A positive correlation between photoperiod and development rate in summer species of Odonata could help to make emergence date appropriate to latitude: a testable hypothesis[1]

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ABSTRACT

In the western Nearctic and the Palaearctic Regions several species of Odonata occur, without evident gaps in distribution, from latitude 50° N northwards to the Arctic Circle (66°30'N) and beyond. The decline in incident solar radiation along this latitude gradient does not appear to be reflected, as might be expected, in progressively later emergence, despite the progress of metamorphosis being dependent on ambient temperature. On the contrary, reports indicate that, in some species, northernmost populations may emerge at least as early as, and sometimes even earlier than, more southerly populations, suggesting that some mechanism exists that enables larval developmental rate to compensate for latitude. Reported responses by late-stadium larvae to photoperiod, placed in the context of seasonal changes of photoperiod at different latitudes, make it plausible to postulate the existence of a single, fixed response to photoperiod that would continuously adjust developmental rate to latitude, at least between 50° and 70° N. In Odonata such a response, to be effective, would be confined to species possessing a Type-2 or Type-3 life cycle, in which more than one stadium precedes metamorphosis in spring or early summer. The hypothesis proposed here does not invoke genetic heterogeneity of response in populations at different latitudes, such as has been detected in certain other insects. The response predicted by the hypothesis may complement, rather than substitute for, other mechanisms of seasonal regulation. Steps are described by which the hypothesis could be tested in Odonata.

INTRODUCTION

Western Canada is of interest to odonatologists because it includes the highest latitudes at which Odonata maintain populations in the Nearctic Region and because it is where many species, commoner and better known in the United States, reach the northernmost limits of their distribution. Some species in western Canada maintain a virtually continuous distribution from about 50° to 70° N, i.e. from southern British Columbia (BC) to the Yukon and Alaska. Reports by Cannings *et al*. (1991), Cannings and Cannings (1997) and Cannings (2002) have done much to characterize this distribution and have provided a major impetus for this paper.

The tree line generally forms the latitudinal limit to the occurrence of resident populations of Odonata: no species of Odonata breeds on the Arctic slope of Alaska (Cannings *et al*. 1991). In Canada the tree line occurs at progressively lower latitudes towards the east, reaching its southernmost limit close to Churchill, Manitoba, at about 58°46' N. This means that the 88 species of Odonata that occur in both British Columbia

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(BC) and the Yukon (Cannings 2002) exist as breeding populations over a wider range of northerly latitudes than anywhere else in the Nearctic Region. Therefore I focus here on the Odonata of western Canada, mainly northern BC and the Yukon.

Another impetus for this paper has been the clarifying research by Norling on the seasonal regulation of those Odonata that have a wide latitudinal range in Sweden (Norling 1976, 1984a, b, c). As Norling (1984b) has remarked, species occurring over such a wide range of latitude will be exposed to a south-north gradient characterized by progressively shorter (and usually cooler) summers, by longer (and usually more severe) winters, and by less predictable weather in summer. They will also experience progressively longer photoperiods between the spring equinox and the summer solstice (i.e. the time of most active pre-emergence development). Such exposure implies an extreme commitment in the northernmost species of these Odonata to early emergence, because inclement weather during the brief northern summer can seriously erode the time available for imaginal maturation and reproduction.

Noting the seasonal placement of the flying season of odonates along this climatic gradient has led me to postulate a hypothetical mechanism whereby the retarding effects of the climatic gradient might be compensated for by a unitary response to photoperiod. In the rest of this report I explain the reasoning leading to the hypothesis and its implications: first, I review what is known about seasonal regulation of Odonata, thus providing the information base with which the hypothesis must be consistent; second, I formulate the hypothesis and explore its implications for several variables;   and third, I present a protocol for testing it.

The full scientific names of all species mentioned in this account, if not in the running text, are given in Table 1.

SEASONAL REGULATION OF ODONATA:
THE BACKGROUND

Norling (1984b) and Pritchard (1982) have placed the topic of seasonal regulation in Odonata in broad ecological perspective. The question of seasonal adjustment according to latitude is a subset of the more fundamental one of how a group of tropical origin such as the Odonata has successfully colonized temperate latitudes. Pritchard (1982) concluded that the Odonata, unlike other aquatic insect orders such as the Ephemeroptera and Plecoptera, remain warm-adapted and have retained cold-intolerant early larval and adult stages; so they have evolved a larval diapause that restricts the cold-intolerant stages to the warmer times of year. This interpretation has been supported by results obtained for several species (Norling 1984b) so that diapause in the egg and/or larva can be regarded as a hallmark of the Odonata (among aquatic insects) that have colonised high latitudes.

Three main Types of odonate life cycle (described below) are encountered in temperate latitudes (Corbet 1960). The first two Types, originally classified as 'spring' and 'summer' species',respectively, have been defined by Corbet and Corbet (1958) and by Corbet (1999). Paulson and Jenner (1971) observed that this dichotomy applies to life cycles in high, but not necessarily low, temperate latitudes. The third Type, a subset of summer species, comprises species that are obligatorily univoltine (completing one generation per year). These Types refer to life cycles, not species. For example, within one population of *Anax imperator* Leach a single population can exhibit two Types of life cycle (Corbet 1957a); and   populations of *Coenagrion hastulatum* (Charpentier) at different latitudes can do likewise. For example, in southern Sweden at 58°42' N, this species is mainly univoltine with a Type-2 life cycle, overwintering mainly in the penultimate larval stadium, (Norling 1984c) whereas in northern Sweden at 63°50' (Johansson and Norling 1994) and 67°50' N (Norling 1984c) it is mainly semivoltine

Table 1

Relative positions of flying seasons of Odonata that occur from southern BC north to the tree line (source: Cannings 2002).

Species	A	B	C	D
Zygoptera				
Coenagrion interrogatum (Hagen in Selys) (2)		x	x	
C. resolutum (Hagen in Selys) (2)		x	x	
Lestes dryas Kirby (3)	x			
L. disjunctus Selys (3)	x			
Enallagma boreale (Selys) (2)	x			
E. cyathigerum Charpentier (2)	x			
Anisoptera				
Aeshna canadensis Walker (2)	x			
A. eremita Scudder (2) *	x			
A. interrupta Walker (2)	x			
A. juncea (Linnaeus) (2)	x			
A. septentrionalis Burmeister (2)				x
A. sitchensis Hagen (2)		x	x	
A. subarctica Walker (2)	x			
Cordulia shurtleffi Scudder (1)	x			
Leucorrhinia borealis Hagen (1)	x			
L. hudsonica (Selys)(1)	x			
L. patricia Walker (1)		x		
L. proxima Calvert (1)	x			
Libellula quadrimaculata Linn. (1)	x			
Somatochlora albicincta (Burmeister) (1)		x	x	
S. franklini (Selys) (1)		x**	x**	
S. hudsonica (Hagen)(1)		x	x	
S. kennedyi Walker (1)		x		
S. minor Calvert (1)	x			
S. semicircularis (Selys) (1)	x			
S. septentrionalis (Hagen) (1)		x		
Sympetrum danae (Sulzer) (3)	x			
S. internum Montgomery (3)	x			
S. madidum (Hagen) (3)	x			
Total species	19	9	6	1

Key to columns:

A Flying season begins earlier in south and ends later in north.

B Flying season begins at same time in south and north.

C Flying season begins at same time in north and south but ends later in south.

D Flying season begins later in south and ends at same time in north and south.

Note: The number in parentheses after each species denotes its probable, typical life-cycle Type (see text). Where pertinent data for North America are lacking (e.g. in *Somatochlora* spp.) the life-cycle Type for the genus has been inferred from Palaearctic congeners.

*The only evidence available (Walker 1958) indicates that *A.eremita* can enter diapause in F-0, a characteristic of the T1 life cycle.

**Unlike Cannings (2002), Walker and Corbet (1978) state that the flying season of *S. franklini* is *later* in the north.

(completing a generation in two years), or even partivoltine (completing a generation in more than two years), with a Type-1 life cycle. A further example of such latitude-dependent variation is *Aeshna juncea* (Linnaeus), which exhibits a Type-2 life cycle in southern Sweden but a Type-1 life cycle in northern Sweden (Norling 1984b). *Aeshna viridis* Eversmann, in contrast, apparently always retains a Type-2 life cycle because its long-day larval diapause prevents larvae from entering the final stadium (F-0) in late summer (Norling 1971). The expression 'T1 species' will be used here as a shorthand for 'species exhibiting a predominantly Type-1 life cycle' and the corresponding abbreviations will be used for the Type-2 and Type-3 life cycles.

The T1 life cycle, typified by spring species

By spending the last winter before emergence in F-0, such species can respond promptly and synchronously to rising temperature in spring; thus they tend to emerge early. Their eggs typically develop directly, hatching about one month or less after being laid, although those of some Palaearctic *Somatochlora* are facultative in this respect, developing directly if laid early in the summer but entering diapause if laid later (Sternberg 1995). Eggs of *S. franklini*, sometimes at least, enter diapause (Walker 1925). Probable T1 examples in Canada are species of *Leucorrhinia* and *Somatochlora*, which, by analogy with their Palaearctic congeners, are semi- or parti-voltine, having life cycles lasting more than one year. *Leucorrhinia intacta* (Hagen) is known to have this Type of life cycle in southern Ontario (Deacon 1975).

The T2 life cycle, typified by summer species

Because they spend the last winter in one or more late stadia preceding F-0, such species typically emerge later than T1 species and with less synchronization (Corbet and Corbet 1958). Likely examples in Canada are species of *Coenagrion*, *Enallagma* and *Aeshna* which, by analogy with their Palaearctic congeners, are probably uni-, semi-, or parti-voltine. The eggs of *Aeshna* species typically overwinter in diapause (for North American species see Lincoln [1940] and Halverson [1984]). Those of *Coenagrion* and *Enallagma* typically develop directly (for Canadian species of *Coenagrion* see Sawchyn [1971] and Baker and Clifford [1981]; and for species of *Enallagma* see Pilon and Masseau [1984]). Despite commencing growth in their last spring in more than one stadium, T2 species can improve their synchronization of emergence by using a system of rising lower temperature thresholds that enable retarded larvae to catch up with more advanced ones (Corbet 1957b; Lutz 1968).

The T3 life cycle, typified by obligatorily univoltine species

These species represent a subset of T2. They typically, but not necessarily (see Corbet 1956a, 1999), overwinter as eggs in diapause. Larval development is completed in two or three months in spring and early summer, and adults die in late summer. Examples from Canada are species of *Lestes* (Sawchyn and Church 1973; Sawchyn and Gillott 1974; Laplante 1975; Baker and Clifford 1981) and from North America species of *Sympetrum* (Krull 1929; Tai 1967; Boehms 1971; Peterson 1975). These observations conform with results for Palaearctic species of these genera (Corbet 1999). In several species of Palaearctic *Sympetrum* and in at least one species from North America, egg diapause is facultative (Tai 1967; Corbet 1999). Like T2 species, T3 species also, theoretically, have available the use of rising temperature thresholds to reduce temporal variation in spring before emergence. From experiments conducted by Krishnaraj and Pritchard (1995) on *Coenagrion resolutum* and *Lestes disjunctus*, it is reasonable to assume that larvae of T2 and T3 species differ in their temperature coefficients for growth, the latter having the higher coefficient as well as having a higher attack coefficient and a more flexible foraging mode.

Some T1 and T2 species, and most T3 species, have evolved cold-resistant (i.e. diapause) eggs. In all such species, however, a relatively high temperature threshold for

hatching after completion of diapause development ensures that the earliest larval stadia are not exposed to low temperature in spring (for T3 species see Sawchyn and Gillott 1974; Boehms 1971; Tai 1967).

The amount of development to be completed in spring before emergence constitutes a major difference between T1 species and the rest. T1 larvae, resuming development in spring, especially at the highest latitudes, are ready to respond almost immediately to rising temperature by initiating metamorphosis, in contrast to those of T2 and T3 which still have one or more larval ecdyses to undergo before metamorphosis can begin. This disparity alone could enable T1 species to emerge earlier at higher latitudes.

Two Episodes in the seasonal regulation of Odonata can be distinguished (Norling 1976, 1984a, b, c). These represent the manifestion of two discrete strategies that can both act, though at different seasons, to ensure that emergence is positioned at an appropriate time of year.

Episode 1. Retardation of larval development in late summer and early autumn so that the larval population overwinters in an appropriate, cold-resistant stage. This process is usually accomplished by the onset of a diapause induced by photoperiod. Initially long (e.g. mid-summer), and perhaps sometimes decreasing, photoperiods (Norling 1984b) postpone entry to one or more late stadia, whereupon short photoperiods prevent development from proceeding further before the onset of winter. This Episode concerns *pre*-diapause development and is well developed in the T1 life cycle in which diapause is induced in F-0; it determines the stadium and/or intrastadial stage in which the last winter will be passed.

Episode 2. The placement of emergence, in spring and early summer, early in the season favourable for adult activity and survival. This Episode concerns *post*-diapause development. It is achieved by responses quite different from those occurring during pre-diapause development. In this Episode, instead of being retarded (as in Episode 1), larval development is *accelerated* under long photoperiods (Norling 1984b). The larval response to photoperiod characteristic of Episode 1 has evidently been reversed among larvae that have experienced a period of low (winter) temperature and/or decreasing (or short) photoperiods.

Norling (1976, 1984a, 1984b) investigated the responses of odonate larvae to photoperiod in populations at different latitudes between 58°42' and 68°20' N in Sweden. Photoperiod influences seasonal regulation in *Leucorrhinia dubia* (Vander Linden) (a T1 species studied by Norling) in late summer (Episode 1), when long photoperiods delay entry to F-0 and then short photoperiods prevent any F-0 larva from initiating metamorphosis. Norling (1976) distinguished five phases of morphological development within F-0, a stadium that had hitherto been regarded as a homogeneous developmental stage. The photoperiodic response of each intrastadial phase differs, ensuring that larvae entering spring in F-0 are in phase 4 which, unlike the phases preceding it, is characterized by larvae being able to respond promptly to increasing photoperiods, by accelerating development. The last intrastadial phase (phase 5) is brief, responsive to temperature, and unaffected by photoperiod. This set of responses results in emergence of *Leucorrhinia dubia* occurring some 7-10 days earlier than if all larvae were to remain static within F-0 and thus fail to reach phase 4 before the onset of spring.

The seasonal progression of photoperiod across the latitudinal range covered by Norling's work changes greatly according to latitude (Fig. 1). Norling (1984a) found that the critical photoperiods inducing diapause in summer (Episode 1) or accelerated development in spring (Episode 2) differed in larval populations at the extremities of this latitudinal range. Such a phenomenon, in which discrete populations at different latitudes differ genetically in their response to a given photoperiod, was already known from the work by Danilevskii and his associates on Lepidoptera between 40° and 60° N in
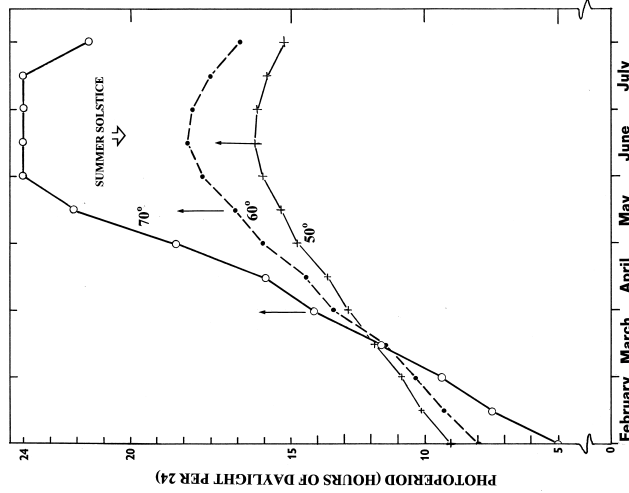
Figure 3. The daily increment of photoperiod (defined as in Fig. 2) at three latitudes during spring and early summer. (Data computed from Wood and Jaramillo (2002) by Dr K. George.)

Figure 2. Progression of photoperiod (defined as in Fig. 1 but with the addition of the Civil Twilights at sunrise and sunset) at three latitudes during spring and early summer. (Data from Beck 1968.)

Figure 1. Progression of photoperiod (defined as the interval between sunrise and sunset) at three latitudes during spring and early summer. Vertical arrows show the extent to which the photoperiod on the date indicated is lengthened by inclusion of morning and evening Civil Twilights. (Data from Beck 1968.)
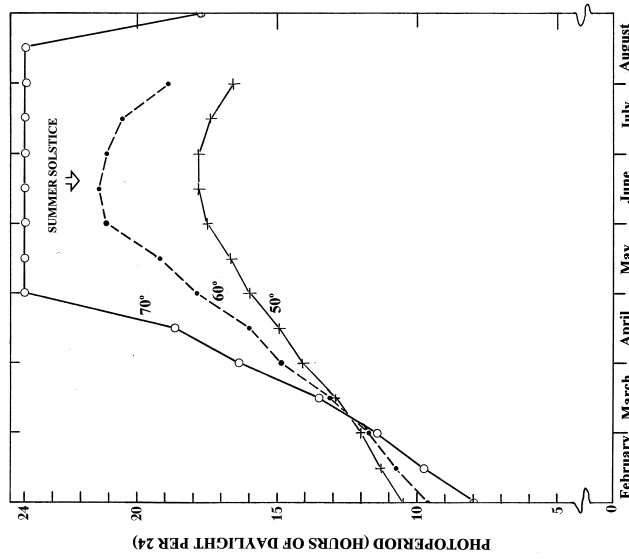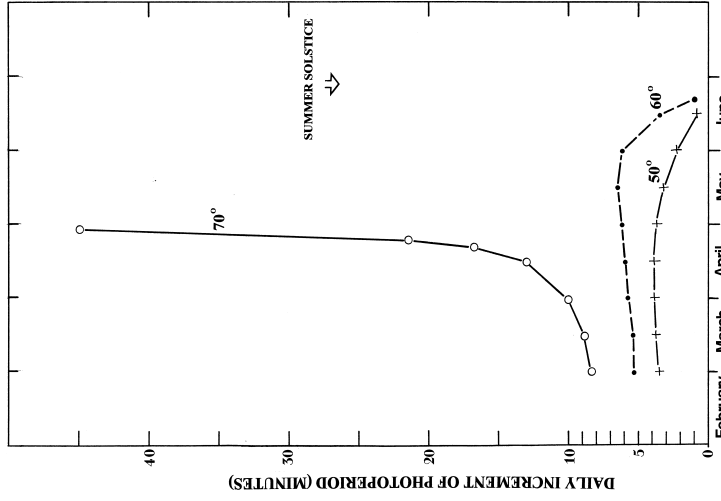
former Soviet Union (Danilevskii 1965, Danks 1987, Saunders 2003) and has since been detected in a calliphorid fly with a wide latitudinal range (Saunders 2001).

This type of response, in which latitude compensation is achieved by genetic heterogeneity of discrete populations, has been detected frequently in species exhibiting latitude-dependent phenology. It therefore occasioned no surprise that Norling (1984a) found such a response in *Leucorrhinia dubia*. However, this type of response is not what I postulate here as a regulating factor in the seasonal ecology of boreal Odonata.

SEASONAL ECOLOGY OF BOREAL ODONATA IN CANADA

Several species (e.g. *Aeshna septentrionalis* (formerly *Aeshna coerulea septentrionalis* Walker), *Coenagrion resolutum, Lestes disjunctus, Leucorrhinia hudsonica* and *Somatochlora hudsonica*) occur from southern BC north to tree line (Cannings 2002). Walker (1953) supposed that the northern limit of *C. resolutum* probably equated to the northern limit of Zygoptera in general. These five species are transcontinental and mainly boreal in distribution (Cannings 2002). In BC the southern limits of several species, as one would expect of predominantly northern taxa, tend to be at high altitude. All these species are widely distributed in the Yukon (Cannings *et al.* 1991). The demands of seasonal regulation upon species with this pattern of distribution must severely test their powers of adaptation and flexibility.

Progressively northern life cycles of Odonata are characterised in some species by an increase in the time taken to complete a generation (presumably reflecting the thermal budget and prey availability) and a narrowing of the range of stadia in which the last winter is spent (Norling 1984b). However, because metamorphosis and emergence are especially sensitive to low temperature, such sensitivity would seem to present a progressive constraint along a south-north gradient characterised by declining day-degree totals (Rae 1951; Boughner 1964). Some clues suggest that compensating mechanisms may be operating to mitigate the effects of such a constraint For example, Walker (1943) noted that adults of *C. interrogatum* appeared as early in the northern part of the species' range as in the south and that consequently a study of the flight period throughout its range might be rewarding. Likewise Walker (1953) noted that the flight period of *Aeshna palmata* may be earlier in Alaska than in Banff. Phenological records for 29 species (six Zygoptera and 23 Anisoptera) from nine genera (Table 1) occurring in Yukon and BC were found (in usable form) in Walker (1953, 1958), Walker and Corbet (1978) and Cannings (2002). Among these species, the recorded flying seasons begin earlier in the south than the north in 19 species (Table 1, column A) and end later in the south than the north in 26 species, a pattern conforming with expectation based solely on the thermal gradient. Two other comparisons, however, are contrary to this expectation: in nine species the flying season begins at about the same time in both the south and north (column B); in six species it begins in both places at the same time but ends later in the south (column C); and in one species (*Aeshna septentrionalis*) the recorded flying season begins *later* in the south (column D). Indeed, Cannings (2002) regards *A. septentrionalis* as the most boreal of Canada's darners.

THE HYPOTHESIS

We have noted examples of insects (e.g. Lepidoptera) in which phenology is made appropriate to latitude by discrete, regional populations exhibiting different, genetically determined response-thresholds to photoperiod that induce or avert diapause (Danilevskii 1965). In such instances it appears that the latitude-compensation may or may not be discontinuous. If discontinuous it can be manifest (along a latitudinal cline) by the existence of races, each adapted to a specific region. There is, however, another, simpler

way in which a photoperiodic response might achieve the compensation for latitude which may be occurring in western Canada.

For two reasons I accord preference here to this alternative hypothesis: first, it does not require the assumption that the responses of populations at different latitudes differ; and second, it postulates a single, unitary response to photoperiod that will result in seamless compensation at all latitudes.

Many years ago (Corbet 1962), perhaps stimulated by Walker's comment about *C. interrogatum,* I theorized that a compensating mechanism might exist whereby, mediated by a response to photoperiod, some Odonata might be able to adjust the rate of seasonal development to latitude. Until now I have been unable to visualise the nature of such a mechanism. My failure to do so in 1962 may have been because I was seeking an all-or-nothing *threshold* response to photoperiod rather than a response manifest in a gradual change in developmental rate.

The hypothesis I now postulate is that:

Some, perhaps many, species of Odonata possess a fixed response whereby the rate of larval development is positively correlated with photoperiod and that, in consequence, emergence at high latitudes occurs earlier than it would have done in the absence of such a response.

THE EVIDENCE

In some species of insects development is accelerated under long photoperiods (the light-growth [LG] effect), although in others long photoperiods have the opposite effect (Saunders 2003). The LG effect is well known but apparently no one has yet suggested that it could play a seminal role in adjusting phenology to latitude. Many species of Odonata exhibit the LG effect (see Danks 1987; Corbet 1999). For example in late-stadium larvae of five species of Zygoptera and the anisopteran *Epitheca* (formerly *Tetragoneuria*) *cynosura* (Say) the rate of development in several late stadia is directly proportional to photoperiod (Jenner 1958); and Dennis Procter (1973) concluded that in BC (at 49°19'N) an increase in (absolute) photoperiod at low temperatures can increase developmental rate as effectively as can a temperature rise in late stadia of *Enallagma boreale*, *Leucorrhinia glacialis* Hagen and *Libellula quadrimaculata.* If we allow the possibility that odonates respond to *changing*, as distinct from *absolute*, photoperiods (see below), then we note from Fig. 3 that the former variable, also, shows a latitude-dependent regression. This variable, manifest as *rate* of change, would also provide a mechanism for enhancing rates of development in spring in northerly populations.

The considerations above apply with particular force to T2 species and to the responses to photoperiod of the last three or four stadia. A somewhat different case is presented by T3 species– the obligatorily univoltine species – in which *all* larval stadia are exposed to the photoperiodic regime of spring.

A recent finding by Johansson and Rowe (1999), obtained in a different context, provides the evidence I need to formulate a hypothesis with confidence. Johansson and Rowe (1999), working in Guelph, Ontario (43°33'N) investigated the LG effect in *Lestes congener* (Hagen), a T3 species. Their hypothesis was structured around the assumption that, because the diapause eggs might hatch in early spring at different times, some larvae from eggs hatching late might find themselves with insufficient time to complete development before the season was too advanced for adults to reproduce. The authors noted that such 'late' larvae, subject to a seasonal time constraint, would be completing a given stadium later in the year and therefore under longer photoperiods than their more advanced conspecifics. As the authors' hypothesis predicted, larvae so placed compensated for their backwardness by accelerating development under long

photoperiods. Later, Johansson *et al.* (2001) demonstrated similar responses in the Palaearctic *Lestes sponsa* (Hansemann), another T3 species. Both *L. congener* and *L. sponsa* responded to long photoperiods by completing the larval stage sooner, albeit by producing smaller F-0 larvae. In the light of my hypothesis, these are significant findings, even though the authors were not addressing the matter of variations in latitude. Their results have obvious implications for a species like *Lestes disjunctus* which (in Canada) occurs from southern BC north to tree line. Eggs of this species are laid in stems of emergent plants, often above the water surface (Sawchyn and Gillott 1974) and are therefore likely to be exposed to highly variable temperatures when they hatch in spring; consequently larvae in different habitats are likely to start development at widely different times, some larvae being far in advance of others. Facing the compelling need to emerge as early as possible in the brief summer ahead, such larvae would benefit greatly from a means of compensating for late hatching. Accordingly we may expect the LG response to be present and well developed in populations of *Lestes disjunctus* also.

We have already noted that several species of Odonata respond to long photoperiods in spring by accelerating development. Two species of Zygoptera, *Coenagrion angulatum* Walker and *C. resolutum,* in Saskatchewan, show this response especially clearly (Sawchyn 1971). The seasonal progression of photoperiod is such that, for the same date in spring (after the spring equinox and before the summer solstice), the photoperiod is longer at the more northerly latitude (Fig. 1). This means that, provided that ambient temperature and prey availability are permissive, larvae possessing such a response to photoperiod will develop progressively more quickly in northerly populations, to an extent that is directly proportional to latitude. Such a (unitary) response alone would achieve the compensatory effect needed to adjust the onset of emergence to latitude, but without the need to invoke genetic heterogeneity between populations. When envisaging the effect of such a compensatory response, we should note that emergence at the highest latitudes may not necessarily be *earlier* than emergence at lower latitudes: the effect may only be that emergence is earlier than it would otherwise have been *without* the operation of a compensatory mechanism.

Implications of voltinism

Voltinism bears on the hypothesis, especially in regard to T2 species, in two respects. It may correlate with the date of first emergence; and also, as a consequence of Johansson and Rowe's (1999) findings, with *size* at emergence.

Regarding the date of first emergence, we may expect the duration of larval development of T2 species to increase with increasing latitude. Norling (1984c) found that *C. hastulatum* was mainly univoltine at 58°42' N, but that cohort-splitting occurred at a higher latitude (67°50'N) so that the study population became semivoltine. This process entailed the life history changing from T2 to T1 and so must have affected the date of first emergence. In western Canada the taxa most likely to be subject to such a change are species of *Coenagrion* and *Enallagma*. In Saskatchewan, at 52°15' N, both *C. interrogatum* and *C. resolutum* are univoltine, overwintering mainly in F-1 (Sawchyn and Gillott 1975). *C. resolutum* has been found to be both uni- and semi-voltine at 51°51' N (Baker and Clifford 1981) and 51°5' N (Krishmaraj and Pritchard 1995). By analogy with *C. hastulatum* in Sweden, one might expect these two Canadian species of *Coenagrion* to become semivoltine at the highest latitudes, but the only available evidence (Cannings and Cannings 1997) indicates that, in the two species of *Coenagrion* being referred to here, univoltinism can persist in the Yukon at least as far north as Koidern (61°58' N) (Cannings and Cannings 1997). If the Cannings' (1997) observation is representative, a response to photoperiod may be affecting development rate in early stadia also, enabling larvae to grow more rapidly during their first summer and enabling them to overwinter in stadia late

enough to permit emergence in the next spring. If such a latitude-compensation effect influences development rate in early stadia, it could offset the tendency for voltinism to increase with latitude in T1 and T2 species. Then the change in voltinism with latitude would be less pronounced in the presence of a latitude-compensating response.

Regarding size at emergence, if there were to be *no* change in voltinism with latitude, one could expect F-0 larvae to be smaller at higher latitudes. However, if voltinism *were* to change with latitude, this effect might be masked or even reversed. Populations of the T2 species *Enallagma cyathigerum* in western Europe reveal a U-shaped relationship between size of F-0 larvae and latitude (Johansson 2003), an effect attributed, speculatively, by the author to the step increase in voltinism observed at about 55°N. No such transition has yet been detected among coenagrionids in western Canada. If one exists, this might influence predictions about a relationship between the size of F-0 larvae and latitude.

In the light of these observations, it would be interesting to determine whether individuals from northern populations of species occupying a wide latitudinal range are *smaller* than their southern counterparts. So far, I have found no indication in the literature that this is so, except for the observations by Walker (1912) that, in *Aeshna* spp, an increase in mean summer temperature correlates with an increase in the length of abdominal segment 3 and in the length of the female anal appendages, and that in *Somatochlora franklini* adults are largest at the species' southern limit in the interior of the continent and smallest on the Labrador coast and in the Rocky Mountains (Walker 1925). The situation may be quite different in the T1 life cycle. *Coenagrion hastulatum* in Sweden in northern populations, at 67°50' N, when exhibiting a T1 life cycle, featured F-0 larvae that were *larger* than elsewhere (Norling 1984c).

TESTING THE HYPOTHESIS

Variables to be considered

Absolute Photoperiod. To simulate photoperiod experimentally one needs to know the lower threshold of light intensity at which a larva registers light as photoperiod. The distributions in Figs 1 and 2 portray regimes of photoperiod at three latitudes derived from regarding photoperiod *either* (in Fig.1) as the interval between sunrise and sunset, moments when the zenith light intensity under a clear sky is about 395 lux, (Danks 1987) *or* (in Fig. 2) as the interval between the beginning (before sunrise) and the end (after sunset) of Civil Twilight, namely Crep 1 (Nielsen 1963), when the corresponding light intensity is about 3.55 lux (Danks 1987). However, having regard to the shaded microhabitats that odonate larvae typically occupy, the lower threshold light intensity at which they register photoperiod is almost certainly very much less than that prevailing under a clear sky (Nielsen 1963; Lutz and Jenner 1964; Saunders 2003; Corbet 1999). So the light intensity above which odonate larvae register photoperiod will probably be more closely approximated by Crep 1 than by either sunrise or sunset. Lutz and Jenner (1964) found that the response threshold of *Epitheca cynosura*, whose larvae live amongst detritus, probably lies below 0.002 lux. Accordingly, to simulate natural photoperiods, those used in an unshaded, experimental situation should be at least as long as those portrayed in Fig. 2.

Changing Photoperiod. To investigate responses to *changing* photoperiod requires so many independent variables to be allowed for simultaneously (see Tauber *et al*. 1986; Danks 1987) that such responses have very seldom been investigated rigorously. Indeed, some lists of supposed examples (e.g. Zaslavski 1988) do not distinguish between responses to gradual (i.e. natural) and discontinuous (unnatural or stepped) changes of photoperiod. Attempts to demonstrate such a response in odonate larvae have been indicative but less than conclusive (Corbet 1956b) although, from the gradual nature of

responses to photoperiod shown by *Aeshna viridis* Eversmann, Norling (1984b) inferred the existence of a response to changing photoperiod. (A response to changing photoperiod *per se* has, however, been rigorously demonstrated in the lacewing *Chrysopa carnea* [Tauber and Tauber 1970].) The latitude-dependent change of this variable (Fig. 3) suggests that, if odonates having an extended south-north distribution were to possess a response to changing photoperiod, this also would provide a means of enhancing rates of development in spring in northerly populations. Such a response might or might not act in concert with a response to absolute photoperiod.

Sun Elevation. Because it declines with latitude, sun elevation progressively extends the duration of twilight, as is evident by comparing values in Figs. 1 and 2. The effect of this variable north of about 60° becomes evident in all Figures, especially Fig. 3, as the summer solstice approaches. Fig. 3 shows that the daily increment of photoperiod changes markedly with latitude, being about 3 and 5 min per day at latitudes 50° and 60° respectively, and exhibiting an abrupt and disproportionate increase from an already higher level at 70°, as the period of continuous daylight approaches. On this account, larvae responding to increments of photoperiod will be receiving a very strong stimulus at the highest latitudes at which Odonata exist.

Microclimate. Although air temperature is inversely proportional to latitude, the temperature close to the ground is to some extent insulated from this trend because of the progressive amelioration of terrestrial microclimate caused by the declining frequency of temperature inversions, especially north of 70° N (Corbet 1969). The water temperature at the bottom of shallow ponds benefits disproportionately from this phenomenon. In a shallow, dark-bottomed pond at 81° N, after retreat of the permafrost, the water temperature (both surface and bottom) remained close to 7°C, a temperature above that of the ambient air throughout June and July (Oliver and Corbet 1966). The bottom sediment of such ponds will benefit further by being insulated from wind-chill. These effects have also been observed by Danks (1971), in a shallow pond at 75° N: they accentuate the microclimatic advantage already possessed by small bodies of water which change far less than terrestrial ones from temperate to arctic regions, the greater specific heat of water imposing a lag that moderates seasonal and diel fluctuations (Corbet 1972). Thus animals able to develop in shallow bodies of water are to some extent buffered against the lower air temperature characteristic of high latitudes.

Testing Procedure

For field studies of seasonal regulation, access to habitats that are productive and readily sampled is a prerequisite for success, a fact convincingly demonstrated in a study of *Anax junius* (Drury) in southern Ontario (Trottier 1971). The survey of BC and the Yukon (Cannings *et al*. 1991; Cannings and Cannings 1997) has established the location of breeding populations of several species over a wide latitudinal range. The logistical implications of monitoring any of these populations in a systematic way are not insignificant but, if such a challenge can be met, exciting opportunities exist for odonatologists wishing to test the hypothesis and thus to explore further Walker's enigmatic statement (1943) that northerly populations of *Coenagrion interrogatum* seemed to be emerging earlier than southern ones. Appropriate, initial steps in such an investigation might be as follows:

1) Determine the phenology of some candidate species at different latitudes. Columns B, C and D in Table 2 provide a list of potentially suitable species. Emergence could best be monitored by collecting exuviae or by recording the presence of teneral adults ─ methods that could be used by a nonspecialist having access to a study site. The best species to choose would be supposed T2 species having a wide latitudinal range,

e.g. *Aeshna septentrionalis, Coenagrion interrogatum or C. resolutum.* Preference should be given to species in columns B, C and D of Table 1.

2) Determine the stadium composition of larvae of such T2 species embarking on development in early spring. This information likewise could be derived from larval samples taken by a nonspecialist able to visit a study site on chosen dates.

3) Infer the voltinism of selected species by determining the stadium composition of larvae (if any) remaining in a water body just after emergence has finished.

4) Determine by laboratory experiment the duration of each (late) stadium, identified in step (2), at permissive temperatures and with prey provided *ad libitum*, , under a range of photoperiods, chosen because they occur naturally between the spring equinox and the summer solstice over the latitudinal range inhabited by the species concerned. For each species use experimental material from several populations derived from a wide latitudinal range. When designing experiments, bear in mind that the hypothesis predicts that in all larvae so derived the rate of development in a given stadium will exhibit the same correlation with a given latitude. Having regard to the threshold light intensity used by larvae to register photoperiod, recognise that photoperiods defined by the interval between the onset of Civil Twilight at sunrise and its termination at sunset (Fig. 2) are more likely to be appropriate for simulation in experiments than those defined by the interval between sunrise and sunset. Attention in experiments should be focused initially on T2 species in which several late stadia embark on development in early spring, although, as opportunity allows, it could also be informative to determine the LG responses of earlier stadia.

Completion of these steps would either falsify the hypothesis (in regard to absolute photoperiod) or allow it to be sustained.

CONCLUSIONS

The foregoing review of phenological records, life-cycle Types and photoperiodic responses of larval stadia poised for development in spring has enabled me to postulate the hypothesis that:

Some, perhaps many, species of Odonata possess a fixed response whereby the rate of larval development is directly correlated with photoperiod and that, in consequence, emergence at high latitudes occurs earlier than it would have done in the absence of such a response.

This hypothesis, which is consistent with experimental data obtained in different contexts, helps to explain, parsimoniously, how more northerly populations of a given species could compensate for declining incident solar radiation by using photoperiodic responses to accelerate post-diapause development in spring. In this way such species could emerge earlier than would have been possible had they been responding to ambient temperature alone. To test this hypothesis could throw useful light on seasonal regulation of northern insects.

Such an investigation might appeal to the investigator whose interests include natural history. To tackle it would present challenges in both the field and the laboratory; and its completion (if the hypothesis were to be sustained) would provide a secure conceptual basis for understanding how Odonata (and other insects) in northern Canada, having different life cycles, adjust their temperature-sensitive reproductive periods to the brief, late-summer characteristic of the region.

Research by Norling (1976, 1984a, b, c) has revealed a complex interplay between responses to photoperiod and temperature in the regulation of larval development of Odonata and has shown that such responses can be modified by a larva's past experience. It is not suggested that the latitude-compensation hypothesis advanced here is to any extent a *substitute* for the matrix of responses discovered by Norling but only that it may *complement* it, enhancing its effectiveness in making the date of emergence yet more appropriate to latitude. The array of other responses by which odonate larvae adjust their developmental rate to season (Danks 1991) is complex and may make it less than straightforward to isolate rigorously the compensatory response postulated in this paper.

ACKNOWLEDGEMENTS

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