REVIEW

Eur. J. Entomol. **96**: 83–102, 1999
ISSN 1210-5759

Life cycles in polar arthropods – flexible or programmed?

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Key words. Arctic, Antarctic, polar, insects, arthropods, life-cycle, seasonal, temperature, climate

Abstract. Climate features that influence life cycles, notably severity, seasonality, unpredictability and variability, are summarized for different polar zones. The zones differ widely in these factors and how they are combined. For example, seasonality is markedly reduced by oceanic influences in the Subantarctic. Information about the life cycles of Arctic and Antarctic arthropods is reviewed to assess the relative contributions of flexibility and programming to life cycles in polar regions. A wide range of life cycles occurs in polar arthropods and, when whole life cycles are considered, fixed or programmed elements are well represented, in contrast to some recent opinions that emphasize the prevalence of flexible or opportunistic responses. Programmed responses are especially common for controlling the appearance of stages that are sensitive to adverse conditions, such as the reproductive adult. The relative contribution of flexibility and programming to different life cycles is correlated with taxonomic affinity (which establishes the general life-cycle framework for a species), and with climatic zone, the habitats of immature and adult stages, and food.

INTRODUCTION

The cold temperatures and marked seasonality of polar regions limit the types of life cycles that are possible in the arthropods living there. However, detailed information about life cycles in polar regions is fragmentary. There is little direct evidence for complex developmental programmes, and instead elements that may indicate if the life cycle is flexible or programmed include whether the overwintering stage is fixed or not, whether it shows winter growth or marked resistance, whether moults are synchronized seasonally, and whether reproduction is continuous (Convey, 1996a).

Recent discussions about polar life cycles have emphasized the value or prevalence of flexibility or opportunism, which allows growth and development whenever conditions are favourable (e.g. Chernov, 1978, 1995; Convey, 1996a, b, 1997a). Such responses allow a species to take advantage of every window of opportunity for development. From this viewpoint, programmed responses such as diapause are uncommon (e.g. Sømme, 1995; Convey, 1996a), because they might suppress development even when conditions happen to be favourable.

However, especially in cold and seasonal environments the life cycles of many arthropod species (at least at some times of year or stages of their life cycle) involve strict temporal programmes. These programmes adjust development in relation to key events, such as adult emergence, or with respect to key resources, such as food plants (sample reviews by Dingle, 1986; Danks, 1987a, b, 1991, 1994a, b).

This paper reviews information about Arctic and Antarctic arthropods to assess the relative contributions of flexibility and of fixity or programming to life cycles there. It concludes, in contrast to the recent emphasis on flexibility, that life cycles in polar regions take a variety of forms, including relatively complex ones; and that depending especially on taxon, zone, habitat, and food, programmed responses are important components of many life cycles.

CONDITIONS

The polar regions from which information on life cycles has been reported are very different from one another. The Antarctic (Fig. 1) is centred on a giant continental glacier whereas the Arctic (Fig. 2) is centred on a cold sea containing islands of various sizes. The three commonly recognized regions of the Antarctic are very dissimilar from one another and from the Arctic (e.g. French & Smith, 1985). Additional information about vegetation, and somewhat different or more detailed zonations, are provided especially by Young (1971), Lewis Smith (1984, 1996), Longton (1988, 1997) and Edlund (1990). The Continental Antarctic is extremely frigid, much more so even than the High Arctic. Because the Maritime Antarctic and Subantarctic comprise chiefly small islands or narrow coastal zones in an extensive ocean, these zones show extreme oceanicity (French & Smith, 1985) unlike typical Arctic sites.

Assessing conditions in these different regions therefore is complex. Moreover, in addition to the great differences in regional climates produced by latitude are differences among sites attributable to continentality, topography, and more local effects.

Arthropods live in microhabitats that, especially when warmed by sunshine, can be extremely favourable compared to the air above them. Some polar soil and plant habitats are moist and have temperatures commonly 10°C and up to 30°C or more higher than ambient air temperatures (see Walton, 1982; Davey et al., 1992; Convey, 1996a, Table 1 for the Antarctic; reviews by Corbet, 1972 and Danks, 1981, 1987b for the Arctic). Shallow waters likewise stay much warmer than the air during the polar

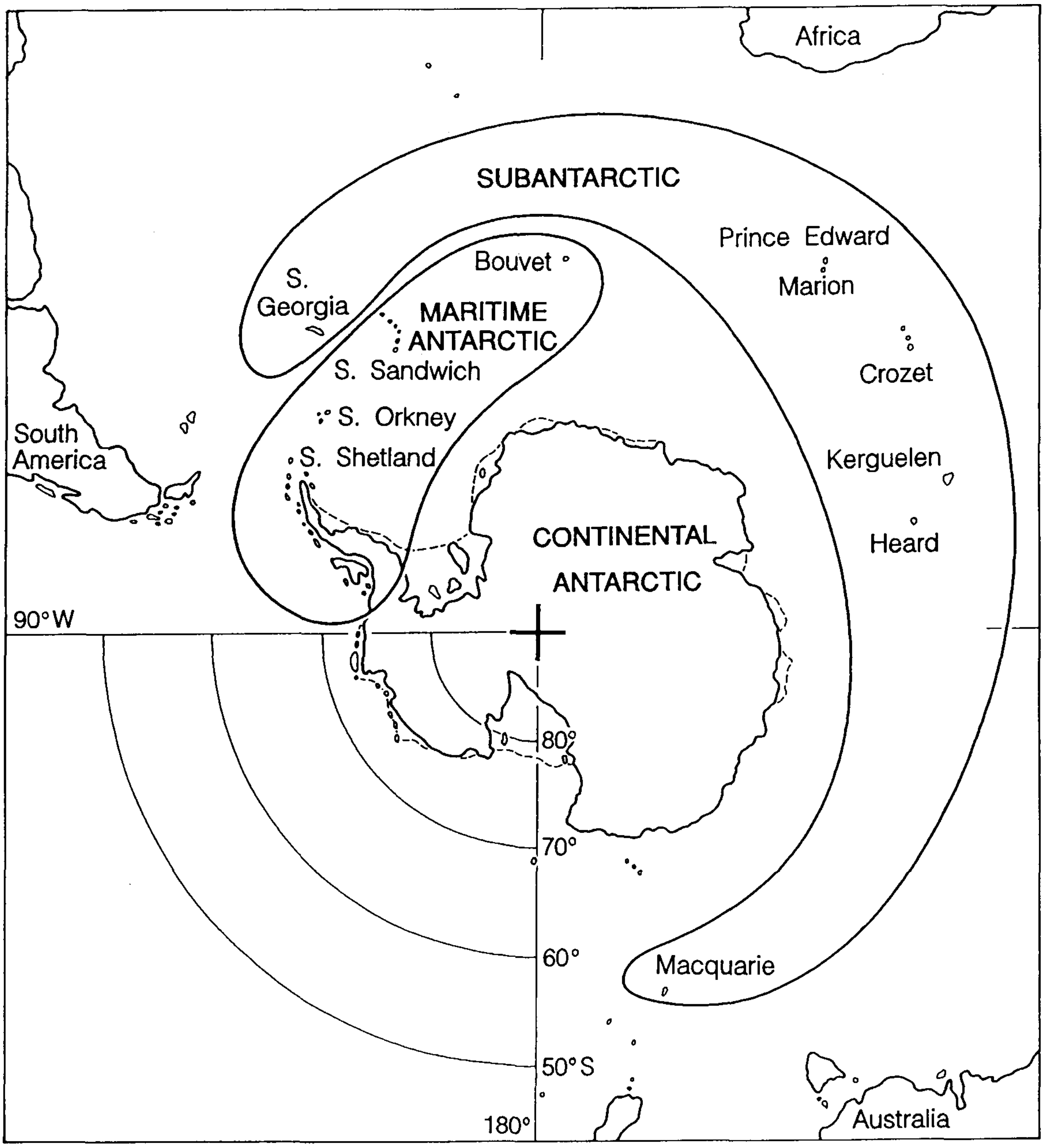

Fig. 1. The Antarctic region, showing generalized Continental Antarctic, Maritime Antarctic and Subantarctic zones. Some authors classify the zones differently (see text for references), in particular because the east side of the Antarctic peninsula tends toward continental conditions.

summer, especially in the Arctic (Oliver & Corbet, 1966; Arnold & Convey, 1998), though the range of temperatures is lower in the Antarctic (Ellis-Evans, 1996). Nevertheless, differences between air temperatures and habitat temperatures appear to be similar in different polar zones, suggesting that general comparisons can be based on ordinary meteorological data, which are easier to obtain and compare.

Constraints on polar organisms can be estimated from climatic patterns by examining the severity, seasonality, unpredictability and variability – in the senses defined below – associated with different climates.

Severity reflects persistent conditions that limit life, such as low summer temperatures and very low winter temperatures. The severity of conditions for growth can be estimated from the number of day-degrees above a given threshold accumulated in a season as well as from mean temperatures. Many polar habitats are also very dry, and moisture is important to the fauna (Kennedy, 1993; Block, 1996; Hodkinson et al., 1996). Coping with severity requires resistance (notably cold hardiness, cf. Block, 1990; Lee & Denlinger, 1991; Danks, 1996), specific microhabitat selection, and other adaptations.

Seasonality reflects the fact that conditions are intermittently favourable on an annual time frame. Such seasonal differences can be estimated by comparing average summer and winter temperatures, for example. They require

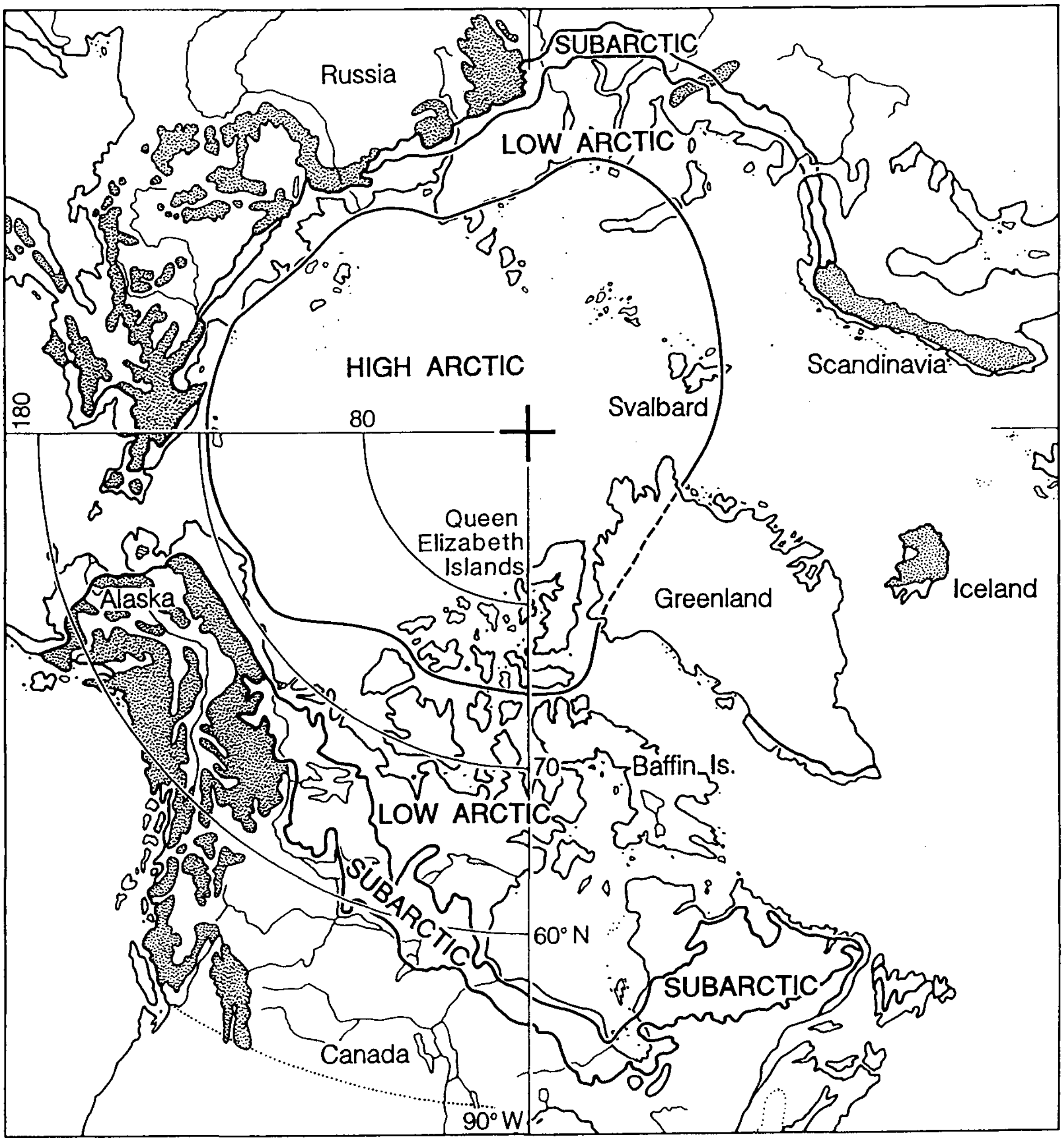

Fig. 2. The Arctic region, showing High Arctic, Low Arctic and Subarctic zones. Stippled areas show northern alpine analogues.

adaptations that limit development and activity to appropriate times of year.

Unpredictability reflects the short-term pattern of conditions, such as the expected range of relevant temperatures in a given month, and hence the need for adaptations to sudden temperature changes, for example. The impact of this range depends also on the mean temperature. For example, temperature patterns in many High Arctic sites are very important because the mean summer temperature is already relatively low; the likelihood of frost in July (the warmest month) may reach 90% (cf. Danks, 1993a, Table 1). Similar changes take place in many Antarctic sites. In Subantarctic sites, in contrast, summer temperatures are cool but remain steadily above freezing.

Variability shows how variable are such features as summer temperature from year to year. Differences between long-term mean temperatures and recorded extremes suggest the level of variability. Such patterns establish the extent of mortality that might be associated with fixed patterns such as emergence at a given time of year.

Table 1 summarizes some information about severity, seasonality, unpredictability and variability for sample sites (there is no such thing as a "typical" site), based chiefly on monthly mean air temperatures. Commonly recognized polar zones (as listed in the table) are used for this comparison, because some alternative schemes (e.g. Longton, 1988, 1997) tend to group Arctic sites with somewhat dissimilar climates. A few temperate sites are included for comparison.

TABLE 1. Some indications of the conditions in different regions based chiefly on mean screen air temperatures (°C). A – Annual; W – Warmest month; C – Coldest month. N/A – not available. Data from Schwerdtfeger, 1970; Vowinckel & Orvig, 1970; Hare & Hay, 1974; Lydolph, 1977; Höflich, 1984; Streten & Zillman, 1984. (These sources were used especially because they include comparable data, but for further general information see also Schwerdtfeger, 1984; Jones & Limbert, 1987; King & Turner, 1997.)

Zone and sample site (°N or °S)	Severity						Seasonality	Unpredictability		Variability			
	W mean	W mean cloud tenths	No. monthly means above 0°C	Day-degree index[a]	C mean	A mean	W to C diff.	W: Av. daily range	C: Av. daily range	W: Diff. of extreme from long-term mean		C: Diff. of extreme from long-term mean	
										Above	Below	Above	Below
High Arctic													
Alert, Ellesmere Is (82 1/2)	3.9	6.7?	2	146	–33.0	–17.8	39.7	3.2	4.1	16.1	9.5	31.9	14.2
Resolute, Cornwallis Is. (75)	4.6	7.5	3	250	–33.7	–16.2	38.3	4.9	6.5	6.8	11.5	15.7	19.8
Mys Chelyuskin, Russian mainland (78)	0.8	N/A	2	43	–31.1	–15.6	31.9	N/A	N/A	23.2	6.8	31.1	17.9
Isfjord, Svalbard (78)	4.5	6.5?	4	354	–12.1	–4.4	16.6	3.2	5.9	11.1	6.3	15.9	16.9
Low Arctic													
Iqaluit, Baffin Is. (64)	7.9	7.5	4	633	–26.5	–8.9	34.4	7.6	7.6	16.1	8.9	30.5	18.5
Baker Lake, Canadian mainland (64)	10.7	6.5	4	843	–32.9	–11.9	43.6	9.9	7	16.3	12.7	21.9	16.1
Chokurdakh, Russian mainland (71)	10.2	N/A	4	746	–36.2	–14.2	46.4	N/A	N/A	21.8	10.2	28.2	15.8
Subarctic													
Ft. Chimo, QU (58)	11.8	7.1	5	1091	–23.9	–5.2	35.7	11.2	8.9	20.2	13.8	29.9	22.1
Churchill, MB (59)	12	6.4	4	1077	–27.5	–7.2	39.5	10.2	7.6	21	14	27.5	17.5
Salekhard, Russian mainland (66 1/2)	13.8	N/A	4	1144	–24.4	–6.7	38.2	11.6	7	17.2	13.8	26.4	25.6
Continental Antarctic													
McMurdo (78)	–3.4	6.4	0	0	–27.8	–17.4	14	5	10	12.2	9	21.6	10
Halley Bay (75 1/2)	–5.0	7.5	0	0	–28.5	–18.7	13.7	5.9	9.1	17.2	7.8	26	24.1
Maritime Antarctic													
Argentine Is. (65)	0.2	8.4	1	6	–11.9	–5.2	12.1	3.9	8.4	9.8	10.8	19.1	31.4
Deception Is., S. Shetlands (63)	1.4	8.9	4	93	–8.0	–2.8	6.6	3.6	4.8	8.6	7	3.4	18.9
Orcadas, Laurie Is. (61)	0.4	9.3	2	29	–10.6	–4.4	11	3.3	9.2	8.6	10.2	18.4	26.3
Subantarctic													
Macquarie Is. (54 1/2)	6.9	6.7	12	1680	3	4.6	3.7	N/A	N/A	5.7	6.3	5.3	5.9
Grytviken, S. Georgia (54)	5.1	7.4	8	751	–1.7	1.7	6.8	N/A	N/A	21.4	8.8	14.9	17.5
Temperate Continental													
Ottawa, ON (45)	20.7	5.5	8	3067	–10.8	5.7	31.5	11.7	8.7	16.3	15.7	21.8	25.2
Temperate Maritime													
St. John's, NF (45)	15.4	7	8	2128	–4.7	4.7	20.1	9.6	6.5	13.6	14.4	19.7	18.3

[a] The day-degree index is based on the simple calculation of day-degrees from monthly mean screen air temperatures, and so is a general indicator only.

The *Continental Antarctic* (Fig. 1) comprises the bulk of the Antarctic continent, excluding parts of the Peninsula. Mean monthly temperatures never rise above the freezing point and vegetation is sparse (chiefly lichens). The relatively few species of arthropods are chiefly soil mites and springtails (Wallwork, 1973; Pugh, 1993; Greenslade, 1995; Lewis Smith, 1996) and are confined to especially favourable localities and microhabitats (cf. Block, 1994). Species of some other groups, like Mallophaga, live on the skin of vertebrates.

The *Maritime Antarctic* includes the Antarctic Peninsula and the island groups of South Shetland, South Orkney, South Sandwich and Bouvet. The summer season is very short, cool and cloudy, with very few seasonal day-degrees C above freezing (as estimated from air temperatures). However, compared to both the Continental Antarctic and all Arctic zones winters are not especially severe (–8 to –12°C mean monthly temperature for the coldest month, similar to cool temperate continental sites). About 160 species of arthropods, again mainly soil mites and springtails (see references above), as well as Mallophaga, have been reported there.

The *Subantarctic* consists of South Georgia, Prince Edward, Crozet, Kerguelen and Macquarie Islands. Summers are cool and cloudy, but the mean air temperature of many sites, and the temperatures of most habitats, are above freezing in most or all months. The Subantarctic islands support a moorland type of vegetation that resembles Arctic tundra in general appearance (Wallwork, 1976; Longton, 1988). The fauna of several hundred species is much richer than in the other Antarctic zones and includes Diptera, Coleoptera and other endopterygote insects.

The *High Arctic* as defined here (Fig. 2) consists of the Queen Elizabeth Islands in North America, which lie north of about 74.5°N, and northern islands and the northernmost mainland in the Palaearctic region. Despite regional differences produced mainly by differences in island size (in particular, the small northwestern Queen Elizabeth Islands are cooler and cloudier than the larger eastern ones), summers throughout the zone are brief, but mean July temperatures in some sites reach 7°C. Winters are long and very cold (below –30°C and unmitigated by sunshine in the continuous polar darkness of winter). Precipitation is very limited; this region is polar desert with most areas colonized only by open vegetation, chiefly clump-forming perennials. Nevertheless, several hundred species of arthropods live there (Danks, 1981, 1990), especially in warm sites and microsites favoured by topographical and other features.

The *Low Arctic*, used here to refer to areas between the High Arctic and the northern limit of trees, is likewise highly seasonal with very cold winters, but generally less severe than the High Arctic. For example, summer is significantly warmer than in the High Arctic, though still relatively arid. More than 2,000 species of terrestrial arthropods have been reported from this region in North America alone (Danks, 1981, 1990).

The *Subarctic* is a zone of scattered trees and tundra patches. Though markedly seasonal with very cold winters, annual temperature sums above freezing normally exceed 1,000 day-degrees C. Thousands of species, including essentially boreal ones at their northern limit, occur in the zone (Danks, 1981, p. 220, 1993b; Danks & Foottit, 1989).

These brief synopses and the data in Table 1 confirm that the polar zones differ greatly from one another. Table 2 summarizes these differences in terms of the important elements of severity, seasonality, unpredictability and variability.

Table 2 confirms that arthropods are least well represented in zones that are most severe. Among other characteristic patterns shown by the table, arctic zones are much more seasonal and tend to be more variable than Antarctic zones. This feature is particularly important where severe winters return rapidly and where conditions such as temperature operate close to the limits for life, so that even a relatively small temperature difference from year to year (or a critical fluctuation during the period of reproduction) may greatly influence the relative success of a given generation.

Also, because of maritime influences, the Subantarctic zone is not very seasonal and is relatively severe only because the summer is so cool, suggesting that information from the zone should be used sparingly in arriving at conclusions about seasonal life cycles in polar regions. Moreover, the Subantarctic fauna – like the Antarctic fauna in general – appears to be depauperate beyond any effects of climate because dispersal to these remote islands is so difficult (Wallwork, 1976; Convey & Block, 1996; Convey, 1997a, b). Note also that data from alpine zones (which have been used commonly for comparison with Arctic and Antarctic information) must be used with care. Alpine conditions differ from those in polar regions in several ways. For example, seasonal patterns of temperature are different, diel cycles of temperature and photoperiod are more marked, and more allochthonous food (such as wind-blown arthropods) is available in alpine sites.

DEGREES OF FLEXIBILITY

The fact that a life cycle is programmed does not mean that it is precisely controlled every step of the way. Many insect life cycles are more or less flexible in some of their stages, but mechanisms exist to restore seasonal synchrony at or before critical times of year. Therefore, it is essential to distinguish patterns of the life cycle as a whole from component features such as cold-hardiness responses (an aspect of resistance to seasonal stresses) or seasonal growth and seasonal reproduction (single aspects of the life cycle). For example, High Arctic mosquitoes are strictly univoltine and overwinter only as drying- and freezing-resistant eggs in diapause. The position of seasonal emergence nevertheless differs widely from one season to the next, depending on weather, and from one pond to the next, depending on temperatures in a given habitat, because the rate of larval and pupal development

TABLE 2. Summary of key features of polar climates – shown as ±, low; +, moderate; ++, high; +++, very high; ++++, extreme – based chiefly on information in Table 1. Numbers of terrestrial arthropod species (including introduced species and ectoparasites, for example) are also given after Block (1984) and Pugh (1993) or estimated from data in Danks (1990, 1993b). For further explanation see footnote.

Zone	Climate feature[a]						Total no. terrestrial arthropod spp. reported from zone
	Severity in summer temp.	Severity in heat accumulation	Severity in winter	Seasonality	Unpredictability in summer (short-term)	Variability in summer (long-term)	
Continental Antarctic	++++	++++	+++	++	++	++	107
Maritime Antarctic	+++	++++	+/++	±/+	++	+/++	164
Subantarctic	++	+/++	±/+	±	?	+/++	585
High Arctic	+++	+++	+++	+++	++	+/++	553
Low Arctic	++	++	+++	+++	+	++	2237
Subarctic	+	+	+++	+++	++	+++	~4000
Temperate Continental	±	±	++	+++	++	+++	~17 000
Temperate Maritime	+	±	+	++	+	++	~12 000?

[a] Climate features of increasing intensity [±, +, ++, +++, (and ++++ for summer severity only)] are scored as follows. Severity in summer temperature: > 20, 20–10, 10–5, 5–0, < 0°C mean in warmest month; Severity in heat accumulation: > 2000, 2000–1000, 1000–500, 500–0, < 0 day-degrees in season; Severity in winter: > 0, 0 to –10, –10 to –20, < –20°C mean in coldest month; Seasonality: 0–10, 10–20, 20–30, > 30 degrees C difference between warmest and coldest month; Unpredictability in summer: 0–5, 5–10, 10–15, > 15 degrees C mean daily range in warmest month, and unpredictability increased by two categories if some daily temperatures pass through freezing then; Variability in summer: < 5, 5–10, 10–15, > 15 degrees C difference (average of positive and negative differences) between monthly means and long-term extremes for warmest month. This more or less arbitrary scheme was chosen to minimize the bias that might have arisen from the careful selection of boundaries.

is regulated by temperature (Corbet & Danks, 1973). Larval and pupal development therefore are flexible locally (at least within a season), but the life cycle as a whole is very closely constrained. Unfortunately more information exists, because it is easier to collect, about single components such as larval growth than about life cycles as a whole.

The sorts of indirect evidence for flexibility that are available, in the virtual absence of complete studies of life cycles in polar arthropods, therefore have to be used with great care. For example, laboratory experiments that fail to provide a key natural seasonal signal or condition may lead to the erroneous conclusion that the life cycle is fully flexible. Field evidence must likewise be interpreted with care. For example, the presence of multiple overwintering stages in polar arthropods can signify several possibilities: flexibility with all stages overlapping; a set of fixed annual cohorts representing several separate but programmed generations; and programming such as diapause that takes effect only at the end of the larval stage and so allows flexible early development but forces programmed adult emergence. These and other possibilities for the relative degree of flexibility in the life cycles of polar arthropods are exemplified in Table 3.

Several species of springtails and mites, and a few insects, appear to have fully flexible life cycles, as suggested by overlapping generations, lack of seasonal synchrony, winter activity, lack of a fixed overwintering stage, lack of build-up of fat for winter, and shorter life cycles where conditions are warmer (cf. Table 3, set 1). Nevertheless, a larger number of species has some programmed components. A particularly common pattern is that early development (typically in habitats that are relatively well buffered, such as the soil or shallow pools) is flexible, but adult emergence into less stable terrestrial or aerial habitats is very closely controlled, ensuring early emergence and rapid reproduction (see Mechanisms below). For example, many species of chironomids ("absolute spring species" of Danks & Oliver, 1972a) emerge only if all growth has been completed the previous year, ensuring the earliest possible start in spring, and hence the longest possible season for reproduction before winter returns.

The converse pattern (Table 3, set 3) is seen in species that develop from egg to adult over one or a small fixed number of seasons, but the adult life span is long and eggs are deposited over a number of seasons, depending partly on the weather. For example, early larval development in the Subantarctic water beetle *Lancetes angusticollis* is completed relatively rapidly, and the final instar takes a further year (Arnold & Convey, 1998), but the adult oviposits over more than one year (Nicolai & Droste, 1984). On a much shorter time scale, several reproductive options occur in High Arctic *Aedes* mosquitoes, in which both obligate and facultative first-cycle autogeny extends the range of alternatives according to the availability of vertebrate hosts for a blood meal (Corbet, 1967).

The life cycles of some polar species appear to be relatively closely programmed throughout (Table 3, set 4). For example, the High Arctic moth *Psychophora sabini* and the Antarctic mite *Alaskozetes antarcticus* both appear to moult only once each year. Larvae of *Psychophora sabini* moult to the next instar in spring before beginning to feed (Danks & Byers, 1972). The natural pattern, at low temperatures, in *Alaskozetes antarcticus* is probably similar, because early stages that grow rapidly under more favourable conditions in the laboratory then spend longer in a pre-moult resting stage (Convey, 1994b).

The life cycle of the High Arctic aphid *Acyrthosiphon svalbardicum* is governed by a fixed sequence of morphs. The fundatrix that hatches from the overwintering egg gives rise to sexual morphs (and to some viviparae which can produce sexual morphs), which in turn produce overwintering eggs (Strathdee et al., 1993).

Rapidly developing univoltine species (Table 3, set 5) are surprisingly well represented even in the High Arctic. They develop through the whole life cycle in one season from a single overwintering stage. The overwintering stage is characteristic of the taxon, and may be the egg (e.g. *Aedes* spp.), the larva (e.g. *Sphagnophylax meiops*) or the adult (e.g. *Bombus* spp.), but rarely the pupa (Danks, 1981).

A feature of many species is some life-cycle variability among individuals, leading to differences in the numbers of years per generation or the numbers of years spent in diapause, for example (Table 3, sets 6, 7). Such variability among individuals experiencing similar conditions is correctly viewed not so much as "flexibility" to take advantage of possible developmental opportunities, but rather as "insurance" (which is a programmed response) against the uncertainty of environmental events. For example, short-term variability prevents a generation late in the year or in an especially cold year that would be likely to fail, and long-term variability reflects the spreading of risk in uncertain environments (for further discussion see Danks, 1981, 1987a, 1994b).

MECHANISMS

Many mechanisms allow life cycles to be adjusted seasonally, including the occurrence, placement, duration, variability and continuity of both development and reproduction (see Danks, 1994a for review). Both graded and discrete responses are used, that is both timed events that can be altered gradually, such as larval growth, and switches between distinct alternatives such as diapause and non-diapause. Nevertheless, both types of responses are conveniently viewed for analysis as comprising discrete alternatives, even for such essentially continuous elements as fast growth versus slow growth, because the temporal flow of the alternatives through the life cycle and how they are controlled is the key to understanding them (Danks, 1991, 1994a).

Mechanisms to accelerate or to delay the life cycle, and factors used for adjustments, are exemplified for polar arthropods in Table 4. The fact that a full array of mecha-

TABLE 3. Characteristic patterns of flexible or programmed life cycles in Arctic and Antarctic arthropods. Areas: CAa – Continental Antarctic; MAa – Maritime Antarctic; SAa – Subantarctic; HA – High Arctic; LA – Low Arctic; SA – Subarctic.

Pattern	Characteristic	Evidence	Example	Area	Reference
1. Always flexible	Duration of development depends only on weather, habitat, etc.	Life cycle greatly shortened under warmer conditions	Apparently in *Hypogastrura concolor* (Hypogastruridae) [as *H. tullbergi*, see Fjellberg, 1986]	HA	Addison, 1977
			Several species of Oribatida		Norton, 1994
			Other insect species		Danks, 1992, Table 2
		Winter activity, feeding or growth	At least early stages flexible in *Cryptopygus antarcticus* (Isotomidae), *Halozetes belgicae* (Podacaridae), and perhaps *Alaskozetes antarcticus* (Podacaridae)	MAa	Convey, 1992
			Suspected in some lake Chironomidae	HA	Welch, 1976
		Overlapping non-synchronized generations	*Cryptopygus sverdrupi* (Isotomidae)	CAa	Sømme, 1986
			Probably *Gomphiocephalus hodgkinsoni* (Hypogastruridae)	CAa	Janetschek, 1967, 1970; Peterson, 1971
			Cryptopygus antarcticus (Isotomidae)	MAa	Burn, 1981, 1984; Schaller, 1992
			Eupodes spp., mainly *parvus* (Eupodidae); probably *Nanorchestes berryi* (Nanorchestidae)	MAa	Booth & Usher, 1986
			Many insects of different Orders	SAa	Convey, 1996a (p. 498)
		Larvae develop over several years, adults survive several years	*Chrysolina* spp. (Chrysomelidae)	LA	Chernov, 1978; Chernov et al., 1993
		Several stages overwinter, no clear cohorts	Probably in *Boreellus atriceps* (Calliphoridae)	HA	McAlpine, 1965; Danks & Byers, 1972
2. Flexible early, programmed late	Duration of immature stages variable, but adult closely controlled	Only fully grown immature stages emerge in spring or early summer; all others postpone emergence (see also Table 4, set 1)	Apparently (emergence synchronized) in *Belgica antarctica* (Chironomidae)	MAa	Edwards & Baust, 1981; Sugg et al., 1983; Convey & Block, 1996
			Synchronized oviposition and hatch in *Paraisotoma octooculata* (Isotomidae)	MAa	Burn, 1984
			Many species of High Arctic Chironomidae	HA	Danks & Oliver, 1972a
			Tipula carinifrons and other spp., *Prionocera* spp., others (Tipulidae)	HA, LA	Lantsov, 1982; Lantsov & Chernov, 1987; Chernov & Lantsov, 1992
			Chironomus prior, *C. tardus* (Chironomidae)	LA	Butler, 1982a, b; Butler et al., 1981
			Pedicia hannai antennata (Tipulidae)	LA	MacLean, 1973, 1975b
		Short-lived adults emerge with fully ripe eggs	*Gynaephora groenlandica* (Lymantriidae)	HA	Oliver et al., 1964
			Tipula carinifrons (Tipulidae)	LA	Lantsov, 1982
			Gymnopais sp. (Simuliidae)	LA	Downes, 1964
			Pedicia hannai and other spp. (Tipulidae)	LA	MacLean, 1973, 1975a
3. Programmed early, flexible late	Development of immature stages programmed, or completed in one season, but reproduction by adult flexible	Adults lay eggs over more than one season	Larval development more or less fixed but adult flexibility in *Lancetes angusticollis* (=*claussi*) (Dytiscidae)	SAa	Nicolai & Droste, 1984; Arnold & Convey, 1998
			[See also Table 4, set 5]		

TABLE 3 (continued).

Pattern	Characteristic	Evidence	Example	Area	Reference
		Facultative autogeny; some adults oviposit at once, others blood feed first, some then oviposit without blood after a delay	*Aedes impiger* (Culicidae)	HA	Corbet, 1967
4. Programmed or staged	Entire life-cycle more or less controlled, e.g. development governed at two or more stages	Only one moult per year	*Alaskozetes antarcticus* (Podacaridae)	MAa	Convey, 1994a, b
			Psychophora sabini (Geometridae)	HA	Danks & Byers, 1972
		Fixed sequence of morph production	*Acyrthosiphon svalbardicum* (Aphididae)	HA	Strathdee et al., 1993
		Successive programmes	Eggs of Arctic black flies hatch in spring, adult emerges with ripe eggs (Simuliidae)	LA	Downes, 1965
5. Rapid	Univoltine, life cycle of fixed duration	Life cycle always completed in a single season, and same stage overwinters	*Aedes* spp. (Culicidae)	HA, etc.	Corbet & Danks, 1973, 1975
			Hydroporus polaris (Dytiscidae)	HA	deBruyn, 1993; deBruyn & Ring, 1999
			Bombus spp. (Apidae)	HA, SA	Richards, 1973; Vogt et al., 1994
			Sphagnophylax meiops (Limnephilidae)	LA	Winchester et al., 1993
			Nysius groenlandicus (Lygaeidae)	HA, LA	Böcher, 1975
			Arctic psyllids (Psyllidae)	LA	MacLean, 1983; Hodkinson, 1997
6. Variable, short-term	Some individuals develop slower or faster than the norm	Some individuals take an extra year for the life cycle	3 not 2 yr in *Dryocoetes* (Scolytidae)	SA	Johansson et al., 1994
		Emergence postponed for one year in cold years	Several species (Chironomidae)	HA	Oliver, 1968; Danks & Oliver, 1972a
			Tipula carinifrons (Tipulidae)	LA	Lantsov, 1982
			Pedicia hannai antennata (Tipulidae)	LA	MacLean, 1973
		Some individuals interpolate an extra generation	Some individuals are viviparae programmed for a third generation in *Acyrthosiphon svalbardicum* (Aphididae)	HA	Strathdee et al., 1993
7. Variable, long-term	Some individuals prolong development or reproduction	Prolonged diapause for more than one season	Species of Muscidae, Anthomyiidae, Olethreutidae, Tenthredinidae	HA, LA	Chernov, 1978
		Reproduction spread out over more than one season	[see set 3 above; and Table 4, set 5]		
		Very prolonged reproduction	Most females deposit only single eggs, averaging only one every 7 weeks in *Alaskozetes antarcticus* (Podacaridae)	MAa	Convey, 1994c

nisms can be listed confirms that the various means for life-cycle programming familiar from temperate species occur in polar species too.

In areas with short seasons, many species promote the earliest possible emergence (Table 4, set 1). In at least some instances, these responses depend on a fixed overwintering resting or diapause stage, typically the prepupa, in which larvae accumulate at the end of the previous season (e.g. Danks & Oliver, 1972a). Several species develop very rapidly (Table 4, set 2) with low temperature thresholds for growth, high growth rates even at relatively low temperatures, a relatively short pre-moult period, and an abbreviated adult stage.

Other species (Table 4, set 3), compared to their temperate relatives, eliminate generations, or stages (adult feeding, mating, and even the adult stage itself). Although such traits as reduced number of generations and parthenogenesis are also known in certain temperate species, of course, they are more common in polar regions (Danks, 1981).

Rapid development is possible even in cold regions through accelerated metabolism at a given temperature and through choice of relatively warm microhabitats. Temperature adaptation has been claimed or demonstrated in several species (Table 4, set 4). However, it is by no means universal nor always convincingly demonstrated, because many other functions besides the potential rate of respiration may constrain polar species (see Danks, 1981, p. 275–276, for discussion), and because a number of other factors influence measured respiration rates (Clarke, 1991). Many polar species choose specific, often warm microsites, and many others – including immature stages – have closely adapted basking behaviours to increase body temperatures in sunshine (see references in Table 4).

Some mechanisms to delay the life cycle assist in appropriate seasonal synchrony. Life-cycle delays may be necessary to ensure that feeding stages coincide with habitats or food supplies that are of low quality, unreliable, or seasonally restricted, or to avoid producing a generation or stage so close to winter that it would be certain to fail. Such mechanisms include slow development or reproduction, and interpolation of a resting stage (Table 4, sets 5, 6). Reproduction may be spread over more than one season. The resting stage characteristic of temperate regions, diapause, does occur in some polar species, even in springtails, a finding that is especially significant because the number of polar studies specifically designed to detect it is so small. Apparently in some Arctic species diapause is coupled with post-diapause control of emergence through temperature thresholds for development (see below). However, Norton (1994) has pointed out that the very slow development of oribatid mites is a primitive character widespread in the group, and not a response to polar environments.

Both directly controlled and cued development help to adjust these life cycles (Table 4, sets 7, 8). Some species adjust the rate of metabolism following an increase or decrease in temperature ("acclimation"), a phenomenon known in some polar chironomids (Table 4) though not in others (e.g. *Belgica antarctica*: Lee & Baust, 1982). Such a short-term adjustment is distinct from the metabolic compensation or faster basal rate already referred to (Table 4, set 4).

Many species use temperature cues or temperature thresholds to control development. For example, in High Arctic chironomids, temperature requirements rise steadily for successive components of spring emergence: 1°C for larval activity, 4–5°C for pupation, and 7°C for adult emergence (Danks & Oliver, 1972a, b; Danks, 1981). Temperature, then, is especially important to polar arthropods, and is commonly used to regulate the life cycle. Conversely, photoperiod becomes much less relevant than temperature toward the poles. It is used differently by some species even in the Subarctic (*Pterostichus nigrita* in Table 4) and not at all by some species in the High Arctic (Danks & Oliver, 1972b for diel emergence of chironomids). Any suggestion for polar latitudes that a lack of photoperiodic response signifies a lack of life-cycle programming therefore is not appropriate.

CORRELATES

Despite a lack of information, the available data suggest that the incidence or balance of flexible versus programmed life cycles in polar species is correlated with the following relatively small number of factors.

First, the phylogenetic placement of species establishes certain basic life-cycle components and certain "preadaptations" to polar conditions (Table 5). For example, primitive oribatid mites develop slowly with low fecundity, iteroparity and long adult life, and even in some temperate species the life cycle lasts for more than a year (Luxton, 1981; Norton, 1994). Even Antarctic species of oribatid mites such as *Alaskozetes antarcticus* do not appear to be specialized (Block & Convey, 1995). Conversely, some species with fixed overwintering stages but characteristically rapid development, such as mosquitoes and psyllids, can complete a generation each year even in the Arctic.

A second major correlate of life-cycle programmes is the conditions experienced, especially according to climatic zone. In particular, the climate of a given zone may limit the life cycles that are feasible there. For example, when the season is very short and severe, most species require more than one year to complete development. Other examples of constraints on life cycles caused by the effects of severe, seasonal or unpredictable climates on above-ground conditions are given below in the context of habitats.

The Continental Antarctic is very severe indeed: temperatures rise above 0°C only in certain habitats, and only for short periods (Sømme, 1986). Few species – especially of insects – survive there, so that few examples can be found to illustrate life-cycle patterns and the range of types is relatively small. Antarctic and Arctic climates are very different, especially the generally smaller range of temperatures (= lower seasonality and variability) of Antarctica. Seasonality is not generally marked in the

Table 4. Sample mechanisms by which the life cycle is adjusted in polar species. Areas: CAa, Continental Antarctic; MAa, Maritime Antarctic; SAa, Subantarctic; HA, High Arctic; LA, Low Arctic; SA, Subarctic.

Mechanism	Details/type	Species	Area	Reference
Acceleration				
1. Rapid start in season	Emergence and reproduction only early in the season (spring or early summer), and hence synchronous	*Eretmoptera murphyi*, ?*Parochlus steinenii* (Chironomidae)	MAa	Block et al., 1984; Convey & Block, 1996
		All High Arctic species (Chironomidae)	HA	Danks & Oliver, 1972a
		Piophila arctica (Piophilidae)	HA	Danks & Byers, 1972
		Trichocera borealis (Trichoceridae)	HA	Danks & Byers, 1972
		Aedes impiger, *A. nigripes* (Culicidae)	HA	Corbet & Danks, 1973
		Hypogastrura tullbergi (Hypogastruridae)	HA	Birkemoe & Sømme, 1998; Birkemoe & Leinaas, 1999
		Many species of Tipulidae	LA	MacLean 1975b
		Bombus spp. (Apidae)	SA	Vogt et al., 1994
2. Rapid development	Low temperature threshold for growth and activity	Low threshold (–0.6°C) for larval activity in *Pringleophaga marioni* (Tineidae)	SAa	Klok & Chown, 1997
		Low thresholds (0.5°C) for activity of larvae and adults of Tipulidae, and adults of Saldidae	LA	MacLean, 1975b
		Lowest thresholds (1°C) in larvae of *Aedes nigripes* and other tundra spp. (Culicidae)	LA, SA	Haufe & Burgess, 1956
	Increased growth rate	Very rapid larval and pupal development in *Aedes* spp. (Culicidae)	HA, LA, SA	Haufe & Burgess, 1956; Corbet & Danks, 1973
		Rapid larval development in *Hydroporus polaris* (Dytiscidae)	HA	deBruyn, 1993; deBruyn & Ring, 1999
		Rapid immature development in *Psylla* spp. and others (Psyllidae)	LA	MacLean, 1983
		Very rapid larval and pupal development in *Chrysomela* spp. (Chrysomelidae)	LA	Chernov, 1978; Chernov et al., 1993
	Rapid moult	*Dineura viridiforsata*, *Nematus calais* and others (Tenthredinidae)	LA	Matsuki & MacLean, 1991; Matsuki et al., 1994; Bogacheva, 1995
	Abbreviated adult stage with rapid reproduction	[See Table 3, set 2]		
3. Elimination of a stage	Reduction in the number of generations typical of temperate regions	None or only 1 viviparous generation in *Acyrthosiphon svalbardicum* (Aphididae)	HA	Strathdee et al., 1993
		Only one worker generation in *Bombus polaris* (Apidae)	HA	Richards, 1973
		Workers eliminated through nest parasitism in *Bombus hyperboreus* (Apidae)	HA	Richards, 1973
	Elimination of free-living adult	Adult liberates eggs without emerging in *Prosimulium ursinum* (Simuliidae)	SA	Carlsson, 1962
	Elimination of mating through parthenogenesis	Species of Ephemeroptera, Trichoptera, Hemiptera (Psyllidae, Coccidae, Miridae), Diptera (Chironomidae, Simuliidae); also Acari, Collembola	Esp. in HA; apparently also in Aa	Review by Danks, 1981, pp. 290–291; see also Convey, 1996b

TABLE 4 (continued).

Mechanism	Details/type	Species	Area	Reference
4. Accelerated metabolism	Elevation of standard metabolism	Activity relatively rapid at lower temperatures in *Maudheimia patronia* (Scheloribatidae)	CAa	Marshall et al., 1995
		Alaskozetes antarcticus (Podacaridae)	MAa	Block, 1977; Block & Young, 1978; Young, 1979
		Parisotoma octooculata (Isotomidae)	MAa	Block, 1979
		Perimylops antarcticus (Perimylopidae)	SAa	Sømme et al., 1989
		Some *Bothrometopus* and *Ectemnorhinus* spp. or populations (Curculionidae)	SAa	Chown et al., 1997
		Amara quenseli (Carabidae), *Simplocaria metallica* (Byrrhidae), *Rhynchaenus flagellum* (Curculionidae)	HA	Stromme et al., 1986; Stromme, 1989
		Folsomia regularis (Isotomidae)	HA	Addison, 1975
		Onychiurus arcticus (Onychiuridae)	HA	Block et al., 1994
	Choice of warm microsites	Basking in *Belgica antarctica* (Chironomidae)	MAa	Peckham, 1971 (p. 164)
		Basking on flowers in *Aedes* (Culicidae) and many other adult insects	HA, LA	Kevan, 1975, 1989
		Larval basking on foodplant and orientation of cocoons in *Gynaephora rossii* and *G. groenlandica* (Lymantriidae)	HA	Kevan et al., 1982; Kukal et al., 1988; Kukal, 1990
		Various basking behaviours in butterflies	HA	Kevan & Shorthouse, 1970
		Larvae of *Aedes* (Culicidae) move to warmest parts of pools	SA	Haufe, 1957
Delay				
5. Slow development	Slow growth	Oribatid mites (but see note in text)	SAa	West, 1982; Norton, 1994
	Reproduction prolonged or lasting more than one season	*Alaskozetes antarcticus* (Podacaridae)	MAa	Block, 1980; Convey, 1994c
		Edwardzetes elongatus (Ceratozetidae)	MAa	West, 1982
		Amblyostegium minimum and *A. pacificum* (Carabidae)	SAa	Davies, 1987
		Apparently in *Hypogastrura tullbergi* (Hypogastruridae)	HA	Birkemoe & Leinaas, 1999
6. Addition of a resting stage	Pre-moult period prolonged	*Alaskozetes antarcticus* (Podacaridae)	MAa	Convey, 1994a, b
		Epirrhita autumnata (Geometridae)	SA	Ayres & MacLean, 1987
	Diapause	Inferred for prepupae of "absolute spring species" of Chironomidae; Tipulidae; etc.	HA	Danks & Oliver, 1972a; MacLean, 1973
		Adults of *Hypogastrura tullbergi* (Hypogastruridae)	HA	Birkemoe & Leinaas, 1999
		Eggs of *Aedes impiger* (and other species) (Culicidae)	HA, LA	Corbet & Danks, 1975; Tamarina & Aleksandrova, 1984
		Eggs of *Nysius groenlandicus* (Lygaeidae)	HA, LA	Böcher, 1975
		Adults of *Protophormia terraenovae* (Calliphoridae)	LA	Vinogradova, 1993, etc.
		Several species of Plecoptera	LA	Inferred by Stewart & Ricker, 1997
	Key threshold for final moult(s)	*Eobrachychthonius oudemansi* (Brachychthoniidae), *Platynothrus skottsbergii* (Camisiidae)	MAa	West, 1982
		[See also set 8, below, e.g. Chironomidae, Dytiscidae]		

TABLE 4 (continued).

Mechanism	Details/type	Species	Area	Reference
Factors used for adjustment				
7. Regulation of rates	Ordinary regulation	Most species develop faster at higher temperatures		Information from all life zones (review by Danks, 1987a, pp. 46–59)
	Temperature compensation	*Chironomus* spp. (Chironomidae)	LA	Bierle, 1971; Butler et al., 1981
8. Use of cues	Temperature threshold or critical range	Spring moult in *Alaskozetes antarcticus* (Podacaridae) only well above 2°C	MAa	Convey, 1994b
		Apparently for emergence of *Belgica antarctica* (Chironomidae)	MAa	Sugg et al., 1983
		Apparently reproductive quiescence at low temperature in *Hypogastrura tullbergi* (Hypogastruridae)	HA	Birkemoe & Leinaas, 1999
	Other thresholds	Moisture may be required for moult in *Cryptopygus antarcticus* (Isotomidae)	MAa	Convey, 1996a
		Freezing temperatures may be required for diapause development in tundra crane flies (Tipulidae)	LA	MacLean, 1975a
	Series of thresholds	Temperature threshold for growth of tritonymph and moult to adult is higher than threshold for deutonymph in *Alaskozetes antarcticus* (Podacaridae)	MAa	Convey, 1994b
		Larvae develop to final instar at 5°C but final instar and pupation requires 7.3°C in *Lancetes angusticollis* (= *claussi*) (Dytiscidae)	SAa	Nicolai & Droste, 1984
		Rising temperatures for growth, pupation and emergence in Chironomidae (see text)	HA	Danks & Oliver, 1972a, b
	Control systems	Circadian control system differs from temperate populations in *Pterostichus* (Carabidae)	SA	Ferenz, 1975; Thiele, 1977; Leyk, 1981

Subantarctic. Consequently, information from that zone has less bearing on the question of whether flexible life cycles are driven by seasonality.

At a smaller scale, conditions vary widely in different habitats. Consequently, the habitat and microhabitat of species are clearly correlated with the structure of their life cycles. For example, mites and Collembola that spend their whole lives in soil tend to have less structured life cycles, because conditions there are buffered. Indeed, for the microfauna interstitial and warm surface-soil habitats are very similar in many climatic zones, as evidenced by species from these habitats that are truly cosmopolitan, such as the oribatid mite *Tectocepheus velatus* (distributed in the High Arctic, Low Arctic, Subantarctic, widely in the Nearctic and Palaearctic regions and in Australia) (Danks, 1981; Marshall et al., 1987) and the springtail *Hypogastrura viatica* (evidently able to live in all zoogeographic regions including the High Arctic, the Maritime Antarctic and the Subantarctic) (Wallwork, 1973; Fjellberg, 1986), and the ease with which such species are introduced by humans (Pugh, 1994; Greenslade, 1995). Nevertheless, a substantial proportion of the Antarctic species of the microfauna are endemic (e.g. Wallwork, 1976; Pugh, 1993; Greenslade, 1995). Species that live on warm-blooded vertebrate hosts in the winter, such as the flea *Glaciopsyllus antarcticus*, show little life-cycle programming (cf. Bell et al., 1988; Whitehead et al., 1991). Mallophaga, relatively well represented even in cold Antarctic zones, spend all of their lives on vertebrate hosts.

On the other hand, most insect species that spend their larval stages in the buffered habitats of soil or water have aerial adults that emerge into the more seasonal and rigorous conditions above ground. The life cycles of these species tend to be seasonally constrained. As might be expected, evidence of programmed adult emergence exists for species of crane flies and chironomids from such habitats. Such a finding emphasizes the need to look at whole life cycles and not simply for flexible larval growth, for example.

Another major life-cycle correlate is food. Synchrony and rapid development are forced in Arctic psyllids, because these species eat the catkins of particular species of willows, a particularly time-limited resource (Hodkinson et al., 1979; MacLean, 1983; Hodkinson, 1997). In contrast, the resources of detritus and the microflora associated with it, which are eaten by typical soil mites and springtails, are much less seasonal. Resources therefore may be either short lived or available all year, and in addition their level can vary widely from year to year. For example, in a given season allochthonous nutrient inputs for aquatic detritivores depend partly on the amount of winter snow and the rate of spring run off, which deposits detritus from terrestrial habitats into aquatic ones.

Finally, the relative local permanence of habitats and food plants, as well as seasonality, determine whether long-term strategies (such as multiple larval overwintering or iteroparity) are possible in a given species. Consequently, the availability or lack of any one of a number of different factors can determine the presence or absence of the species in a given region.

CONCLUSIONS

The information reviewed above suggests that recent opinions about the scarcity of programmed life cycles in polar environments have arisen chiefly from an absence of salient observations, especially the relative lack of direct information about entire life cycles and the lack of direct experiments, rather than from the true absence of life-cycle programmes. I conclude that previous conclusions and generalizations are premature, such as Sømme's (1995) opinion that diapause is rare in Arctic, Antarctic and alpine species, and Convey's (1996a, b, 1997a) opinion that seasonality and unpredictability force flexibility in Antarctic environments. The sub-category of "passive" development recognized by Chernov (e.g. 1978) likewise is not a single grouping, because development over several years can be structured in a number of ways and does not depend only on long and opportunistic larval life (cf. Table 3; see also Danks, 1992).

The flexible aspects of polar life cycles therefore have often been emphasized, but it is worth noting that a great deal of flexibility is inherent in the life cycles of typical arthropods from temperate regions, some of it correlated with unpredictable conditions or resources, for example, and some with the possibility of growth all year. It is well known that constraints such as temperature, humidity, oxygen, food or crowding can slow development directly or reduce adult size (see Danks, 1992, 1994a for some examples) without compromising the life cycle as a whole. From a seasonal perspective, for example, the life cycle may last from months to years in different habitats in the same region (e.g. Winstanley, 1979), the number of generations interpolated between successive winters may vary among years, habitats or microhabitats (e.g. Farkas & Brust, 1986), many species show cohort-splitting (e.g. Pritchard, 1979; Danks, 1992, 1994a), and many species overwinter in multiple instars some of which may have diapause but some of which are merely quiescent at the same time (e.g. Brown, 1980, 1983). Some other species that normally enter diapause lack diapause in buffered habitats such as springs and caves (e.g. Di Russo et al., 1994), and in milder climates (Danks, 1987a), where even many aphids overwinter as vivipara rather than in the usual winter egg stage (e.g. Blackman, 1974; Dixon, 1985). Changes in the number of larval instars as a result of temperature or starvation are common, as in some Lepidoptera (e.g. Morita & Tojo, 1985; Clare & Singh, 1990; Kamata & Igarashi, 1995). A large number of life-cycle pathways can be generated within a species from opportunistic responses of this sort, as well as through programmed options (e.g. Knülle, 1987, 1991; Danks, 1991, 1994a). Given the limitations of data about species from polar regions, it is difficult to compare the prevalence of flexibility there with its prevalence in temperate regions. Nevertheless, demands on species are more extreme in polar than in temperate regions, so that several

TABLE 5. Some correlations between features of a taxon and life-cycle characteristics.

Basic feature of taxon	Other typical correlates	Typical polar life cycle	Sample taxa	Sample reference
Slow development, evolutionarily conservative	Often stenothermal	Long, slow (potentially flexible) life cycle, multiple overwintering	Oribatida	Norton, 1994
Flexible development	Small size, generalized habits	Variable/flexible	Some Acari and Collembola	(See Table 3, set 1)
Occupies buffered habitats		Potentially flexible development	Many aquatic and soil species; also ectoparasites	Danks, 1981
Overwinters in a fixed late larval stage		Potentially synchronized spring emergence	"Absolute spring species" in many taxa, including Chironomidae, Tipulidae, Lepidoptera	Danks & Oliver, 1972a; Danks & Byers, 1972
Long adult life		Relatively rapid larval development, iteroparous adult	Coleoptera	Danks, 1992
Rapid development, overwinter in one stage	Small size	Rapid univoltine	Culicidae Psyllidae	Corbet & Danks, 1973 Hodkinson et al., 1979; MacLean, 1983
Generalized foods, physiology, etc.		Various life-cycle options, including larval overwintering	Chironomidae	Danks, 1971
Food restricted, specialized, or of low quality	Limited seasonal window	Usually long, overwintering as larva in feeding stages	Some larger Lepidoptera	Danks, 1987b, 1992
Complex morphological changes with generations		Sequenced or variable programmes	Aphididae Some Collembola	Strathdee et al., 1993; Cassagnau & Lauga-Reyel, 1987; Fjellberg, 1995
Good performance even under cold conditions		Rapid development, low thresholds, spring emergence, etc.	Taxa that evolved in cold regions, e.g.: Chironomidae Trichoceridae Other cold-adapted taxa [as well as some taxa with characteristically rapid development, e.g. Diptera-Cyclorrhapha, or spring emergence]	 Brundin, 1966; Danks, 1971 Dahl, 1970 Downes 1962; Danks, 1990 (Table 4); Convey, 1997a

adaptations are more frequent or more marked there (Danks, 1981).

Some of the differences of opinion about the prevalence of flexibility probably arise too from the great differences between the Antarctic and Arctic zones. Not only are the climatic conditions different (see Conditions, Correlates), but also the success and recency of colonization differ between the Arctic and the more remote lands of the Antarctic, and – partly stemming from this – the diversity, composition and typical habitats of the fauna also vary. For example, the Continental and Maritime Antarctic have relatively few species, chiefly soil-dwelling mites and springtails, whereas mites and springtails but also many insects live in the High and Low Arctic. The Arctic therefore has a greater number of species, and may have a wider range of life-cycle options.

Notwithstanding these differences, the features noted above illustrate the variety and complexity of life cycles in polar arthropods. Some species indeed have highly flexible life cycles (as in some but not all soil arthropods), but others have relatively closely governed life cycles (such as a single moult each spring). However, the life cycles of most polar species do not show one or the other extreme but instead combine elements of flexibility and programming at different stages, depending on the species and its life style (Table 3). Beyond these responses (though we lack information from polar regions), genetic morphs that are differently programmed can provide more than one developmental option – a kind of programmed flexibility – and are most prevalent where conditions are unpredictable or variable so that the optimal choice in a given season cannot be determined from cues available during that season (see Danks, 1994a for general examples).

In particular, even species with life cycles that appear to be largely flexible have programmed elements at the season or stage when timing is most significant, such as the emergence of the adult in spring. Erroneous life-cycle decisions incur severe fixed penalties, and evidently even relatively modest life-cycle modifications and intermittent temporal programming provide significant advantages for survival (Danks, 1994b). In addition, some degree of insurance or risk spreading (achieved through variability) has advantages in most habitats over precise and universal seasonal or annual coincidence (see Danks, 1983, 1987a for discussion). In other words, life cycles consist of successive responses, no one of which can be overlooked in trying to understand them. In turn, the components can be correlated with regional, habitat and microhabitat conditions (especially with respect to temperature patterns), with taxon, and with food resources (see Correlates). In particular, environmental conditions help to determine what life cycles are feasible in a given area (Danks, 1994b). Analysis of the severity, seasonality, unpredictability and variability of climates and habitats that is more detailed than has been customary (see Conditions, and compare Table 2) therefore is necessary.

Evidence from polar arthropods, then, coincides with the lessons from the more abundant information that is available for temperate regions in confirming that flexibility and opportunism are by no means the only way to cope with highly seasonal or unpredictable environments. Certainly there is room for selective opportunism. However, in most habitats including polar ones a successful life cycle normally cannot be maintained merely through simple, unstructured, opportunistic responses to the environment. This conclusion suggests that life cycles evolve not so much to ensure that growth can be fitted in but rather so that critical stages of the life cycle, notably reproduction, coincide with conditions that are favourable. Consequently, even in polar regions, specific adaptations for life-cycle timing are generally required, not just the flexibility to muddle through.

ACKNOWLEDGEMENTS. I thank P. Convey, British Antarctic Survey, Cambridge, for especially helpful comments on the manuscript.

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Received September 28, 1998; accepted March 26, 1999