REVIEW

Eur. J. Entomol. **93**: 489–505, 1996
ISSN 1210–5759

Overwintering strategies of terrestrial invertebrates in Antarctica – the significance of flexibility in extremely seasonal environments

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Antarctica, invertebrate, life history flexibility, diapause, quiescence

Abstract. Antarctic terrestrial communities are characterised by their geographical isolation and the survival of extreme environmental stresses. Of particular significance to life history strategies of organisms in continental and maritime Antarctic zones is the pronounced seasonality, with short (1–4 month) cold summers and long (8–11 month) winters. Activity and growth are largely limited to the summer period, although maintenance costs, undetectable in the short-term, may become significant over winter. Sub-Antarctic invertebrate communities experience a less rigorous regime, as climatic extremes are ameliorated by their oceanic environment, with positive mean temperatures occurring over 6–12 months. Here, year-round activity and growth of invertebrates are common.

This paper considers our limited knowledge of the life histories of sub-Antarctic and Antarctic terrestrial invertebrates, to identify features correlated with seasonal and/or climatic cues. There is little evidence for diapause, although seasonal patterns of variation in cold tolerance and cryoprotectant production in direct response to desiccation and decreasing temperatures have been reported. A rapid response to feeding and growth opportunity is shown by maritime Antarctic species, irrespective of season, although moulting does not occur over winter. Associated reduction of feeding, along with arrested growth and reproductive activity due to the low thermal energy budget over winter are probably sufficient to explain the peaks of moulting and reproduction often observed at the end of winter. Generally there is a high level of flexibility in the observed species life histories, with varying developmental duration and much overlap of generations being the norm, particularly in maritime and continental Antarctica.

A formal diapause may be a disadvantage in maritime and continental Antarctic zones, as it would reduce the opportunity of capitalizing on short periods of optimal environmental conditions, and could be erroneously triggered by severe conditions during summer. In contrast, the development of specific overwintering strategies including diapause may be unnecessary or even irrelevant in much of the sub-Antarctic, where seasonality is greatly reduced and the risk of severe or stressful environmental conditions during winter is negligible.

INTRODUCTION

Antarctica is conventionally separated into three major zones – the sub-, maritime and continental Antarctic (Lewis Smith, 1984; Longton, 1988). There is greater similarity between communities within than between zones. The continental Antarctic consists of the majority of the Antarctic continent with the exception of the west coast of the Antarctic Peninsula and associated island groups. The maritime Antarctic includes those parts of the Peninsula and additionally the South Shetland, South Orkney and South Sandwich Island groups and Bouvetøya. The sub-Antarctic comprises the major island groups of the Southern Oceans (South Georgia, Marion and Prince Edward Islands, Îles Crozet, Îles Kerguelen, Heard Island and Macquarie Island) (Fig. 1).

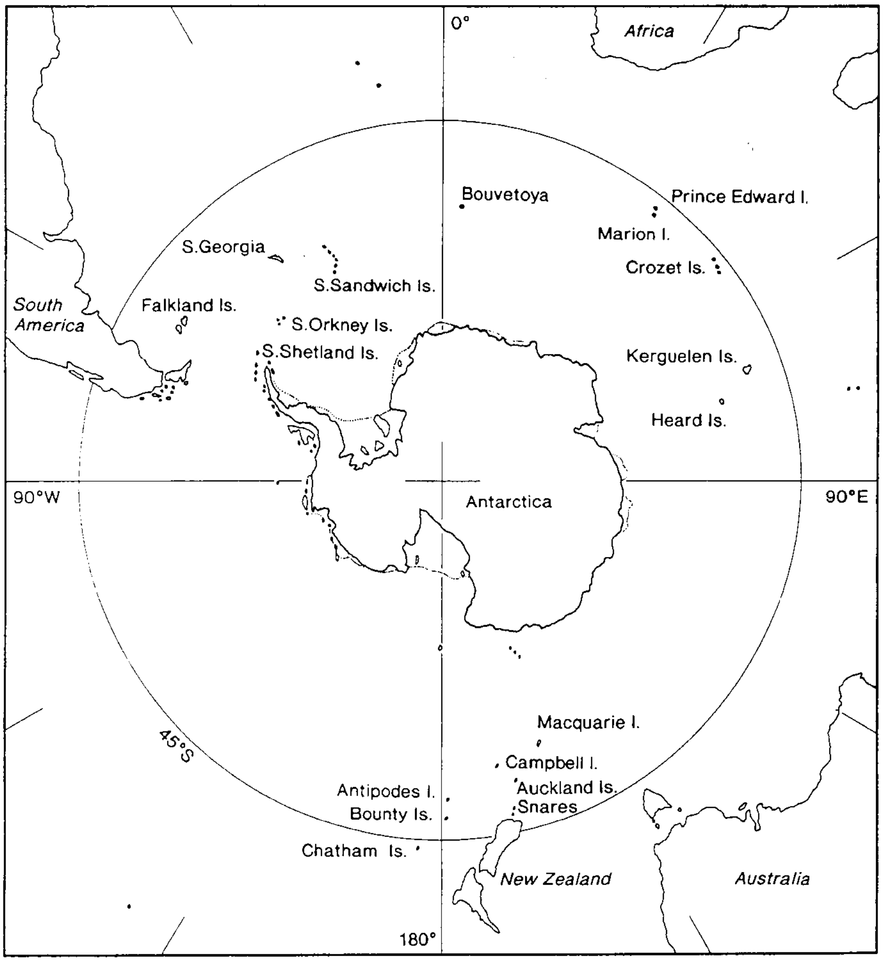

Fig 1. Map of the Antarctic region, indicating areas mentioned in the text, and their relationship to the other southern hemisphere continents.

Compared to northern polar and temperate regions, the terrestrial fauna and flora of all three Antarctic zones are species-poor, probably largely due to their isolation from the other southern continents, and the relatively recent and continuing recession of permanent ice sheets. General faunal and floral descriptions are given by Block (1984), Lewis Smith (1984) and Longton (1988). The invertebrate fauna of the continental Antarctic is most restricted, being limited to small areas of ice-free ground and rock faces. Very low annual water input is typical, to the extent that more extensive ice-free areas, such as the "Dry Valleys" of the Victoria Land, are described as cold deserts. Such environments therefore often face severe water stress. The arthropod fauna consists of a small number of species of mites (Acari) and springtails (Collembola). Microinvertebrates such as nematodes may be the dominant or only animal group represented in cold desert soils (Freckman &

Virginia, 1991; Powers et al., 1995). The maritime Antarctic is generally wetter, at least during summer, due to the oceanic influence and has developed much larger areas of bryophyte and lichen-dominated fellfield, moss carpet and moss bank. Again, Acari and Collembola are dominant, although two species of Diptera are resident with restricted distributions. Groups of "higher" arthropods (predominantly Diptera and Coleoptera, but also Lepidoptera, Hymenoptera, Hemiptera, Siphonaptera, Thysanoptera and Araneae) are better represented on the sub-Antarctic islands (Gressitt, 1970). This may be related to the presence in the sub-Antarctic of habitats dominated by tussock-forming grasses and woody herbs, although Chown (1990) highlights the high insect diversity that may be found in epilithic habitats not dominated by angiosperms.

Overwintering tactics, both behavioural and physiological, are likely to be most highly developed in environments showing the greatest variation between summer and winter conditions (extreme seasonality). Reliable seasonal cues may be more likely to exist and be identifiable in such environments. Seasonal variations in temperature are likely to be of greatest significance to invertebrates of the Antarctic, as they will define the thermal energy budget within which the organism must survive, the availability of free water, and any requirement for adaptations to avoid damage due to extreme cold or heat. Seasonal changes in free water availability are important in many Antarctic habitats (Kennedy, 1993). This is particularly true for inhabitants of continental cold deserts where, additionally, water availability is only in part related to temperature, as the major source of water in these environments is the spring melt.

TABLE 1. General summary of microclimatic data for a range of sites within the continental, maritime and sub-Antarctic zones. (n.d. = no data)

Zone	Months with positive mean air temperatures	Site	Range of microhabitat temperatures (°C)	
			Winter	Summer
Sub-Antarctic	6 to 12	Grytviken, Husvik (South Georgia) (c. 54°S)	> –4	–1 to +30
		Marion Island (c. 47°S)	n.d.	–4 to +34
Maritime Antarctic	1 to 4	Signy Island (South Orkney Is.) (c. 60°S)	–20 to +3	–5 to +35
		Two Step Massif (Alexander I) (c. 72°S)	–33 to –10	–4 to +31
Continental Antarctic	0 to 1	Dronning Maud Land	–34 to –10	–10 to +34
		Wilkes Land	n.d.	–10 to +40
		South Victoria Land	n.d.	–10 to +11
		Ross Island	n.d.	–8 to +25

References:
Sub-Antarctic – Lewis Smith & Walton (1975), Holdgate (1977), Smith (1982), Heilbronn & Walton (1984), Chown & Crafford (1992), MacAlister (unpublished data).
Maritime Antarctic – Lewis Smith (1972), Walton (1982), Pickup, (1990a), Davey et al. (1992), Kennedy (1995), Convey & Lewis Smith (unpublished data).
Continental Antarctic – Janetschek (1967b), Block (1985), Sømme (1986), Lewis Smith (1988), Marshall et al. (1995), Newton (1996).

Walton (1984) presents a wide-ranging discussion of environmental conditions prevailing in the different Antarctic zones. Table 1 summarises typical ranges of microhabitat temperatures experienced at sites in each of the three zones (obviously variation at a single site may not cover the range experienced in the zone as a whole). It is clear that the continental and maritime Antarctic both have highly seasonal climates. Mean summer temperatures are lower in the continental Antarctic and although similar microhabitat maxima are recorded, the probability of temperatures considerably below 0°C exists during the summer period, which may itself be as short as one month. Winter temperatures in both zones are low enough to preclude invertebrate activity and to lead to the development of extensive cold tolerance. However, the maritime Antarctic also experiences periods of thaw during all winter months, leading to the possibility of short periods of invertebrate activity. In contrast, the sub-Antarctic has a cool but not extreme climate year-round, with relatively low seasonal variation in temperatures due to oceanic damping.

GENERAL STRATEGIES FOR WINTER SURVIVAL

The ecology and physiology of invertebrate overwintering in temperate and northern polar environments have been extensively studied, and are comprehensively reviewed by Mansingh (1971), Tauber et al. (1986), Danks (1987, 1990, 1991, 1992), Schuster & Murphy (1991, part three) and Leather et al. (1993), amongst others. Likewise, there is a considerable literature on the related subject of cold tolerance strategies in temperate and polar invertebrates (e.g. Baust & Rojas, 1985; Zachariassen, 1985; Cannon & Block, 1988; Sømme, 1989; Block, 1990; Bale, 1993).

Unfortunately, the terminology used by different authors to describe overwintering states often overlaps and is sometimes contradictory. Strategies are generally considered under two main classes, quiescence and diapause. Quiescence is an immediate and reversible response to prevailing environmental conditions, and diapause is a fixed consequence of specific environmental cues ("token cues") leading to a fixed or variable period of developmental or reproductive arrest (Tauber et al., 1986; Danks, 1987). Mansingh (1971) includes a third class of "oligopause", representing an intermediate stage with longer periods of winter inactivity than in quiescence, requiring preparatory accumulation of energy reserves. The term "dormancy" has been used to describe periods of inactivity in all three of the above states, and is therefore of limited use (see Tauber et al., 1986, for a clear discussion of the terminology associated with overwintering states). Migration (i.e. complete avoidance of unsuitable environmental conditions by leaving the geographical area) is generally considered as an alternative strategy to diapause (e.g. Danks, 1987). However, it is underlain by at least some of the same physiological and behavioural changes as diapause (Tauber et al., 1986), and these authors consider that both dormancy and migration may be different manifestations of the diapause syndrome.

In the current study, four aspects of overwintering strategies are recognised that may be utilised by invertebrates. The occurrence of the two major strategies of quiescence and diapause (as described above) will be examined in detail. In addition, two aspects of life history and ecology that may allow survival in, or exploitation of, parts of a habitat that is otherwise too harsh for a given species – winter activity and local avoidance of suboptimal conditions – will be considered (after Leather et al., 1993). Seasonal migrations are not observed in Antarctic terrestrial invertebrates, and the topic will not be considered further here.

In the absence of specific studies of Antarctic species, evidence correlated with the occurrence of quiescense or diapause must be extracted from studies of a range of features of life history and physiology. Three features relating directly to phenology may be considered – the identification of specific overwintering life stages, any occurrence of seasonal moult synchronisation, and occurrence of reproductive arrest. Evidence relating to more specific developmental activities may also be examined – the occurrence of winter activity (including feeding, growth and moulting), and the seasonal accumulation and use of energy reserves. Finally, seasonal influences on the development and loss of cold tolerance adaptations can be examined.

The primary aim of this paper is to examine how far the general strategies of overwintering mentioned above can be applied to terrestrial invertebrates occurring on the Antarctic continent and sub-Antarctic islands. Although there are a number of descriptions of life history patterns and detailed experimental studies of the physiological mechanisms of cold tolerance of various Antarctic species, there has been little attempt to tie this information together, and to field studies. This paper will attempt to draw together a wide range of life history and physiological studies, to identify seasonal patterns in the observed variations, and relate these to environmental cues.

TACTICS EMPLOYED BY ANTARCTIC SPECIES

Observed strategies – Continental Antarctic

The paucity of published information relevent to the life histories of Antarctic terrestrial invertebrates is highlighted by the fragmentary studies of a small number of continental Antarctic species. With temperatures conducive to growth, even at the microhabitat level, occurring for as little as 1–2 months during the short summer, long development times and extended life cycles have been proposed, although not explicity proven, for Collembola such as *Cryptopygus sverdrupi* (Sømme, 1986), *Gomphiocephalus hodgsoni* (Janetschek, 1967a, 1970) and Acari such as *Maudheimia wilsoni* (D.J. Marshall, pers. comm.). All these species are likely to be able to overwinter in most, if not all, life stages, although *M. wilsoni* may have a peak of egg-laying activity early in summer, which dies away as winter approaches (D.J. Marshall, pers. comm.). Within this pattern, rapid development through individual instars may be possible. Janetschek (1967a) reported instar durations as short as 6.4 days for *G. hodgsoni*, which if continued throughout development would allow sexual maturity to be reached in 38.5 days. This would allow the species to take advantage of the short summer period of "mild" weather.

In the extreme environment of the continental Antarctic, freeze-thaw cycles may be a daily occurrence in summer, with night-time temperatures below –15°C (e.g. Marshall et al., 1995). Therefore it is advantageous for individuals to maintain a high level of cold tolerance even during summer. Field-collected summer specimens of *C. sverdrupi* had supercooling points below –20°C, while actively feeding on various algae (Sømme, 1986). Similarly *G. hodgsoni* had a lower limit of survival of –28°C (Janetschek, 1970), and supercooling points down to –30°C as did the mite *Stereotydeus mollis* (Block, 1985). The springtail *Isotoma klovstadi* has a lethal cold temperature between –50 and –60°C (Pryor, 1962). There is also evidence that continental Antarctic plant species may show a similar constant level of cold tolerance year-round (Melick & Seppelt, 1994). No studies of cold tolerance of any continental invertebrate during winter have been made, although it is likely that they will experience temperatures considerably lower than their summer supercooling capacity. However, Sømme (1986) demonstrated a significant reduction in supercooling point in *C. sverdrupi* acclimated at progressively lower temperatures. Virtually no information is available on potential seasonal responses to environmental conditions or cues, with the exception of the observation of Pryor (1962) that *I. klovstadi* enters aestivation in response to very low levels of relative humidity (< 15%), which occur in many continental Antarctic sites as terrestrial habitats dry out after the initial spring thaws. This is likely to be an opportunistic response to an immediate cue.

Alternative tactics may be available to micro-invertebrates such as nematodes (Wharton, 1995) and tardigrades (Ramløv & Westh, 1992). Cryptobiosis (reversable cessation of metabolism) may occur, often in the form of anhydrobiosis, such that individuals may survive exposure to extreme (and biologically unrealistic) low temperatures (between −180 and −271°C) (Hadley, 1994, Chapter 2). This ability has been identified experimentally in a continental Antarctic tardigrade (Sømme & Meier, 1995) and maritime Antarctic nematodes (Pickup & Rothery, 1991) but its relevence to field survival is unclear, as these groups also have well-developed cold tolerance strategies in the hydrated state. Cryptobiosis has been reported in only a few instances in arthropods (Collembola and Diptera) (Hadley, 1994), and in no Antarctic species. Continental Antarctic individuals of the nematode *Panagrolaimus davidi* are able to survive intracellular freezing (Wharton & Ferns, 1995), which has previously been considered fatal to whole organisms. It should also be noted that studies of two Arctic tardigrades describe overwintering predominantly as specialised frozen cysts, and less frequently as adults or eggs (Westh & Kristensen, 1992).

Preliminary conclusions that may be drawn from these studies are that continental Antarctic invertebrates show great flexibility in those aspects of their life cycle relevent to overwintering tactics, particularly with the ability to overwinter in all life stages and associated variation in development times leading to the general occurrence of overlapping generations. Predictably, physiological cold tolerance abilities are well-developed and, unusually, may not be reduced by feeding activity (the presence of gut contents usually provides nucleating agents for ice formation, thereby reducing cold tolerance in freeze-susceptible species; Cannon & Block, 1988; Block, 1990). There is no evidence for the use of programmed environmental cues to influence overwintering strategy or life history. Indeed such a response might be disadvantageous in that it could restrict an organisms' ability to take advantage of local but unpredictable availability of microhabitat conditions suitable for activity. This would further reduce the opportunity for development in an already highly truncated summer season.

Observed strategies – Maritime Antarctic

A wider, though still disjointed, range of studies have been carried out on the ecology and physiology of overwintering terrestrial invertebrates in the maritime Antarctic. This literature covers some Acari, Collembola and Diptera, with more limited information available on Nematoda and other microscopic groups.

As described for continental Antarctic species, the ability to overwinter in all or most life stages is widespread, with the associated occurrence of overlapping generations in field populations, and widely varying developmental rates. This pattern is true for the common and widely distributed species *Alaskozetes antarcticus* (Acari) (Convey, 1994a) and *Cryptopygus antarcticus* (Collembola) (Burn, 1981; Block, 1982; Convey, 1994b), and also the prostigmatid mites *Eupodes* spp. and *Nanorchestes berryi* (Booth & Usher, 1986). However, other species show more limited overwintering abilities. All three Diptera present in the region (the resident chironomids *Parochlus steinenii* and *Belgica antarctica* and the introduced *Eretmoptera murphyi*) overwinter as larvae, *B. antarctica* predominantly in the second and fourth instars (the others unknown), with adults and eggs only being found during summer (Convey & Block, 1996; Sugg et al., 1983). The prostigmatid mite *Ereynetes macquariensis* (Booth & Usher, 1986) and the mesostigmatid *Gamasellus racovitzai* (Lister, 1984) may have an annual life cycle and overwinter predominantly as the final instar nymph, with a moult to adult and oviposition concentrated in early spring. The springtail *Parisotoma octooculata* overwinters twice, as the egg and 4th or 5th juvenile instar, which has been suggested as evidence for a relatively late colonisation of the polar region by this temperate genus (Burn, 1984a). Within these more structured life cycles, a proportion of individuals overwinter successfully in other juvenile instars and flexibility in development times remains possible.

Unlike continental Antarctic terrestrial habitats, where winter temperatures are unlikely to rise high enough to allow any form of invertebrate activity, positive air temperatures are experienced briefly in all winter months in much of the maritime Antarctic (refs given in Table 1). This leads to the possibility of winter activity and feeding, but carries the potential costs of increased metabolic maintenance demands below any threshold for assimilation and a risk of loss of cold tolerance associated with hydration and/or feeding. Infrequent opportunistic winter activity and feeding appears to be the norm, with the opportunity defined by thawing of the overwintering site. Species overwintering in moss clumps or associated with encrusting lichens (e.g. the collembolan *C. antarcticus* and the oribatid mite *Halozetes belgicae*) are therefore more likely to experience brief thaws during winter than those that overwinter deeper in the peat profile (Diptera) or effectively surrounded by ice under rocks (the oribatid mite *A. antarcticus*). Such winter activity and feeding during thaws have been demonstrated in *C. antarcticus, A. antarcticus* and *H. belgicae* (Convey, 1992). This appears to be a rapid opportunistic response to short-term variation in local environmental conditions, however, there is no empirical evidence available on its effect on individual cold tolerance, or on the speed of response to, or mortality caused by, the subsequent return to normal winter temperatures. The gut clearing response of *C. antarcticus*, eliminating potential ice nucleators at the onset of decreased temperatures, is known to be rapid, although it is not clear whether this is an active response or simply a function of cessation of feeding (Burn, 1982; Sømme & Block, 1982) (the latter authors also highlight the possibility that some food types may not affect supercooling capacity).

The metabolic costs of overwintering may be significant. Energy reserves may be depleted by low respiration rates sustained over long periods, in the absence of opportunity for assimilation. The springtail *C. antarcticus* has a positive temperature threshold for net assimilation (Burn, 1984b), whilst feeding activity ceases as temperatures approach 0°C. Respiration has been detected at –4°C in the mite *A. antarcticus* (Block, 1977). *A. antarcticus* experiences mass loss during winter (Convey, 1994a), which may be associated with seasonal depletion of fat reserves (Convey, 1992). Winter use of energy reserves is a significant cost for many temperate invertebrates (Leather et al., 1993).

A common feature both of species overwintering in defined instar(s) and those overwintering with more flexibility is synchronisation of moulting in spring. This may lead to synchronised egg production and peaks of subsequent instars, although it is often not possible to follow population cohorts due to the broad variation in growth rates typically observed. Synchronisation of adult emergence is seen on a very local scale in different populations of the fly *Belgica antarctica* (Sugg et al., 1983), probably related to rising microhabitat temperatures, and in the related chironomids *Eretmoptera murphyi* (Block et al., 1984) and *Parochlus steinenii* (Richard et al., 1994). The mite *A. antarcticus* only completes a single instar each year, with the moult of most individuals synchronised in spring. This may in part be a constraint due to the long premoult period of inactivity characteristic of the Cryptostigmata, but it is also advantageous allowing maximisation of summer feeding opportunities (Convey, 1994a). Spring moult synchronisation caused by thermal cues is well-known in insects generally, and has been suggested as a pre-adaptation for (northern) polar environments (Corbet, 1964; Oliver, 1968).

Moulting represents a period of great vulnerability to arthropods – the apparent arrest in moulting by Antarctic invertebrates over winter suggests that risks would be involved. The exact form of these has not been indentified, but the risks of desiccation or ice nucleation during ecdysis are likely to be important. In the field, the mite *A. antarcticus* enters an inactive premoult phase, apparently cemented to the substrate and fully hydrated, well before the onset of winter, but does not moult until spring, approximately eight months later (Convey, 1994a). Laboratory cultures of this species kept at constant temperatures show a shorter premoult period and, importantly, indicate that a temperature between 2 and 7°C may be required for moulting to occur (Convey, 1994c). An alternative limit for collembolans such as *C. antarcticus*, which overwinter in a partially dehydrated state (Cannon et al., 1985), may be a lack of liquid water required during and after moulting.

Cold tolerance in Antarctic arthropods has been widely studied (reviewed by Cannon & Block, 1988), and as mentioned above has also been described in Antarctic tardigrades and nematodes (Pickup, 1990a,b; Wharton & Brown, 1991; Sømme & Meier, 1995; Wharton & Ferns, 1995). It involves both behavioural (habitat selection, choice of diet, cessation of feeding, gut clearance) and physiological (supercooling, cryoprotectant synthesis, use of ice nucleating agents, thermal hysteresis/antifreeze proteins) responses. Antarctic arthropods can be divided broadly into two classes, those which do not survive any ice formation within the body ("freeze intolerant", dying at their freezing temperature) and those which can tolerate extracellular ice formation ("freeze tolerant") (Cannon & Block, 1988), although a wider range of intermediate classes can be identified in groups from less extreme environments (Bale, 1993). Of relevance to the current discussion are the possibility of seasonal variation in cold tolerance, and the cues used for its induction and their timing in its development.

Seasonal variation in cold tolerance (measured by the supercooling point or the temperature of ice crystallisation) has been shown in field-collected material of the common freeze-intolerant microarthropods *A. antarcticus*, *H. belgicae* and *C. antarcticus*, and is related to variation in the concentrations of cryoprotectants (Block, 1980; Lee & Baust, 1981; Cannon & Schenker, 1985). Similar variation can be induced experimentally in these and two other species of mite (*Nanorchestes antarcticus* and *Stereotydeus villosus*) by acclimation to low temperatures, starvation and desiccation (Young, 1979; Young &

Block, 1980; Cannon, 1986; Block & Sømme, 1982; Sømme & Block, 1982). These cues may act either separately or together, and again seem to lead to immediate opportunistic response to local environmental conditions. The primary cue for antifreeze accumulation and ice nucleation activity in most arthropods has been linked to temperature (Baust, 1982; Zachariassen, 1982), although photoperiod may also play a role (Horwath & Duman, 1983). The possible influence of photoperiod on the development of cold tolerance in Antarctic species has only been investigated in *A. antarcticus* and *B. antarctica*, where it appears to play no role (Block, 1980; Baust, 1982). It has been suggested that daylength variation is a poor predictor of environmental conditions in polar regions, due both to a lack of stimulus during summer periods of 24 h daylength (not the case in most of the maritime Antarctic, north of the Antarctic Circle) and the increased risk of harsh conditions in these regions in any season.

Not all species show this response – the mite *Gamasellus racovitzai* shows no variation in supercooling point with starvation and temperature acclimation during summer (Block & Sømme, 1982). *Belgica antarctica* shows seasonal variation in cryoprotectant levels in response to temperature and feeding cues (Baust, 1982; Baust & Lee, 1983) but no variation in cold tolerance, which is suggested as a relict feature (Baust, 1980). Similarly, the levels of potential cryoprotectants found in the dipteran *Eretmoptera murphyi* are too low to contribute significantly to cold tolerance, but still vary seasonally (Block et al., 1984). Nematodes show a range of seasonal patterns of cold tolerance, probably influenced by temperature and hydration levels (Pickup, 1990a; Wharton & Brown, 1991), some with seasonal variation in supercooling capacity and others not. Some species may be able to switch between freezing tolerant and intolerant strategies (Pickup, 1990b).

The levels of supercooling ability found in all freeze-intolerant maritime Antarctic invertebrates so far examined are sufficient to allow survival of the environmental temperatures they are likely to experience (Table 1 and refs therein; Cannon & Block, 1988). However, two of the three dipterans found in the maritime Antarctic (*Belgica antarctica* and *Eretmoptera murphyi*) utilise the alternative strategy of freeze-tolerance (Baust & Edwards, 1979; Harrisson & Block, 1988). These use ice nucleators to promote extracellular freezing at high sub-zero temperatures, and have a lower lethal temperature below their supercooling point. The lower lethal temperature of *E. murphyi* has not been determined precisely, but that of *B. antarctica* is approximately –10°C year-round (Baust & Edwards, 1979), and therefore the species must survive in more favourable microhabitats, avoiding the extreme temperatures experienced in the maritime Antarctic (Baust, 1980). The third dipteran, *Parochlus steinenii*, has been studied only in summer (Shimada et al., 1991), showing a lower lethal temperature several degrees above its supercooling point. This species is restricted to the South Shetland Islands, and may be a recent introduction to the maritime Antarctic (Convey & Block, 1996).

The overall pattern that may be emerging from this diverse range of studies is that, as with continental Antarctic species, there is little evidence of programmed responses to environmental cues having a major role in defining invertebrate overwintering strategies. The temperature limit to moulting described in *A. antarcticus* may represent an important exception, but no studies of this feature in other species have been made. Again, flexibility in development rates and the presence of overlapping generations are widespread, although there is also evidence of synchronisation of major events in the life cycle (moulting, oviposition) by rising temperatures during spring. Species are present, particularly Diptera, which have more structured life cycles with overwintering predominantly in specific instars. Behavioural and physiological features are important in the development and maintenance of cold tolerance (in those species showing seasonal variation), but appear to be rapid opportunistic responses to prevailing local environmental conditions (temperature, water and food availability). These may take advantage of taxonomically-imposed "resting" periods in development, such as the long premoult period typical of the Cryptostigmata.

Observed strategies – sub-Antarctic

Several more advanced groups of arthropods are relatively well represented on the widely-spaced islands of the sub-Antarctic, particularly Diptera, Coleoptera and Lepidoptera (Gressitt, 1970). With more species present, including predatory Coleoptera, Arachnida and Hymenoptera, food webs are more complex. Diversity of micro-arthropods (Acari, Collembola) is also greater than that found in the maritime and continental Antarctic regions (e.g. Pugh, 1993). However, biological studies in the sub-Antarctic have concentrated on the larger, more obvious groups, meaning that there are few studies directly comparable with those of micro-arthropods described above. There is also little published information on seasonal variation in the physiological characteristics of sub-Antarctic invertebrates.

The position of most sub-Antarctic islands means that they experience cool but positive temperatures year-round, with seasonal variation damped by the oceanic influence (see above and Table 1). Even the large colder islands of South Georgia and Heard Island experience soil surface temperature minima of only c. –4°C (Table 1), although more extreme habitats exist at higher levels above the soil on plants (Smith, 1982; Smith & Headland, 1983), or on the islands' mountain ridges. This means that survival of extreme low temperatures may not be relevent to wintering strategies of invertebrates in many sub-Antarctic habitats (Worland et al., 1992).

Many ecological studies of Diptera and Coleoptera have identified extensive overlap of generations in the field, combined with all life stages being present in most months if not all year round. In the Coleoptera these features are shown by the Perimylopidae of South Georgia (Block & Sømme, 1983; Meyer-Arndt, 1984; Ernsting et al., 1995), Curculionidae of Marion Island (Chown & Scholtz, 1989a) and Carabidae of Îles Crozet (Davies, 1987), as well as introduced Carabidae on South Georgia and Îles Kerguelen (Jeannel, 1940; Ernsting et al., 1995). These studies also indicate that growth (including moulting) occurs during the winter months and that adults of all species may survive and reproduce for several years. As with maritime Antarctic micro-arthropods, there may be seasonal peaks of moulting (particularly to adult) and of oviposition, and a shorter period of oviposition arrest during winter (e.g Davies, 1987; Ernsting et al., 1995). Overlapping generations and probable year-round development have been identified in the dipterans *Anatalanta aptera* and *A. crozetensis* on Îles Kerguelen and Îles Crozet (Tréhen, 1978, 1982; Tréhen & Vernon, 1982), *Paractora dreuxi* on Marion Island (Crafford, 1984) and *Antrops truncipennis* on South Georgia (Harrison, 1970) and the lepidopterans *Embryonopsis halticella* and *Pringleophaga marioni* on Marion Island (Crafford & Scholtz, 1986). *E. halticella*, *P. kerguelensis* and *P. crozetensis* are reported to be univoltine on Îles Kerguelen and Îles Crozet (Chauvin & Vernon, 1982). Unlike the Coleoptera, these latter groups may show rapid larval development (Diptera) due to short-lived availability during all seasons of their shoreline food source (seaweed/carrion) and short-lived adults (Diptera and Lepidoptera).

West's (1982, 1984) study of the life history of three South Georgian oribatid mites, the only published life history study of sub-Antarctic micro-arthropods, identified similar patterns, with all stages of each species present year-round. All three species also showed considerable growth and moulting during the winter months, with two (*Edwardzetes elongatus* and *Eobrachythonius oudemansi*) showing a peak of egg-hatching during autumn, possibly synchronised by a decline in habitat temperature.

There are few examples of more seasonally-structured life cycles, the best-described being that of the dytiscid water beetle *Lancetes claussi* (Nicolai & Droste, 1984). This species shows a clear temperature-mediated arrest in development in larval stage IV, which does not moult to the pupa until water temperatures exceed 7.3°C, leading to a peak of adult emergence and oviposition in early summer. As above, adults may survive over several seasons. Other short-lived adult Diptera do not pupate or emerge during winter (e.g. the chironomid midges *Parochlus steinenii* and *Eretmoptera murphyi* on South Georgia) as their freshwater or inland habitats may be frozen and/or snow-covered. No life cycle studies have been made on these or similar species in the sub-Antarctic.

A number of sub-Antarctic Coleoptera and Lepidoptera have a herbivorous diet (Chauvin & Vernon, 1982; Crafford & Scholtz, 1986; Crafford & Chown, 1987; Chown & Scholtz, 1989b; Sømme et al., 1989a), in contrast to the predominantly detritivorous / algivorous / fungivorous diets of most sub- and maritime Antarctic Diptera and micro-arthropods. If, as Remmert (1986) proposed, there is a lower temperature threshold for the maintenance of a herbivorous diet of about 6°C, species with this diet may be unable to extend their range farther south than the sub-Antarctic.

Physiological studies of South Georgian Coleoptera (including *Hydromedion sparsutum, Perimylops antarcticus*, *Oopterus soledadinus*) and Diptera (*Eretmoptera murphyi*) have concentrated on summer-collected animals and covered cold tolerance, freezing survival and ice nucleation (Block & Sømme, 1983; Worland et al., 1992, 1993), respiratory metabolism (Sømme et al., 1989b) and desiccation resistance (Ring et al., 1990). These species are freezing tolerant, at least over periods of several hours. The coleopterans show a limited increase in cold tolerance with low temperature acclimation (Block & Sømme, 1983; Worland et al., 1992). Low enzyme activation energies are indicative of cold adaptation (Sømme et al., 1989b), a result also found by Crafford & Chown (1993) studying the respiratory metabolism of Marion Island Lepidoptera and Coleoptera. The dipteran *Anatalanta aptera* is freezing susceptible, and is capable of supercooling to approximately −11°C (Vannier, 1987; Vernon & Vannier, 1987). *H. sparsutum* and *P. antarcticus* can also withstand significant desiccation, although water loss rates are higher than non-polar species from arid regions (Ring et al., 1990). Larvae of three species of weevil (Coleoptera, Curculionidae) from Marion Island can withstand similar rates of water loss (Chown & van Drimmelen, 1992). However, with the generally damp climate, habitat temperatures only decreasing to just below 0°C, and winter activity and feeding common as described above, these features are unlikely to be of great ecological significance.

There is very limited evidence of physiological change in advance of winter conditions. *H. sparsutum* shows some fat deposition in late summer (P. Convey & T. Wilmer, unpublished data). Cultured *Anatalanta aptera* (Diptera) may also contain high levels of fat (43% dry mass) which is used as an energy reserve during periods of starvation (Vernon, 1986). Use of this lipid, or feeding, is associated with a decrease in cold hardiness for this species (Vernon & Vannier, 1987).

The lack of seasonality experienced on most sub-Antarctic islands in comparison with the maritime and continental Antarctic zones may be the most significant influence on life history. Cool temperatures year-round combined with a low or non-existent risk of extreme winter lows allow activity and development to be continuous. Similarly, food availability varies little with season, although in the case of shoreline Diptera it may be at least partly opportunistic. Flexibility is again an important feature, but here it is associated with reduced seasonality and near-continuous opportunity for activity rather than with the extreme seasonality and unpredictable opportunities for activity and growth experienced in the regions farther south. Studies of the insects of Marion and Prince Edwards Islands, (Crafford et al., 1986) and the terrestrial invertebrates of Macquarie Island (Greenslade, 1990) have also recognised the importance of flexibility in life history strategy in sub-Antarctic invertebrates.

CONCLUSIONS

Overall, very few specific studies on the mechanics of overwintering in Antarctic terrestrial invertebrates have been made. Therefore no unequivocal conclusions can be drawn on such subjects as the use and timing of cues for entering or leaving an overwintering state, whether any such state has a fixed duration, or even whether any form of "programmed" diapause exists, as against immediate responses to local cues signalling entry into or exit from a (variable length) quiescent state. The general conclusions described below are drawn from circumstantial evidence provided by studies of a wide range of often geographically-separated species, as described in the preceding sections.

1) There is no evidence for predetermined responses to environmental cues occurring before the onset of adverse conditions in any of the three Antarctic zones under consideration. Sømme (1995) similarly concluded that diapause is not widespread in polar species. Rather, major responses such as gut clearance, cessation of feeding and cryoprotectant synthesis appear to be controlled by immediate factors in an individual's local environment, and are sufficiently rapid to allow advantage to be taken of periods of "mild" weather during winter thaws on an opportunistic basis. Responses to decreasing temperatures, desiccation and food quality have been identified, but not to changes in photoperiod. However, evidence of possible seasonal patterns of energy reserve accumulation, and of autumn/winter arrest in oviposition, suggest the use of earlier cues, before the onset of winter conditions.

2) In all three zones, decreased or zero growth rates overwinter due to low thermal energy budget may lead to synchronisation of life cycle events in early spring (i.e. moulting and oviposition). This may lead to a peak of oviposition, and allows full advantage to be taken of feeding and growth opportunities during the subsequent summer. However, very variable growth rates, and the possibility of overwintering (active or inactive) in all or most life stages are typical of many groups, leading to considerable overlap of

generations. Arthropod groups with more limited overwintering life stages are unusual in the maritime Antarctic (limited to Diptera) and not present in the continental Antarctic.

3) The sub-Antarctic zone is thought to present fundamentally different constraints on life history to the two more southerly Antarctic zones: year-round development is generally possible, relatively small seasonal variation in temperatures effectively means that highly-developed overwintering or diapause abilities may not be required, leading to a partial uncoupling of life history from seasonal cues, and a large degree of flexibility in development patterns. In contrast, in maritime and continental Antarctic zones, apparently similar flexibility is achieved by having rapid responses to immediate environmental cues at all stages in the life cycle, and well-developed ability to survive extreme levels of temperature and desiccation.

4) Arthropod groups poorly or not represented in the maritime and continental Antarctic (especially Diptera, Coleoptera and Lepidoptera) may lack the flexibility in overwintering tactics which is seen in the dominant micro-arthropod groups of those regions (Collembola, Acari) as well as microinvertebrates such as Nematoda and Tardigrada. Lepidoptera and Coleoptera may also face a phylogenetic constraint, in that few members of these groups worldwide utilise a detritivorous diet.

ACKNOWLEDGEMENTS. I am grateful to W. Block and P.J.A. Pugh (British Antarctic Survey) for stimulating discussions. Along with L. Sømme and an anonymous reviewer, they also gave constructive criticism of an earlier draft of the manuscript.

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