationship between growth (production) and respiration.

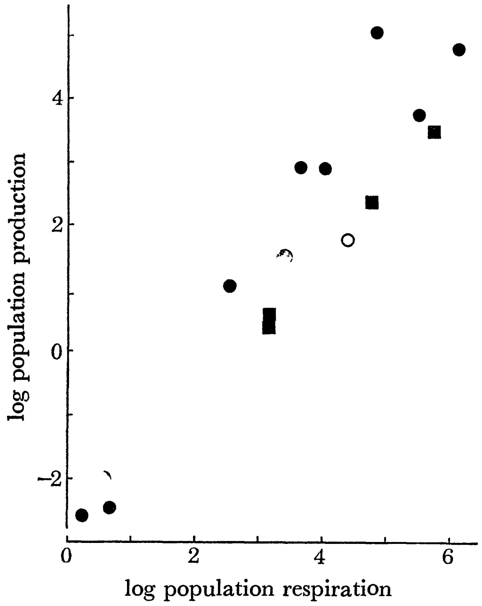

Figure 13. Relation between population production and population respiration for a variety of long-lived poikilotherms (●), including fish (■) (data from McNeill & Lawton 1970), and also *Notothenia neglecta* (○, Everson 1970*b*).

In a review of a wide variety of species from different groups and differing habitats McNeill & Lawton (1971) showed there was a strong correlation between population respiration and population production for homoiotherms and short-lived poikilotherms. They also published results for a series of long lived (life span greater than 2 years) poikilotherms but felt that the data were too widely scattered to produce a valid relationship. These results are plotted in figure 13 along with the results of Everson (1970) for *Notothenia neglecta* at Signy Island. Unfortunately there are no other results of Antarctic population production and respiration available to add to this.

Notothenia neglecta is a species that might be expected to show cold adapted metabolism since it lives continually at a temperature near to zero centigrade and also has a slow growth rate. If it were cold adapted it would be expected to have an above average figure for population respiration when related to production. This is clearly not the case, since the result falls in line with the other fish species considered. One may assume that *N. neglecta* is not cold adapted. This single result suggests that in the Antarctic marine ecosystem metabolism and growth follow the same general trend suggested by McNeill & Lawton (1971) rather than metabolism being elevated by cold adaptation.

There are several very interesting lines of investigation which follow from this tentative hypothesis. In this paper several species have been shown to have a fast growth rate, two of these, *Euphausia superba* and *Notothenia rossii*, live pelagically and since neither is neutrally buoyant it can be argued that they expend more energy living in this way than comparable demersal species and thus fast growth (equivalent to production) would be associated with high population respiration. In the case of the demersal species *Laternula*, *Adamussium* and *Gaimardia* there is no information on which to base any theory – further information on growth, metabolism, gonad production and life histories of populations would therefore be of extreme interest.

This paper would have not have been possible without the cooperation and help of all the marine biologists in the British Antarctic Survey, in particular M. G. White, A. Clarke and J. G. H. Maxwell. I am particularly indebted to A. Clarke, J. G. H. Maxwell and Dr R. Ralph for making available their unpublished results.

Finally I would like to thank Nigel Bonner for reading and amending the manuscript.

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