

THE UNIVERSITY OF CALGARY

Life Histories and Functional Responses of Two  
Coexisting Zygopterans

by

Rangathilakam Krishnaraj

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DEPARTMENT OF BIOLOGICAL SCIENCES

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JUNE, 1994

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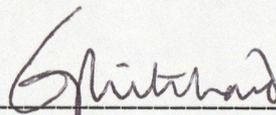
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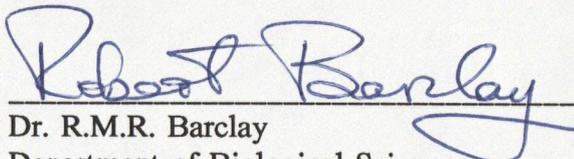


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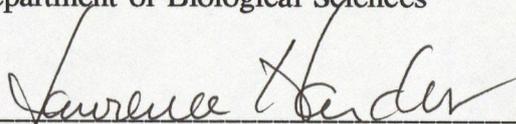
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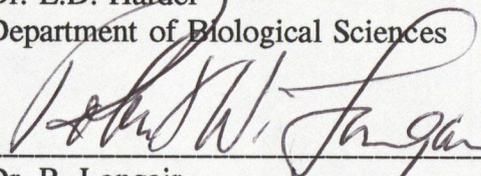
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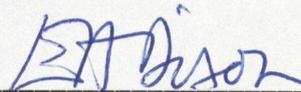
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## ABSTRACT

The objective of this study was to examine the contribution of feeding behaviour to differential larval growth rates of two dragonflies, *Coenagrion resolutum* (Hagen) and *Lestes disjunctus* Selys, at the University of Calgary Research Pond. *C. resolutum* followed a mixed univoltine-semivoltine strategy, with direct egg development, whereas *L. disjunctus* followed an obligatory univoltine life cycle, with an eight month egg diapause. The larvae of *L. disjunctus* grew 5 times faster than the larvae of *C. resolutum*, completing their development in approximately 90 days. Under constant laboratory conditions *L. disjunctus* grew 1.4 to 3.3 times faster than *C. resolutum*, the differential increasing with increasing temperature. Functional response experiments gave variable results, but small and medium *L. disjunctus* fed at a greater rate than the corresponding sizes of *C. resolutum*, attack coefficients were greater for *L. disjunctus*, and handling times were generally shorter.

## ACKNOWLEDGEMENTS

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My special thanks are due to my husband **Dr. Sankaran Krishnaraj**, for his timely help, enduring support and encouragement, without which I could not have finished this thesis. I would also thank all my family members for their moral support.

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*Dedicated to my Grand Father*

**Udumalai Narayana Kavi**

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## LIST OF ABBREVIATIONS

F instar	final instar
F-1 instar	final minus one instar
F-2 instar	final minus two instar
F-3 instar	final minus three instar
F-4 instar	final minus four instar
F-6 instar	final minus six instar
F-8 instar	final minus eight instar
Got 1	Glutamate oxaloacetate transferase 1
Got 2	Glutamate oxaloacetate transferase 2
Gpi	Glucose -6-phosphate isomerase
Idh 1	Isocitrate dehydrogenase 1
Idh 2	Isocitrate dehydrogenase 2
Ldh	Lactate dehydrogenase
mA	milliamperes
ml	millilitre
m	metre
mm	millimetre
min	minutes
<i>n</i>	sample size
<i>p</i>	probability
<i>s</i>	seconds
Std.Err	standard error
$\mu$ l	microlitre

## CHAPTER 1

### GENERAL INTRODUCTION

Dragonflies are basically warm adapted insects of tropical origin which have evolved various life cycle patterns that have enabled them to colonize temperate regions. Pritchard (1982) suggested that temperate-zone odonates might employ any of the following four strategies in order to survive the winter: 1) migration; 2) cold tolerance in all stages; 3) cold tolerance in some stage(s) and seasonal adjustment of the life cycle; and 4) habitat selection and seasonal adjustment of the life cycle. Of these four strategies the third is the most common in temperate-zone dragonflies. Mid- to late-instar larvae are usually cold-tolerant and seasonal adjustment occurs through the intervention of diapause, usually in the egg or larval stages.

Based on the positioning of diapause in the life cycle of temperate-zone Odonates, Norling (1975) classified odonate life cycles into two groups. His first group was an obligatory univoltine life cycle in which the species overwinter in a well-defined diapausing stage. Commonly the eggs are the overwintering stage in this group and larval development is rapid, as exemplified by the genus *Lestes* (Corbet, 1956a; Gower and Kormondy, 1963; Sawchyn and Gillott, 1974a & b; Baker and Clifford, 1981). (A similar life history pattern is shown by *Anax junius* Drury, where migration is substituted for egg diapause as a means of escaping winter conditions. Trottier [1966 & 1971] has described migratory populations of *A. junius* in Montreal and southern Ontario, where the adults fly in from the south during early spring and

lay eggs. Larval development is completed in approximately three months with adults emerging in late summer. These adults then presumably fly south.)

In Norling's second life cycle type the ability of the species to overwinter in a wide range of larval instars, and sometimes in the egg stage, allows for slower larval growth and extension of the life cycle over more than one year, if conditions warrant. In this type of life cycle, photoperiod is important in seasonal regulation in temperate regions (Norling, 1984a). A long-day diapause in various late instars during summer prevents untimely emergence in late summer or autumn when the cold-sensitive adults, eggs, or early instar larvae could experience cold conditions, and a short-day diapause synchronizes adult emergence during the following spring and summer. However, emergence in the following year depends on the size or the developmental stage of the overwintering larvae. Only those larvae overwintering above a certain winter critical size (WCS) show growth to emergence during the following season and larvae which are below the WCS will be prevented from emerging by the long-day diapause.

Whether a larva reaches the WCS or not depends primarily on water temperature; the higher the temperature within a range of about 10-30°C, the faster the growth. Depending on the response of larvae to water temperature in a particular habitat, the growth rates of larvae living in those habitats may vary. Thus, *Argia vivida* Hagen took one, two or three years to complete its life cycle in streams with annual temperature ranges of 11-31°C, 0-33°C and 5-20°C respectively (Pritchard, 1989). All three populations showed short-day diapause in their final winter. However, larvae in the second population did not reach WCS before their first winter

and so went into long-day diapause in the following summer, whereas larvae in the third population did not reach WCS before their second winter and so growth was delayed in their second summer. Differences in growth rate between individuals of the same population may also result from larvae having different responses to temperature or living at different temperatures, for example in shallow as opposed to deep water.

Given variation in growth rates between individuals due to photoperiod and temperature, cohort splitting and variation in voltinism can occur even within the same population. Norling (1971, 1976, 1984a & b) has given very detailed accounts of cohort splitting in Swedish populations of *Aeshna viridis* Eversm., *Coenagrion hastulatum* (Charpentier) and *Leucorrhinia dubia* (Vander Linden). Ingram and Jenner (1976) observed a small second (bivoltine) generation of the otherwise univoltine *Enallagma aspersum* if a critical stage (F-3) was reached before 1 August; otherwise a long-day diapause slowed development and led to overwintering until the following spring. If larvae of *Coenagrion resolutum* (Hagen) (Baker and Clifford, 1981), *Coenagrion puella* (L.) and *Ischnura elegans* (Vander Linden) (Parr, 1970) are in F, F-1 and F-1 instars (respectively) before the first winter, then they will complete their emergence in the following summer; otherwise they emerge during the next summer, extending the life cycle from 1 to 2 years. *Pyrhosoma nymphula* (Sulzer) is normally semivoltine in western Europe (Macan, 1964 & 1977; Lawton, 1970 & 1971; Corbet and Harvey, 1989), but the life cycle may be extended from 2 to 3 years in dense populations (Macan, 1977).

Alternatively, Macan (1977) suggested that differences in diet were possibly

responsible for cohort splitting in *Pyrrosoma nymphula*. In general, dragonfly larvae feed on any moving prey below a certain size. Their diet is mainly composed of Chironomidae, Coleoptera, Cladocera, Copepoda and other small aquatic arthropods (Pritchard, 1964; Lamoot, 1977; Thompson, 1978a; Baker and Clifford, 1981; Breene et al., 1990). The diet reflects the relative abundance of different prey in the environment, the size and habits of the prey, the ease with which prey are caught and devoured (Pritchard, 1964), predator species, predator age, season of the year (Lamoot, 1977; Blois, 1985), habitat complexity and prey activity (Folsom and Collins, 1984). Although some studies suggest that dragonfly larvae prefer large prey (Fischer, 1972; Kime, 1974; Blois, 1982; Chowdhury et al., 1989) and prey with high calorific value (Fischer, 1972), most species are general feeders and do not show any preference for different prey species in nature, provided that they are of appropriate size.

Thus, diet might principally affect growth rate within a population through feeding rate. Amount of food taken by different larvae may be influenced by microhabitat (Macan, 1977) or territorial behaviour (Baker, 1980), although Baker and Clifford (1981) and Baker (1981a) showed that neither of these mechanisms appeared to operate in the field. Alternatively, individuals may grow at different rates because of different abilities to detect, orient to, pursue, capture, consume and digest prey, that is through the attack coefficient and handling time components of the functional response to prey density (Holling, 1959).

In this thesis I compared growth rates of two zygopteran species, *Lestes disjunctus* Selys (family Lestidae) and *Coenagrion resolutum* (Hagen) (family

Coenagrionidae), whose life histories belong to different categories of Norling's classification, although they coexist in ponds in Alberta (Baker and Clifford, 1981). First, I followed the life cycles of the two species in the University of Calgary Research Pond to confirm that *L. disjunctus* does indeed fall into Norling's first life history type and that *C. resolutum* falls into the second category (Chapter 2). Then, I reared the two species at fixed temperatures in the laboratory in order to describe the relationship between growth rate and temperature (Chapter 3). Finally, to explain the faster growth rate of *L. disjunctus*, I tested the hypothesis that *Lestes disjunctus* feeds at a higher rate than *Coenagrion resolutum*, due to a higher attack coefficient and a shorter handling time (Chapter 4).

## CHAPTER 2

LIFE HISTORIES OF *COENAGRION RESOLUTUM* AND *LESTES DISJUNCTUS*

## 2.1 INTRODUCTION

*Coenagrion resolutum* is one of the most common and widely distributed odonates in Canada, ranging further north than any other species except *C. interrogatum* (Hagen) (Walker, 1953), but it has been little studied (Sawchyn and Gillott, 1975; Baker and Clifford, 1981). *Coenagrion* species may follow a univoltine (Sawchyn and Gillott, 1975; Waringer and Humpesch, 1984) or a mixed univoltine/semivoltine life history strategy (Parr, 1970; Baker and Clifford, 1981; Norling, 1984b). The eggs of *C. resolutum* hatch soon after they are laid and the larvae overwinter in a wide range of instars, taking 1-2 years to complete larval development in Canada (Sawchyn and Gillott, 1975; Baker and Clifford, 1981).

In Canada, *Lestes disjunctus* occupies a variety of habitats from marshy ponds to slow moving weedy streams and is one of the most widely distributed species in the genus (Walker, 1953). Its life history has been studied in the prairies by Sawchyn and Gillott (1974a) and Baker and Clifford (1981). Most lestids living in temperate regions appear to be univoltine in nature and undergo successful larval development in a variety of aquatic habitats including temporary ponds (Corbet, 1956b; Lutz, 1968a; Paulson and Jenner, 1971; Sawchyn and Gillott, 1974a & b; Baker and Clifford, 1981). Survival in the latter environment is due to the ability of most species to arrest development before eclosion. The eggs hatch only after diapause (which normally

takes about 6 to 8 months during winter) and when the water temperature is above about 10°C. Once the larvae hatch, they complete their development in 2 to 3 months.

In spite of the Odonata being better known taxonomically than any other group of aquatic insects in Canada (Walker, 1953 & 1958, Walker and Corbet, 1975), identification of larvae, especially early instar larvae, still presents considerable difficulty. At the University of Calgary Pond there are five species of Coenagrionidae (*Coenagrion resolutum* Hagen, *Enallagma boreale* Selys, *E. cyathigerum* Charpentier, *E. ebrium* (Hagen), and *E. hageni* Walsh) and four species of Lestidae (*Lestes congener* Hagen, *L. disjunctus* Selys, *L. dryas* Kirby and *L. unguiculatus* Hagen). Larvae of three of the species of *Lestes* are currently morphologically separable only by the dubious characteristic of labial length:width ratio (Walker, 1953; Cannings and Stuart, 1977), and Walker (1953) could only suggest that a 6-segmented versus a 7-segmented antenna might separate larvae of the genera *Coenagrion* and *Enallagma*. However, this character is not stable enough to work even for last instar larvae and, because segments are added during development, certainly does not work for earlier instars. Baker and Clifford (1980) encountered similar problems and found characters that would separate larvae of the two genera in Alberta. I found that these characters worked quite well for medium and large-sized larvae but were inadequate for separation of small larvae. Within *Enallagma*, characters on the caudal lamellae are used to separate species, but these are notoriously variable and lamellae are often missing or distorted through regeneration. Furthermore, no characters are known that

will separate female larvae of *Enallagma ebrium* and *E. hageni* (Cannings and Stuart, 1977).

I selected electrophoretic means of identification to solve these problems. Over the last 20 years, electrophoresis has been applied to many areas of biology (Richardson et al., 1986), perhaps most successfully for distinguishing between closely related species (Ferguson, 1980). Although, until recently, there were few reports of electrophoresis on dragonflies (Anderson et al., 1970; Knopf, 1977; Schott and Brusven 1980; Maibach, 1985), Zloty (1992), Zloty, Pritchard and Esquivel (1993), and Zloty, Pritchard and Krishnaraj (1993) have now established the technique as a means of associating larval and adult dragonflies. I used cellulose acetate gel electrophoresis because it has a number of very useful characteristics, not the least of which is its sensitivity, which allows analysis of very small quantities of extract (0.5-2  $\mu$ l), so that even 1st-instar larvae can be identified.

Before addressing the effects of temperature and functional response on growth rates, it was necessary to first confirm that the growth rate of *Lestes disjunctus* larvae was indeed faster than that of *Coenagrion resolutum* larvae in the populations upon which I intended to work. Therefore, this chapter is devoted to a description of the life histories and growth rates of the two species in the University of Calgary Research Pond.

## 2.2 METHODS

### 2.2.1 Study area

The University of Calgary Research Pond is a permanent pond in the western part of the University campus (51°5'N, 114°7'W), Calgary, Alberta, Canada. The pond is about 28 m long, 18 m wide and 2.25 m deep at the centre (Fig. 2.1). The depth is maintained during the summer by adding water when necessary from the University's irrigation system. The pond freezes over from late October to the end of March. Emergent vegetation is represented by a mixed stand of *Typha latifolia* L. and *Scirpus acutus* Muhl. ex. Bigel. around the northern end of the pond, extending half-way down the eastern side; the rest of the eastern side and the entire western side is covered with *Carex rostrata* with a sparse growth of *Scirpus acutus* and the southern end of the pond is devoid of emergent vegetation. *Chara* sp. and *Potamogeton richardsonii* (Benn) Rybd. grow throughout the open water area of the pond. The bank of the pond is surrounded by a dense growth of *Bromus inermis* Leyss and *Caragana arborescens* Lam. Water temperature was continuously recorded (except for September 1993) by a Ryan thermograph, placed at about 50 cm depth in the south eastern corner of the pond from 20 April to 8 December 1992 and from 9 April to 27 October 1993. Water temperature was measured once during the period when the pond was frozen over on 26 January 1993.

### 2.2.2 Sample collection

Sampling of *C. resolutum* and *L. disjunctus* started on 6 April 1992 and subsequent samples were taken at bi-weekly intervals until 24 August 1992, then at 3-week intervals until 27 October 1992, and again at two-weekly intervals from 9 April 1993 until mid-September 1993. Larvae were collected from the *Carex-Scirpus* zone and from shallow, open-water areas with a 'D' frame dip net which had an inner bag of mesh size 0.8 mm and an outer detachable bag with a mesh size of 0.2 mm. After each sampling, the inner net contents were transferred to a white enamel tray, the debris was removed and the sample was transferred to a plastic bucket for transport to the laboratory. The outer net bag was also placed in the bucket without removal of its contents.

Upon returning to the laboratory with the larval samples, I transferred the contents of the outer fine-mesh net to a beaker containing water, stirred well and let stand for about 30 min. Then small amounts of the top layer of the sediment were transferred in turn to a petri dish and small larvae were removed under a magnifying lens. Whenever *Lestes* larvae or small coenagrionid larvae were present, about 40 individuals from each sample from each family randomly were frozen at - 86 °C for electrophoretic identification (see section 2.2.3) and the rest were preserved in 70% alcohol. The contents of the coarse-mesh net were transferred to large enamel trays and coenagrionids and lestids were sorted visually on the basis of the shape of the labium. 30-40 individuals from each family, depending on the sample size, were frozen for electrophoresis. The remaining larvae were preserved in 70% alcohol. The

preserved larvae were then sorted into *C. resolutum*, *Enallagma* spp., *Lestes congener* and *Lestes* spp. with the keys provided by Cannings and Stuart (1977). Head width, wing pad length and caudal lamellae lengths were recorded for all larvae from each sample using a binocular microscope fitted with a calibrated ocular micrometer.

### 2.2.3 Species identification

In preliminary work Zloty, Pritchard and Krishnaraj (1993) scored 28 loci in *Enallagma*, 29 in *C. resolutum*, and 23 in *Lestes*. *Coenagrion resolutum* was genetically well separated from *Enallagma* (Zloty, 1992) and so could be differentiated at most of the 28 loci, but it was necessary to run six loci to get three fixed differences between *E. cyathigerum* and the other two species of *Enallagma*, and the 28 scored loci in total revealed only one fixed difference between *E. ebrium* and *E. hageni* (Table 2.1). The four species of *Lestes* were separable on the three-or-more criterion by using the five loci shown in Table 2.2.

To associate larvae with readily identifiable adult damselflies, adults were obtained by aerial netting and were taken to the laboratory in envelopes. In the laboratory all insects required for electrophoresis were dry-frozen in 1.5 mL polypropylene micro-centrifuge tubes (Fisher Scientific Ltd.) and stored individually at -86°C in a Revco Ultima 1090 Chest Freezer. I used known adults of both sexes, samples of morphologically unidentifiable larvae, and a range of morphologically identifiable larvae to monitor changes in enzyme composition during development.

The protocol of Hebert and Beaton (1989) was followed with some

modifications in the staining procedure described by Packer and Owen (1989) and Richardson et al. (1986). To perform the analysis, the frozen sub-samples were partially thawed and the thoracic portions of individual larvae with head width >1.5 mm were excised and placed in 1.5 ml microtubes. Depending on the volume of tissue, 5 to 10  $\mu$ l of double distilled water was added. The tissue was ground with a glass homogenizer and centrifuged at 10,000 rpm for 60 to 90 s. The supernatant was then transferred into sample wells by an Eppendorf digital pipette (0.5-10  $\mu$ l) for transfer to a Cellulose Acetate Gel plate presoaked in CAM buffer (8.4 g citric acid, 10 ml N-(3-aminopropyl)-morpholine in 1l of double-distilled H<sub>2</sub>O, pH 6.1) with the help of an applicator. Whole larvae with head widths <1.5 mm were ground directly in the sample wells with a sharp needle and then applied onto the gel plates. Electrophoresis was carried out for 45 to 60 min by applying 250 Volts and 8 mA/plate of current at room temperature (21°C). At the end of the time, the samples were stained for specific enzymes.

Misidentification could occur if enzyme mobilities changed during development, but the statistical aspects of electrophoretic determination compromised complete assurance that changes did not occur between unidentifiable and identifiable larvae and adults. However, if a large number of specimens were tested and no changes in enzyme mobility between adults and morphologically identifiable larvae were found and small larvae with electrophoretic profiles matching each of the known adult profiles were found, then one could assume that there were no size-associated changes in the mobilities of diagnostic loci. Clearly, the more fixed differences

between species that were used, the lower was the probability of a mismatch occurring. Therefore, I strived to obtain differences between species at three or more loci. In fact, no changes in enzyme mobility between adults and morphologically identifiable larvae were found in any species and small larvae with electrophoretic profiles matching each of the known adult profiles were found for all species.

Having characterized the species, I estimated the numbers of each species in field samples. First, I determined the proportional representation of each size class of *C. resolutum* and *L. disjunctus* in the sub-samples of larvae that were subjected to electrophoresis. Then, I multiplied these values by the total number of unidentifiable larvae in each size class in the field samples. Large *C. resolutum*, which could be identified without electrophoresis, were then added.

#### 2.2.4 Life history analysis

Examination of the data collected from the field samples suggested the presence of two groups of *C. resolutum* larvae with different growth rates. To separate the two groups, the cumulative frequency of head widths from each sample was plotted on probability paper (Harding, 1949) and mean head widths of each group read from the plots at the 50% point. The mean head widths of *L. disjunctus* were determined by dividing the sum of all head widths for this species in each sample by the total number of individuals present in the sample. Average growth rates per day were calculated for both species from these mean head widths.

## 2.3 RESULTS

### 2.3.1 Pond temperature

Temperatures were read from the thermograph charts at 6-hour intervals and used to calculate daily mean temperatures (Figs. 2.2 & 2.3). At the beginning of May 1992 the water temperature was about 12°C; it fell during May and then rose to a maximum of 22°C in mid-June. Temperatures fell again in July and then rose again. From mid-August the temperature declined until the pond started to freeze at the end of October. Water temperature below the ice varied from 0°C at the surface to 5.2°C at the substrate in the centre of the pond. In 1993 the temperature was cooler than in 1992 but more constant from May through August (Fig. 2.3). At the beginning of May, 1993 the temperature was about 9°C and rose to a maximum of 18.6°C during mid-June. Temperatures declined after mid-August as in 1992 and the pond froze on 27 October 1993.

### 2.3.2 Life history of *Coenagrion resolutum*

Larvae of *C. resolutum* occurred in the vegetated zone rather than in open-water areas. When sampling started in April 1992, larvae ranged in size from about instar F-8 to F (Fig. 2.4). Final-instar larvae were probably semivoltine individuals from the 1990 cohort; the rest were from eggs that hatched in 1991. By early May 1992, the non-final instar larvae (the 1991 cohort) comprised two groups - a semivoltine group of smaller-sized individuals growing at a rate of 0.006 mm/mm/day from 19 April to 29 June and a univoltine group of larger individuals growing at 0.005 mm/mm/day

(Fig. 2.5). The semivoltine component would not emerge until 1993, but the univoltine group merged with the semivoltine component of the 1990 cohort, and adults emerged in June and July 1992. Mating pairs were seen in the field until the third week of August and females oviposited in the stems of *Carex* sp. and *Scirpus* sp.

These eggs started to hatch in about mid-July of 1992 as indicated by the appearance of second instar larvae (head widths <0.3 mm) in the sample collected on 14 July (Fig. 2.4). By October there were signs that this cohort consisted of two groups - one consisting of semivoltine individuals from 1992 and one containing semivoltine individuals from 1991 plus the 1992 univoltine component. Sampling was discontinued during ice cover, but identical size-frequency distributions in the October 1992 (Fig. 2.4) and April 1993 (Fig. 2.6) samples showed that no growth occurred during this period. Growth resumed in spring 1993 (Fig. 2.6) at rates of 0.005 mm/mm/day between 22 April and 2 July for the semivoltine component and 0.004 mm/mm/day for the univoltine group (Fig. 2.7), slightly slower than in 1992 (Fig. 2.5). Estimates of the proportion of the 1992 cohort that was semivoltine ranged from 40-50% in the samples, which was lower than in 1993 (56-72%). Adults emerged from the merged 1992 univoltine and 1991 semivoltine cohorts from the third week of May to the beginning of July. Growth during the second half of 1993 was identical to that in the same period of 1992.

### 2.3.3 Life history of *Lestes disjunctus*

Larvae of *L. disjunctus* were collected mainly from shallow, open-water areas

of the pond. Larvae were not present in the sample of 6 April 1992 nor in samples taken from the second week of August 1992 through 9 April 1993, but 2nd instar larvae appeared in the samples from late April in both years (Figs. 2.8 & 2.9). As the water temperature rose through May and June, larvae grew rapidly at rates of 0.022 mm/mm/day during 1992 and 1993 (Figs. 2.5 & 2.7). Growth was quite synchronous in both years and there was no cohort splitting. Adult emergence commenced during the third week of June and continued until the first week of August. Mature adults were seen from the first week of July until the third week of August, and tandem pairs were laying eggs in the stems of *Carex* and *Scirpus* over this period.

About half of the larvae collected during late July and early August 1993 were parasitized by a mermithid nematode. Because I did not notice these parasitoids until this time when many larvae had metamorphosed, the actual rate of parasitism in the population was not estimated.

## 2.4 DISCUSSION

The population of *Lestes disjunctus* in the University of Calgary Research Pond followed an invariable univoltine life cycle during the study period, as reported in earlier studies in Canada (Sawchyn and Gillott, 1974a; Baker and Clifford, 1981) and for other *Lestes* species elsewhere (Corbet, 1956b; Gower and Kormondy, 1963; Pickup et al., 1984). The first appearance of very small larvae in April samples indicated that the eggs laid during summer went into diapause and did not hatch until the following spring. The larval development was completed in approximately 90 days

and the growth rate was faster than *C. resolutum* in both years. This short developmental period in *L. disjunctus* is an adaptation for life in temporary ponds, the usual habitat of species in this genus.

The number of *L. disjunctus* larvae collected during most of the sampling periods at the University Pond were lower (especially in 1993) than those of *C. resolutum*, indicating that the population size of *L. disjunctus* is smaller. Perhaps *L. disjunctus* is not able to thrive well in the permanent pond, where daily mean temperatures would be lower than in temporary ponds. Another reason could be competition for food and habitat and predation by species of Coenagrionidae, which do not occur in temporary ponds. A third reason could be nematode parasitism which was observed in *L. disjunctus* and very rarely in species of *Enallagma*, but not in *C. resolutum*.

In contrast, a mixed univoltine-semivoltine life cycle was followed by the population of *C. resolutum* and eggs hatched immediately without an egg diapause (see also Baker and Clifford, 1981). Whether larvae are semivoltine or univoltine appeared to be established in autumn, because the two size groups were quite evident in the following spring. The semivoltine cohort could develop from eggs laid by late-flying adults in August. Larvae from these eggs would be subjected to much lower temperatures than larvae that hatched earlier and their growth would be considerably slowed. In addition, the late-hatching larvae would have to compete for food with larger larvae. This could be particularly important in this species in which Baker (1980) has shown that small larvae were excluded by large larvae from better feeding

areas in the laboratory.

A comparison of growth rates of *L. disjunctus* and *C. resolutum* during the period April to June when they co-occur, showed that *L. disjunctus* did indeed grow faster than *C. resolutum* in the University Research Pond as predicted. Of the factors discussed in Chapter 1 that might influence growth rate, distributional differences may be important because *L. disjunctus* tended to occupy shallower, open water with potentially higher temperatures. The temperature responses of the two species will be examined in Chapter 3.

Food quality is an unlikely reason for the differences in growth rate. Examination of gut contents of larvae collected from 2 June to 2 July 1993, when the two species were about the same size, showed no qualitative difference in the prey taken by the two species. Chironomids, ostracods, dixids, corixids, ephemeropterans, ceratopogonids and acarines were the prey found in both species. Chironomids were the commonest prey in both diets. Large *C. resolutum* ate many newly-hatched *Lestes* larvae in April. *Lestes disjunctus* guts were always completely filled, whereas those of *Coenagrion* were often small and only partially filled. Hence *L. disjunctus* may have a greater rate of food intake than *C. resolutum*, as discussed in Chapter 4.

Table 2.1 Electrophoretic identification of four species of Coenagrionidae at six loci.  $R_f$  values (relative mobilities in mm with *Coenagrion resolutum* as the standard [100]) are shown in parentheses.

Species	Got1	Got2	Idh1	Idh2	Ldh	Gpi
<i>Coenagrion resolutum</i>	A (100)	C (100)	A (100)	A (100)	A (100)	C (100)
<i>Enallagma cyathigerum</i>	B (105)	A (96)	B (104)	B (101)	C (105)	B (99)
<i>E. ebrium</i>	B	B (98)	C (105)	B	B (103)	A (98)
<i>E. hageni</i>	B	B	C	B	B	B

Table 2.2 Electrophoretic identification of four species of *Lestes* at five loci.  $R_f$  values (relative mobilities in mm with *Lestes congener* as the standard [100]) are shown in parentheses.

Species	Got1	Got2	Idh1	Idh2	Gpi
<i>Lestes congener</i>	A (100)	B (100)	D (100)	C (100)	A (100)
<i>L. disjunctus</i>	B (103)	B	B (97)	A (93)	C (104)
<i>L. dryas</i>	B	A (98)	A (92)	B (94)	B (101)
<i>L. unguiculatus</i>	B	B	C (98)	B	A

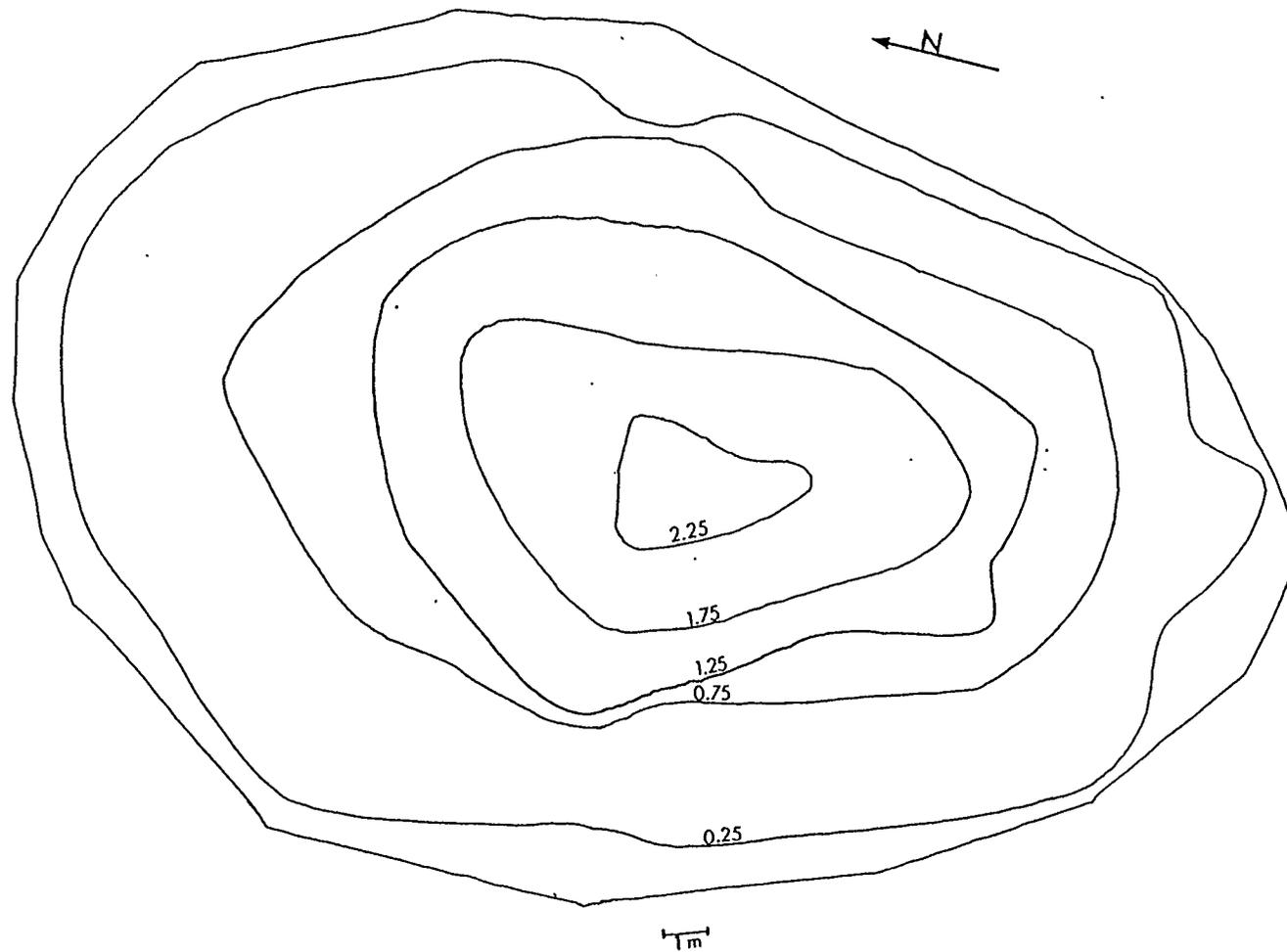


Figure 2.1 A topographical view of the University of Calgary Research Pond. Contours at 0.5 m intervals are shown. 21

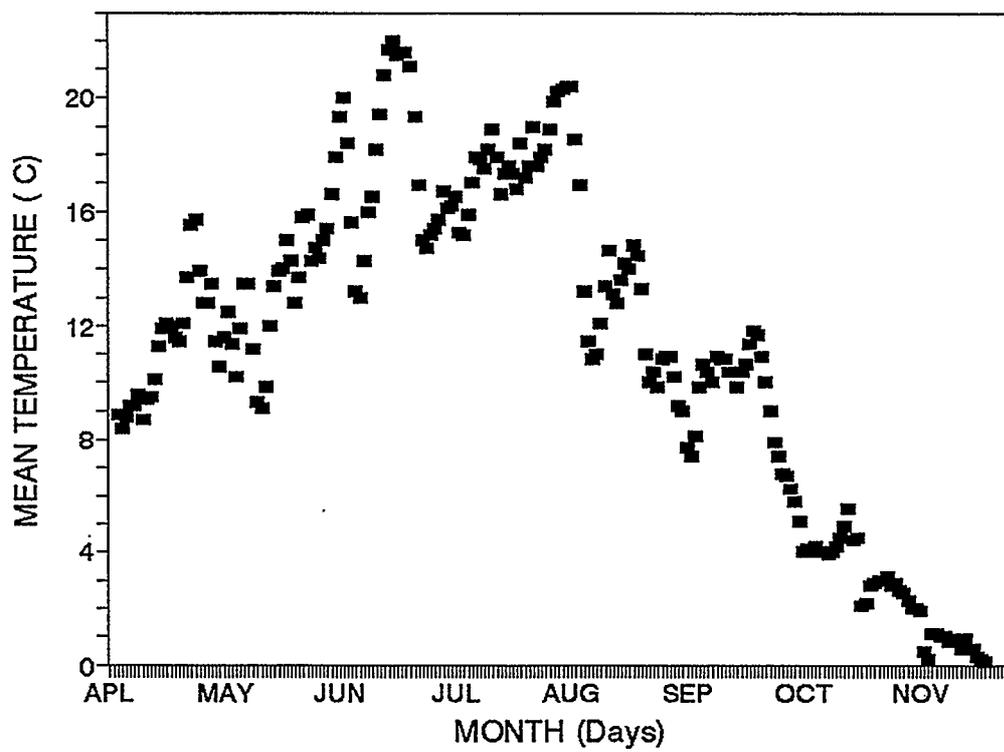


Figure 2.2 Daily mean temperatures recorded from the University Research Pond during the sampling period of 1992.

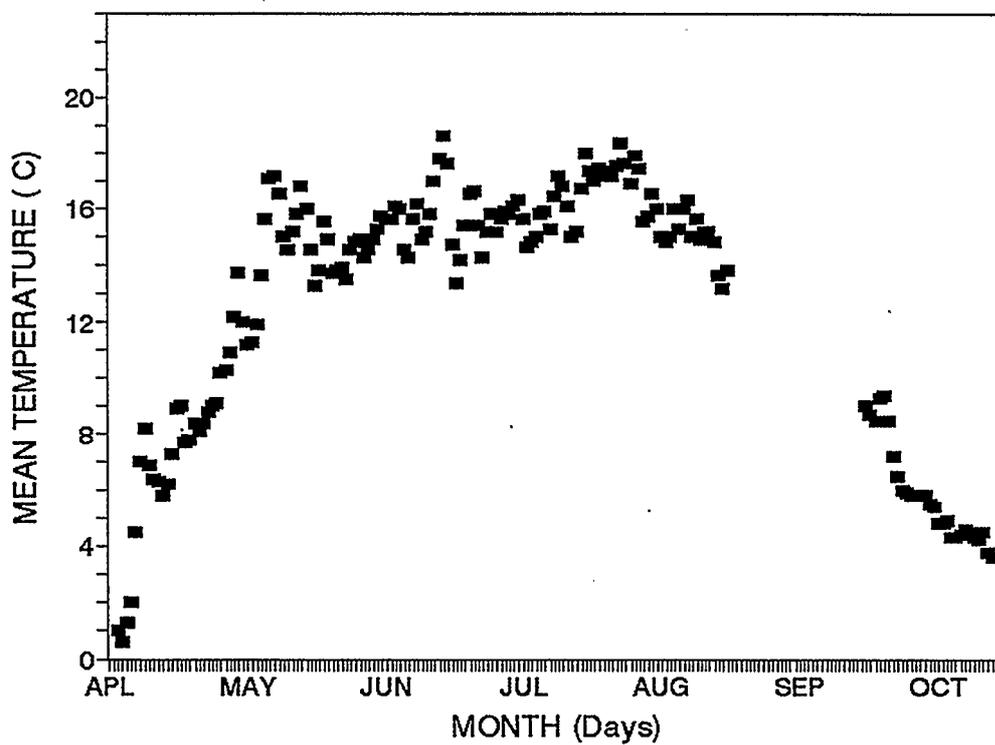


Figure 2.3 Daily mean temperatures recorded from the University Research Pond during the sampling period of 1993.

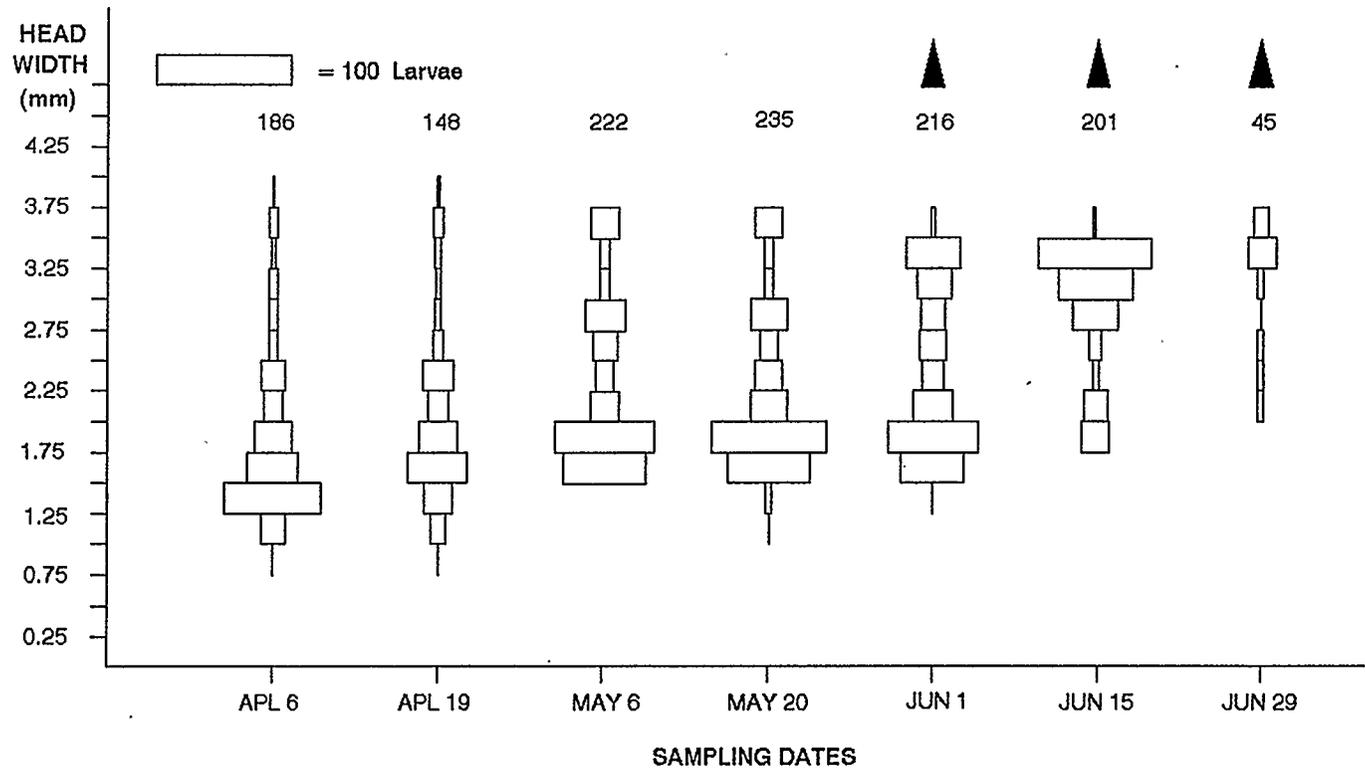


Figure 2.4 Progression of developmental stages of larvae of *Coenagrion resolutum* at the University of Calgary Research Pond during April - October, 1992. Vertical arrows indicate adult emergence; horizontal boxes indicate number of larvae in various stages on an arithmetic scale; numbers give the sample sizes.

....continued

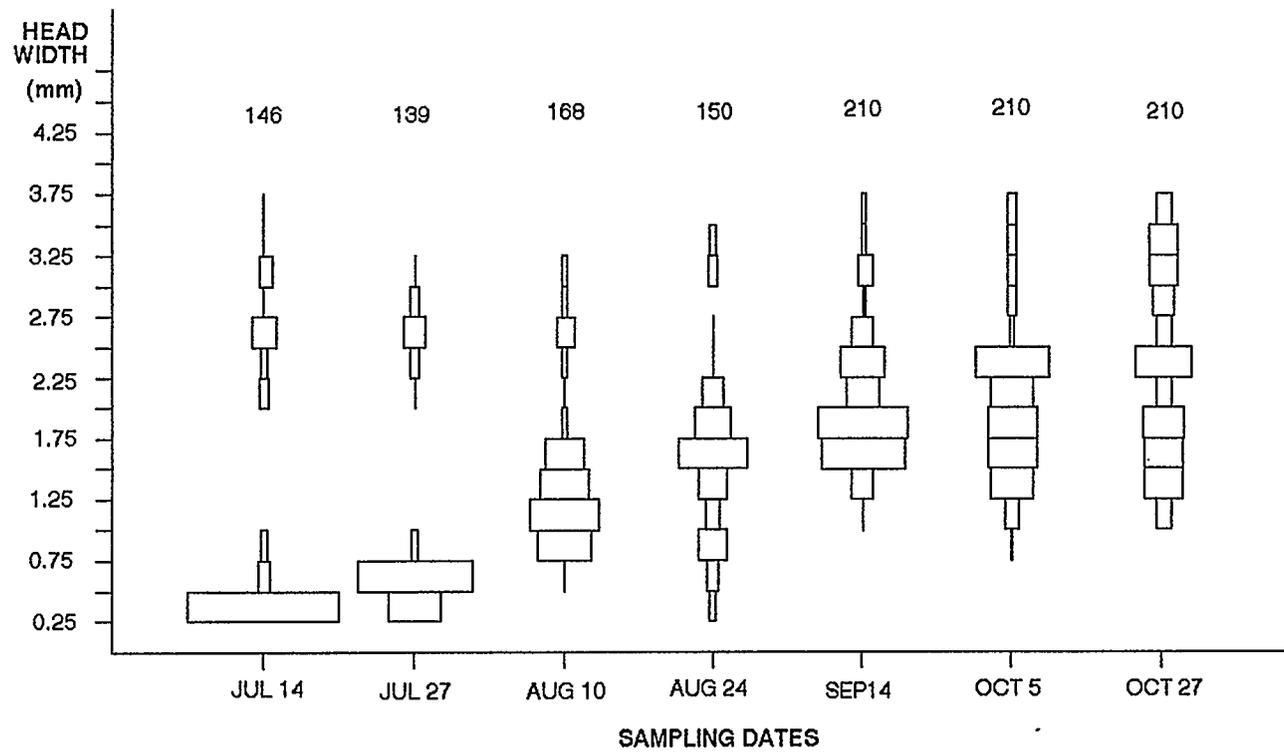


Figure 2.4 Continued.

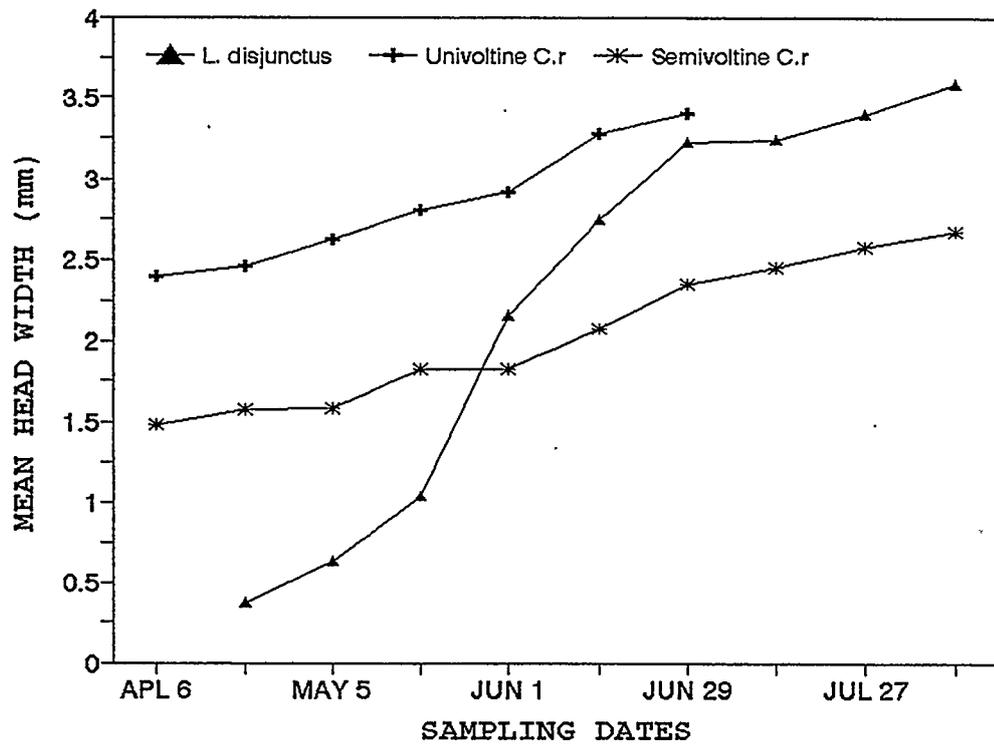


Figure 2.5 Size dynamics of the semivoltine and univoltine cohorts of *Coenagrion resolutum* and of *Lestes disjunctus* during the period of coexistence in 1992.

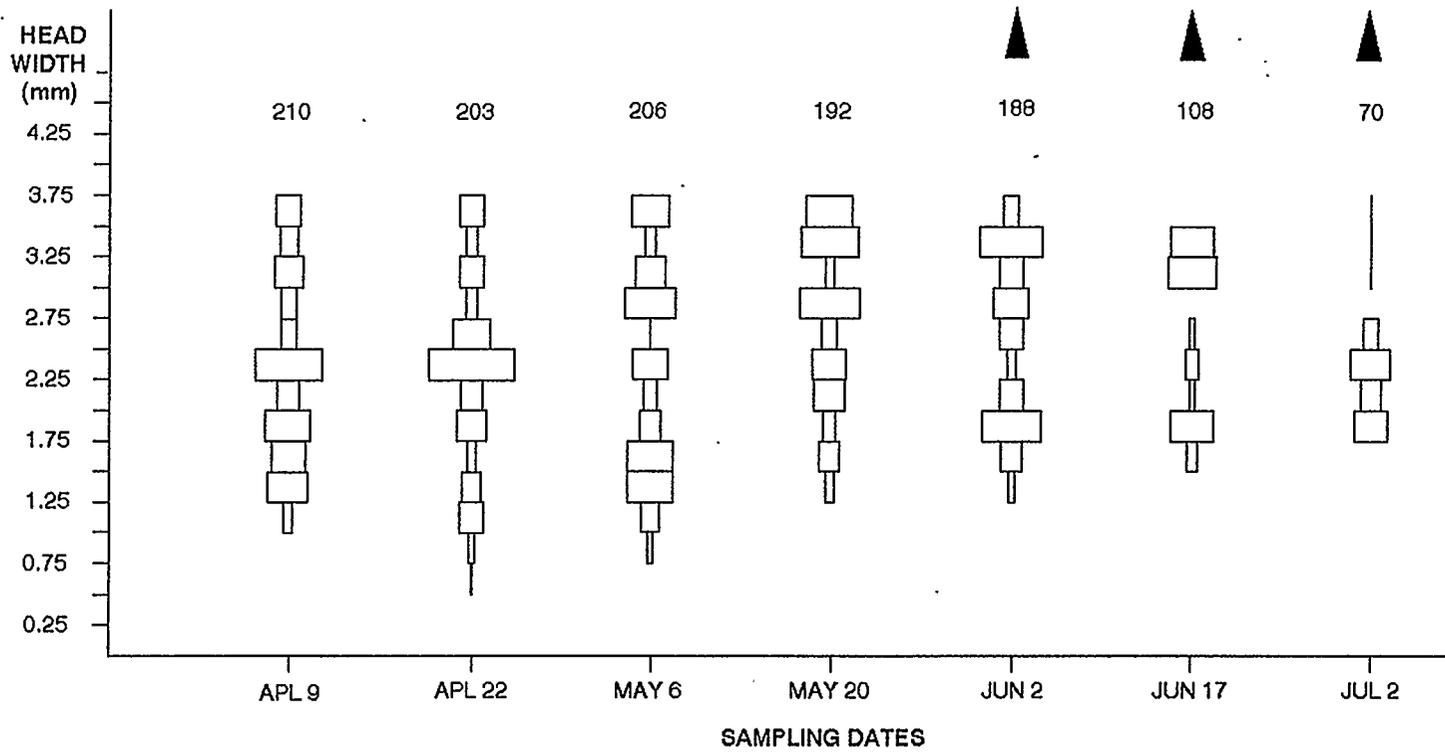


Figure 2.6 Progression of developmental stages of larvae of *Coenagrion resolutum* at the University of Calgary Research Pond during April - October, 1993. Conventions as in Figure 2.4.

.....continued

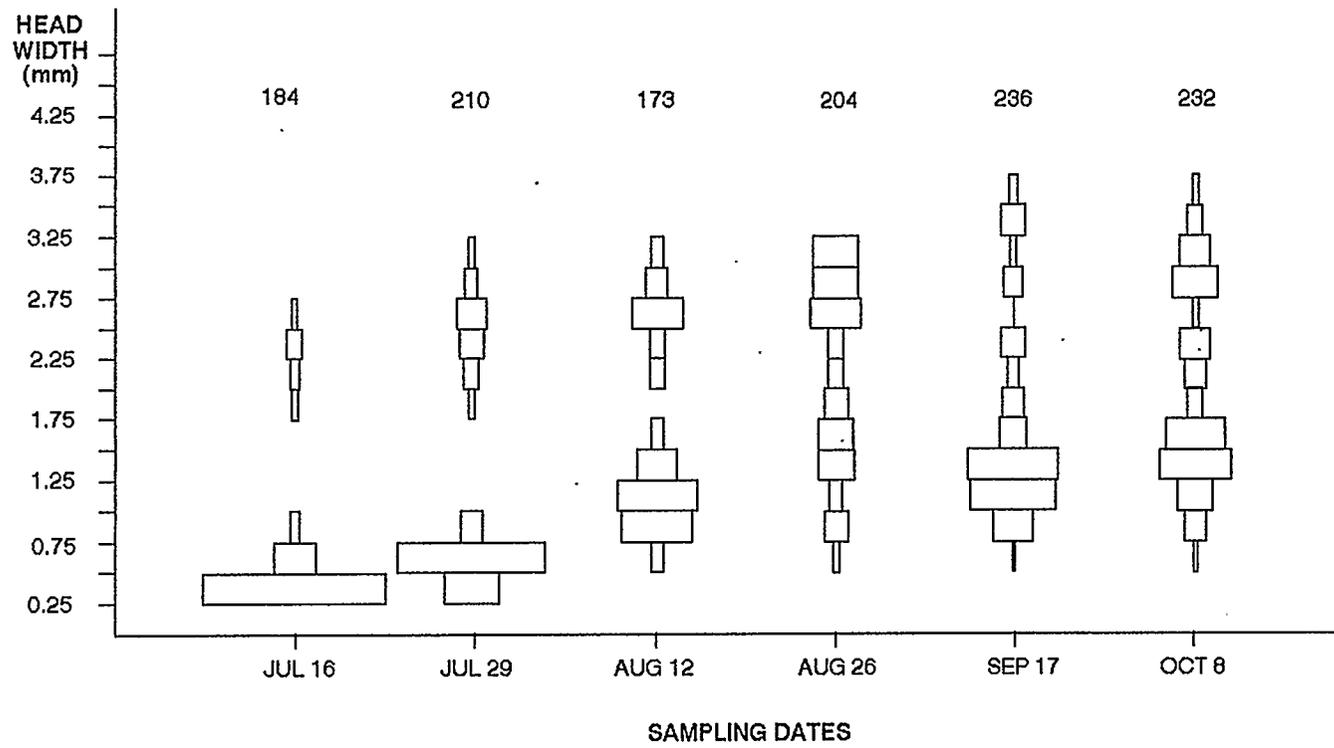


Figure 2.6 Continued.

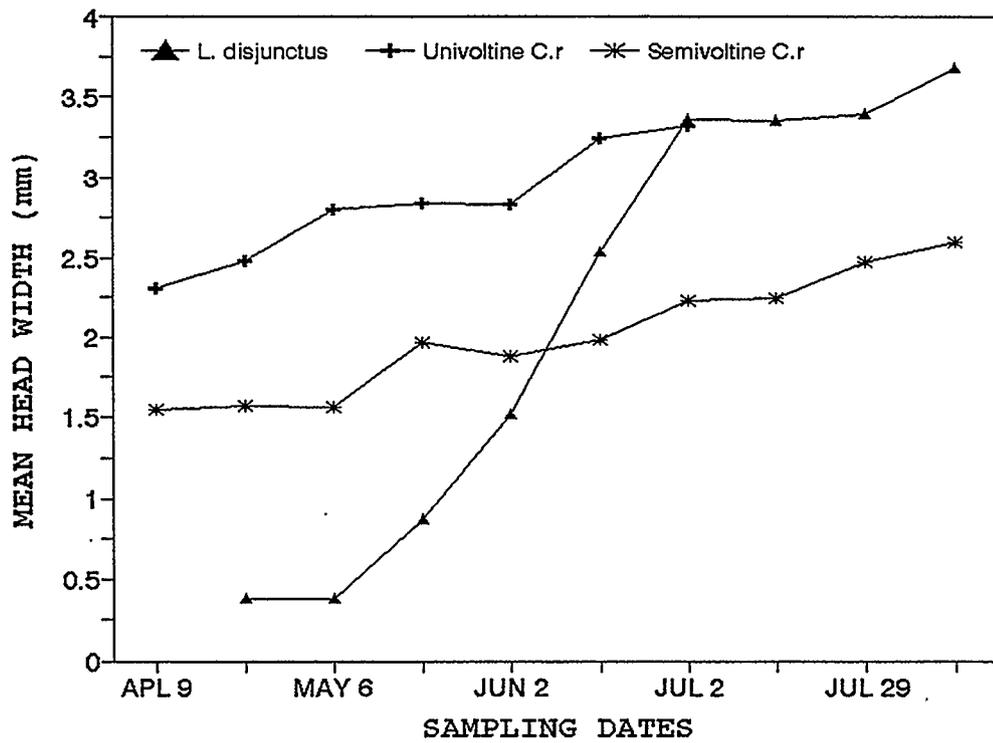


Figure 2.7 Size dynamics of the semivoltine and univoltine cohorts of *Coenagrion resolutum* and of *Lestes disjunctus* during the period of coexistence in 1993.

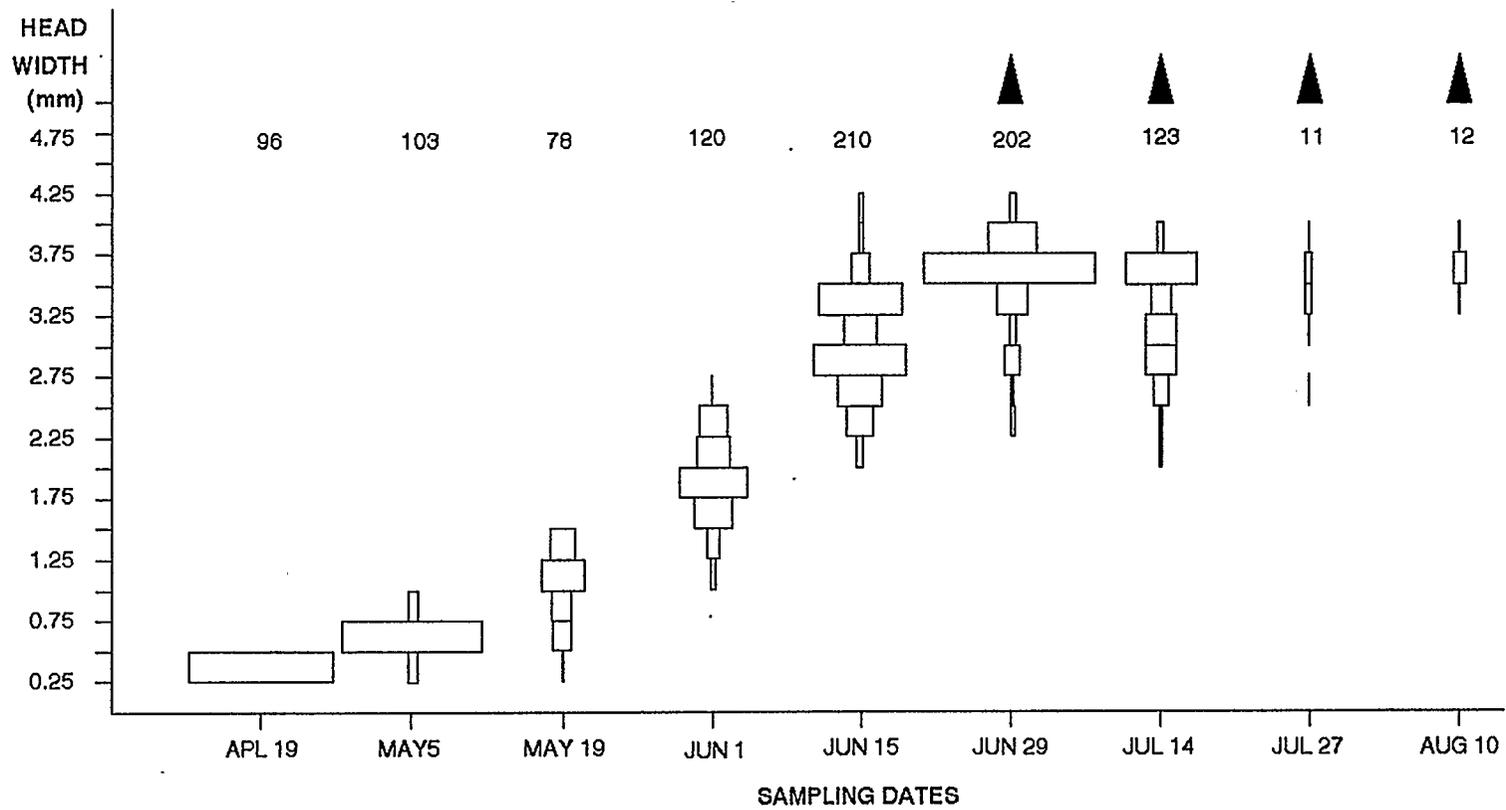


Figure 2.8 The life history of *Lestes disjunctus* at the University of Calgary Research Pond during 1992. Conventions as in figure 2.4.

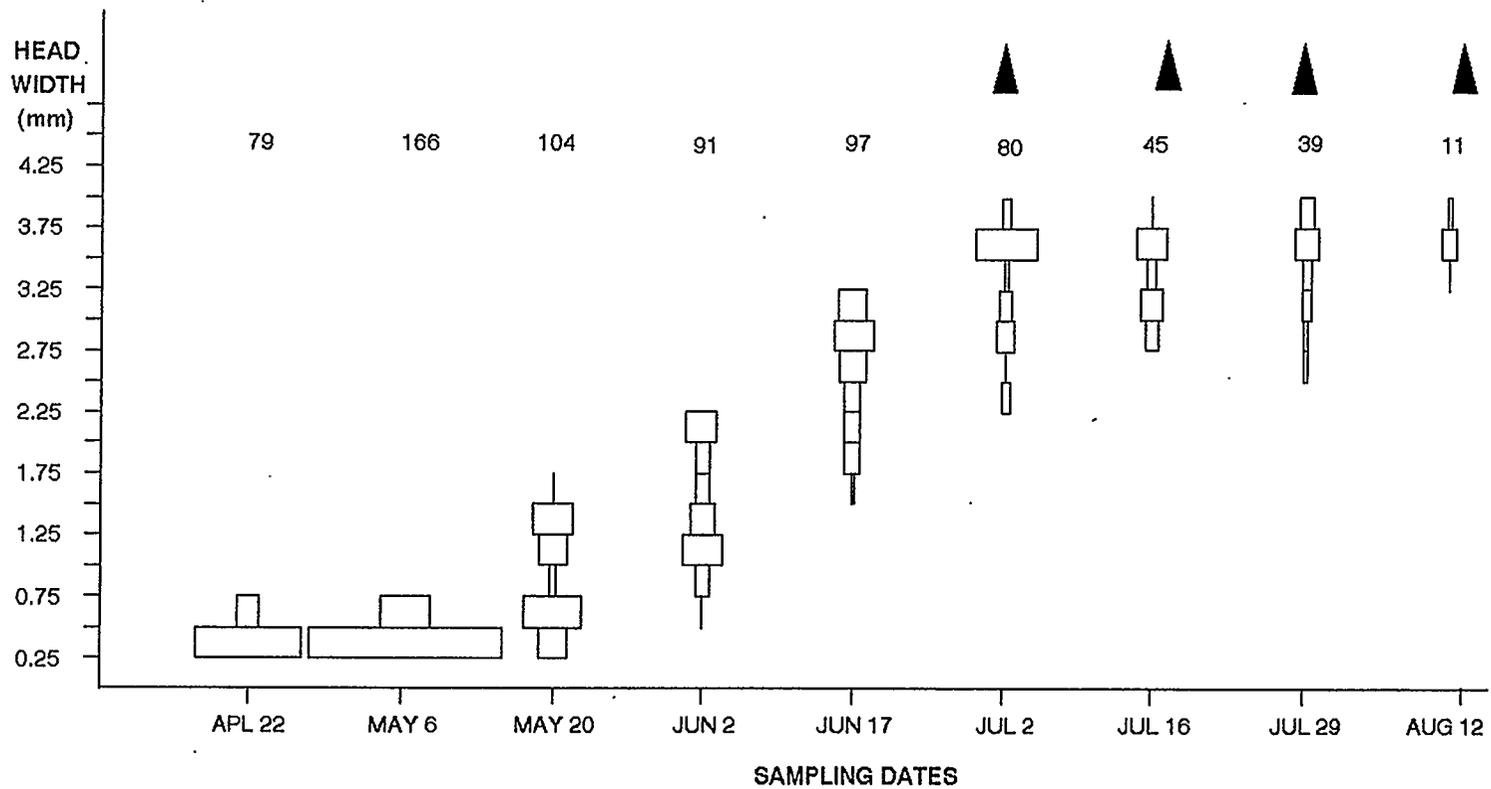


Figure 2.9 The life history of *Lestes disjunctus* at the University of Calgary Research Pond during 1993. Conventions as in figure 2.4.

## CHAPTER 3

GROWTH RATES OF *COENAGRION RESOLUTUM* AND *LESTES DISJUNCTUS*

## 3.1 INTRODUCTION

The growth rates of larval odonates are determined mainly by their responses to temperature and photoperiod (Norling, 1984a). The effects of photoperiod and temperature on growth rates vary depending on the time of the year and the developmental stage of the larva. In general, short days (<13 h) and low temperatures (<15°C) prolong development, while moderate day lengths (13-18 h) and temperatures >15°C promote rapid development in larvae of *Lestes eurinus* (Lutz, 1968b), *Tetragoneuria cyanosura* (Lutz, 1974), *Enallagma hageni* and *E. aspersum* (Ingram and Jenner, 1976), *Coenagrion hastulatum* (Norling, 1984b) and *Argia vivida* (Pritchard, 1989). Long days (>18 h) and high temperatures (>20°C) delay development of young larvae (<F-3 instar) and promote rapid development to emergence in older larvae (>F-4) in *C. hastulatum* (Norling, 1984b). Prolonged development can result in cohort splitting (see Chapter 2) or can cause extra moults as in *E. hageni* and *E. aspersum* (Ingram and Jenner, 1976).

When the effect of temperature alone is considered (during the period where the day length does not seem to affect the growth rate or when the day length is held constant) no larvae are reported to grow below 8°C (Pritchard, 1982 and references therein). Even though larvae are better survivors of the cold winter conditions of temperate regions than are eggs and adults, the minimum temperature threshold for

larval growth is relatively high; the low temperature threshold for development of *Ischnura elegans* (Vander Linden) is 8°C (Thompson, 1978a), 11°C for *Argia vivida* (Leggott and Pritchard, 1985) and 12°C for *Coenagrion puella* (Waringer and Humpsech, 1984). Above this threshold, growth rate increases with increasing temperature to a maximum, beyond which it decreases with increasing temperature. The maximum growth rate of larvae occurs at temperatures between 20-25°C in most odonates (*Lestes eurinus* (Lutz, 1968b), *L. sponsa* (Fischer, 1972), *Coenagrion puella* (Waringer and Humpsech, 1984), *C. puella*, *Ischnura elegans* and *L. sponsa* (Pickup and Thompson, 1990)).

In this chapter I report on growth rates of larvae of *Coenagrion resolutum* and *Lestes disjunctus* under constant temperatures within the range experienced during the period of coexistence in the field. During this period, daylength does not seem to affect larval growth. My null hypothesis was that the response of larval growth to temperature was the same for both species.

## 3.2 METHODS

### 3.2.1 Culturing of *Daphnia magna* Straus.

I selected *Daphnia magna* as the prey species in this experiment because cladocerans are common prey in the diet of Zygoptera larvae in nature and species of *Daphnia* are the most commonly used prey in experiments involving dragonflies. *Daphnia magna* was cultured in 26 cm x 15 cm x 11.5 cm plastic containers filled with artificial pond water. The artificial pond water was prepared by dissolving 12.5

g  $\text{Ca}(\text{NO}_3)_2 \cdot \text{H}_2\text{O}$ , 12.5 g  $\text{NaHCO}_3$ , 6.0 g  $\text{Mg}_2\text{SO}_4 \cdot 7\text{H}_2\text{O}$ , and 2.5 g KCl individually in 50 ml of distilled water and adding each solution in order to 49.8 litres of distilled water (Agriculture Canada Research Station, Lethbridge, pers. comm.). The *D. magna* cultures were maintained at 23° C and a 16:8 hours light:dark regime. The water was constantly aerated and about 50 ml of a dense *Chlamydomonas* suspension was added to each container as food every other day.

### 3.2.2 Experimental procedure

Larvae of *L. disjunctus* were collected from the University Pond during April and May 1992 and *C. resolutum* were collected in September 1992 and September 1993. Head widths and wing pad lengths were measured and larvae in a range of sizes from 1-3 mm head width were used in the experiment. Larvae were housed individually in small plastic containers filled with 75 mL of dechlorinated tap water, and were placed at seven different temperatures, approximately 2.5° C apart as shown in Tables 3.1 & 3.2. Temperature was recorded twice daily. To eliminate photoperiodic effects, a single cycle of 16:8 hours light:dark regime was used. About 50-65 *L. disjunctus* and 40-50 *C. resolutum* larvae were kept at each temperature.

The larvae were fed *ad libitum* with appropriately sized laboratory cultured *D. magna*. Occasionally, when *D. magna* production was very low or the cultures needed restarting, oligochaete worms (*Enchytraeus* sp.) were substituted as prey. Larvae were checked for moulting every day. After the first moult, a larva was removed from the container, its head width and wing pad length recorded, and then replaced. These

measurements were repeated after the second moult and the larva was preserved. Small larvae (less than 1.5 cm in head width) were frozen individually in small plastic vials at  $-86^{\circ}\text{C}$  for identification by electrophoresis (see Chapter 2). After electrophoretic identification, data from species other than *L. disjunctus* and *C. resolutum* were ignored from further analysis. Average temperatures experienced by individual larvae were calculated from daily temperature recordings.

### 3.2.3 Statistical analysis

Growth rate was calculated from the formula given by Travis (1980):

$$G_n = \frac{L_{n+1} - L_n}{T_n} \cdot \frac{1}{(L_{n+1} + L_n)/2} \quad (3.1)$$

where,

$G_n$  = mean specific growth rate of instar n (mm/mm/day)

$L_n$  = head width of instar n (mm)

$L_{n+1}$  = head width of the next instar (mm)

$T_n$  = total days spent in instar n (days)

$\% G_n = G_n * 100$

To separate the effects of size and temperature on % Growth, a multiple regression analysis with size and temperature as independent variables was carried out. Linear, logarithmic and power functions were fitted to the regression of % Growth on size and temperature to determine the best fit. The parameters of this equation were

then compared by size and temperature for the two species with Analysis of Covariance (ANCOVA). Differences in growth rates between species at each temperature were tested with a pairwise contrast.

### 3.3 RESULTS

#### 3.3.1 Effect of temperature on larval growth rates

Percentage growth rate (%G<sub>n</sub>) decreased with larval size within temperatures (Figs. 3.1 & 3.2) and increased with increasing temperature in both species. The best overall fit to the data was given by the equation:

$$\ln \% G = a + b_1 \text{ size} + b_2 \text{ temperature} + b_3 \text{ temperature}^2 \quad (3.2)$$

where  $\ln \% G$  = logarithm to base e of %G<sub>n</sub>

$a$  = constant

$b_1$  = partial regression coefficient for size

$b_2$  = partial regression coefficient for temperature

$b_3$  = partial regression coefficient for square of the temperature.

The third term (temperature<sup>2</sup>) was necessary to account for the decrease in growth rate at high temperatures. The coefficients for both species obtained from the multiple regression are given in Table 3.3. All values are significantly different from zero ( $P < 0.001$ ).

Figure 3.3 shows the predicted mean % growth rates for the two species over the temperature range of the laboratory experiments. The pair-wise contrast test

showed significantly higher predicted mean growth rates in *L. disjunctus* at all temperatures ( $P < 0.001$ ). Figures 3.4 & 3.5 show the growth rates for individuals of the two species, calculated from Equation 3.2, again using the average size, but also taking into account the residuals from the multiple regression analysis. Hence, individual variation is revealed.

For *C. resolutum*, % growth increased with increases in temperature up to 22.5°C and decreased at 25°C (Fig. 3.3). In contrast, for *L. disjunctus* % Growth increased throughout the experimental temperature range (Fig. 3.3). Based on the first-order differential equation of Equation 3.2 with respect to temperature, growth was maximized at  $T^* = -b_2/2b_3 = 22.4^\circ\text{C}$  for *C. resolutum* and 28.8°C for *L. disjunctus*.

Mean % Growth was always higher for *L. disjunctus* at any given temperature compared to *C. resolutum*. ANCOVA showed no significant interactions for growth rate between size and species ( $F_{1,312} = 1.18$ ;  $P > 0.25$ ) or between temperature<sup>2</sup> and species ( $F_{1,313} = 0.45$ ;  $P > 0.5$ ). Hence, these non-significant terms were removed from further analysis. Significant effects were then found for the response of growth rate to size ( $F_{1,314} = 22.92$ ;  $P < 0.001$ ), temperature ( $F_{1,314} = 70.06$ ;  $P < 0.001$ ), interaction between temperature and species ( $F_{1,314} = 20.62$ ;  $P < 0.001$ ), and temperature<sup>2</sup> ( $F_{1,314} = 38.06$   $P < 0.001$ ) for both species (see Table 3.4 for partial regression coefficients). The effect of temperature on growth rate was significantly higher for *L. disjunctus* than for *C. resolutum*.

### 3.4 DISCUSSION

In Chapter 2, I showed that *L. disjunctus* grew faster than *C. resolutum* in the University Pond and I suggested that this may have resulted from *L. disjunctus* larvae occupying warmer parts of the pond. In this chapter I have shown that *L. disjunctus* larvae grow faster even without a temperature difference in microhabitat. *L. disjunctus* grew faster than *C. resolutum* at all laboratory temperatures, the differential increasing with increasing temperature. Furthermore, the predicted temperature for maximum growth was more than 6°C higher in *L. disjunctus* than in *C. resolutum*, indicating that the growth rate of *L. disjunctus* would be very much faster than that of *C. resolutum* at temperatures above 22.5°C.

The results are consistent with those reported by Pickup and Thompson (1990) for the European *Lestes sponsa* and *Coenagrion puella* reared at 12, 16, and 20°C. The growth rate was higher in instars 6, 7 and 8 than in the penultimate and final instars of both species, but the rate of development was consistently faster in *L. sponsa*. Thus, the difference in growth rate response to temperature observed in the present study is possibly a universal generic difference.

Thus, in summary, the laboratory experiments support the field observations and lead to acceptance of the alternative hypothesis that the response of larval growth rate to temperature was different in the two species. Having established the relationship between growth rate and temperature, I now proceed to investigate feeding rates (functional response) of the two species.

Table 3.1 Mean temperatures maintained in the controlled environmental chambers during the experimental periods for *Coenagrion resolutum*.

Chamber	Mean (°C)	± Std.Err
Fall - 1992		
1	9.9	0.11
2	12.4	0.07
3	15.0	0.04
4	17.7	0.05
5	20.0	0.06
6	22.7	0.05
7	25.3	0.07
Fall - 1993		
1	9.7	0.24
2	11.2	0.57
3	15.2	0.07
4	17.5	0.07
5	20.3	0.13
6	22.3	0.07

Table 3.2 Mean temperatures maintained in each controlled environmental chamber during the experimental periods for *Lestes disjunctus*.

Chamber	Mean (°C)	± Std. Err
1	10.0	0.17
2	12.8	0.24
3	14.5	0.24
4	17.7	0.09
5	20.1	0.11
6	22.5	0.10
7	25.0	0.14

Table 3.3 Partial regression coefficients ( $\pm$  Std. Err) estimated from the regression of % growth on size and temperature for *Coenagrion resolutum* and *Lestes disjunctus* ( $P < 0.001$ ).

Effect	<i>C. resolutum</i>	<i>L. disjunctus</i>
Intercept	-4.200 $\pm$ 0.573	-2.741 $\pm$ 0.752
Size	-0.231 $\pm$ 0.074	-0.501 $\pm$ 0.114
Temperature	0.403 $\pm$ 0.061	0.363 $\pm$ 0.074
Temperature <sup>2</sup>	-0.009 $\pm$ 0.002	-0.006 $\pm$ 0.002

Table 3.4 Partial regression coefficients for size and temperature from analysis of covariance for *Coenagrion resolutum* (C) and *Lestes disjunctus* (L) ( $P < 0.001$ ).

Effect	Slope value	$\pm$ Std. Err
Size	-0.294	0.061
Temperature - C	0.372	0.048
Temperature - L	0.427	0.048
Temperature <sup>2</sup>	-0.008	0.001

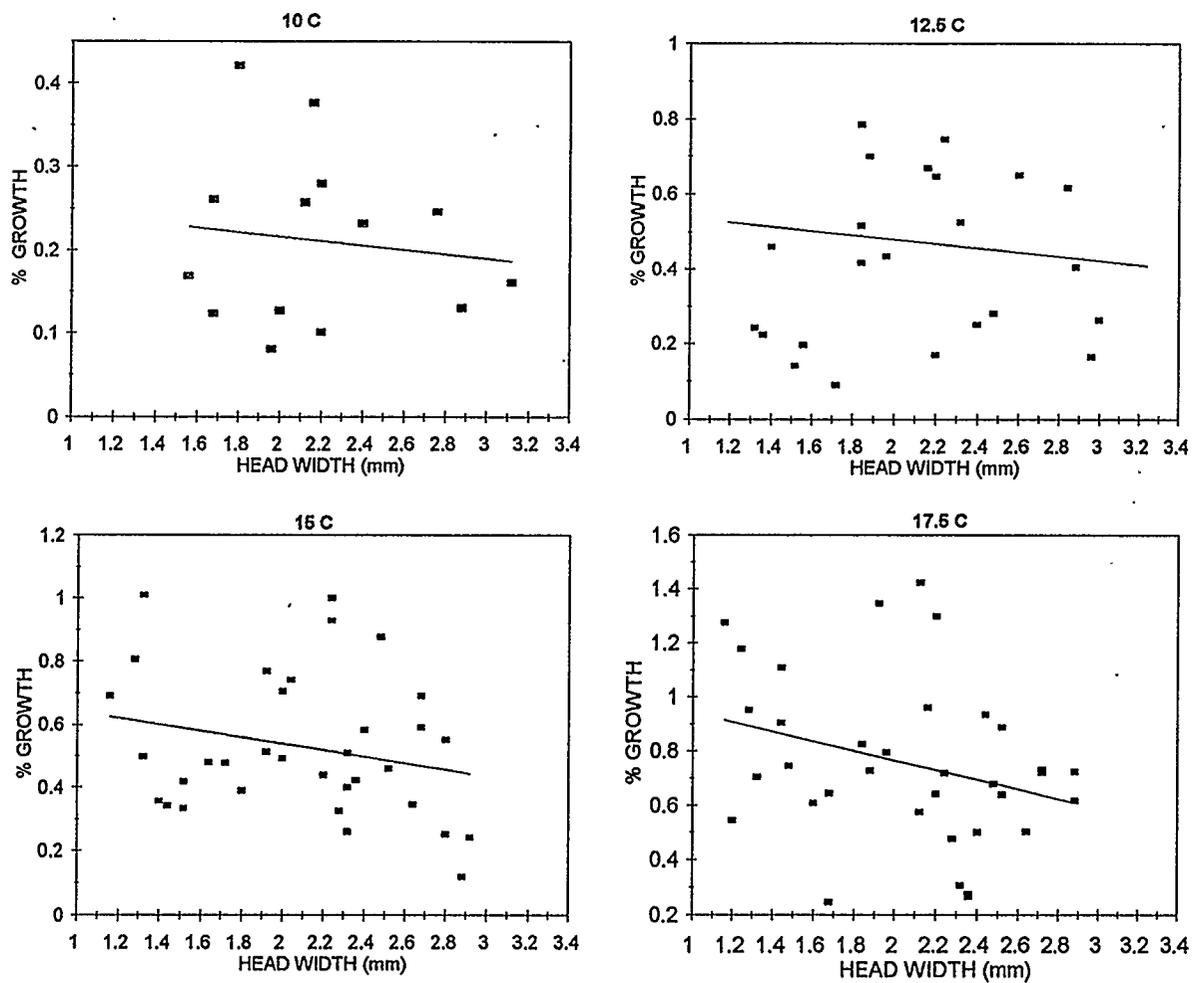


Figure 3.1 The relation between % growth rates and size for larvae of *Coenagrion resolutum* at different temperatures. Least squares linear regression lines are shown. ....continued.

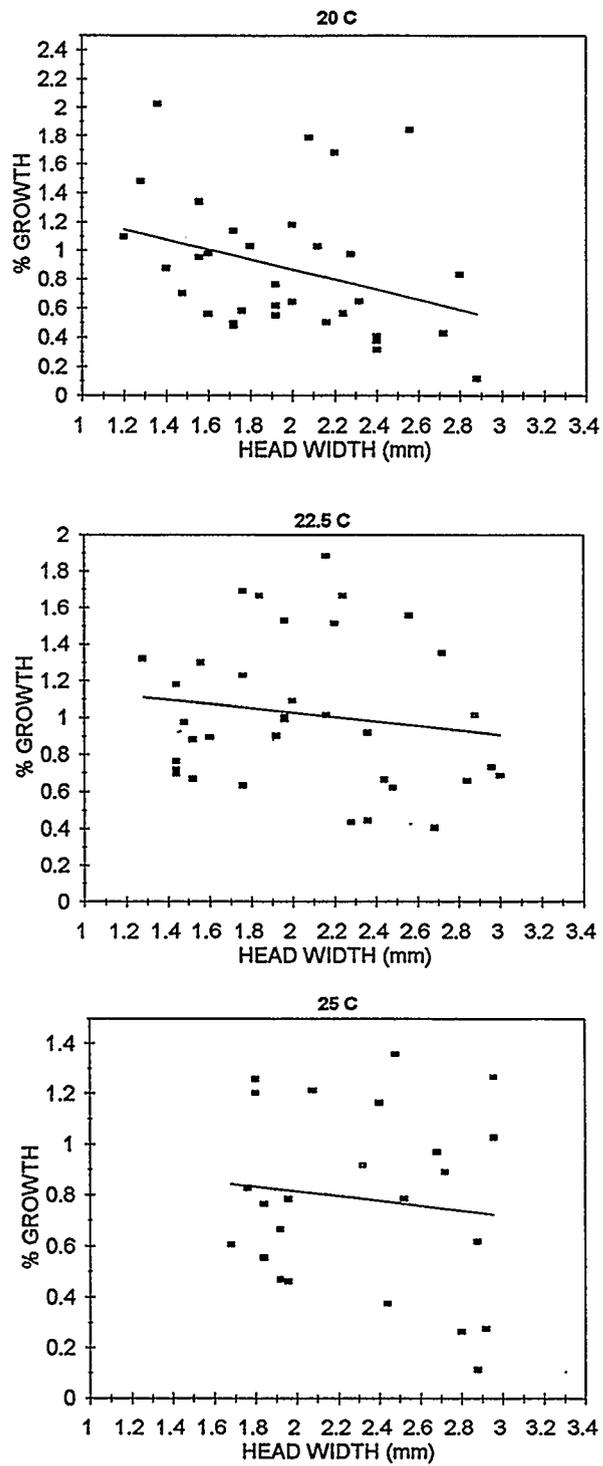


Figure 3.1 Continued.

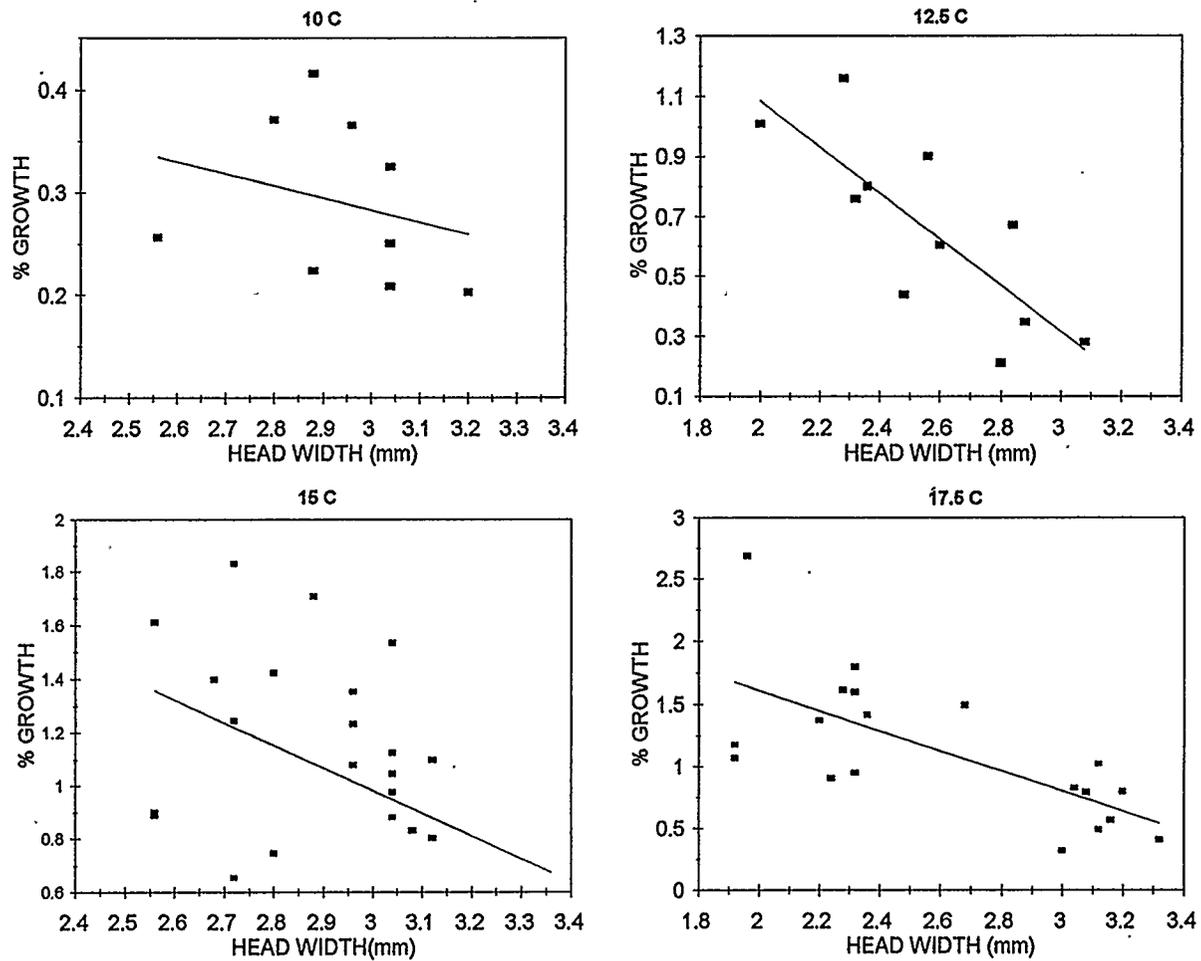


Figure 3.2 The relation between % growth rates and size for larvae of *Lestes disjunctus* at different temperatures. Least squares regression lines are shown. ....continued.

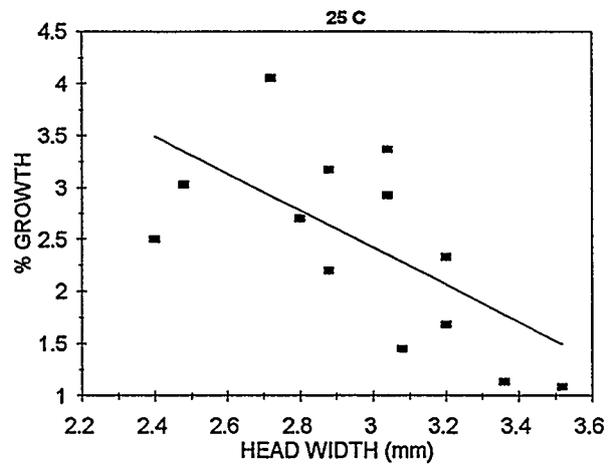
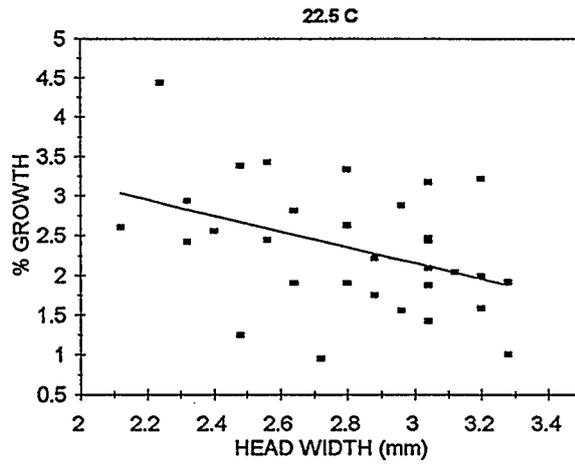
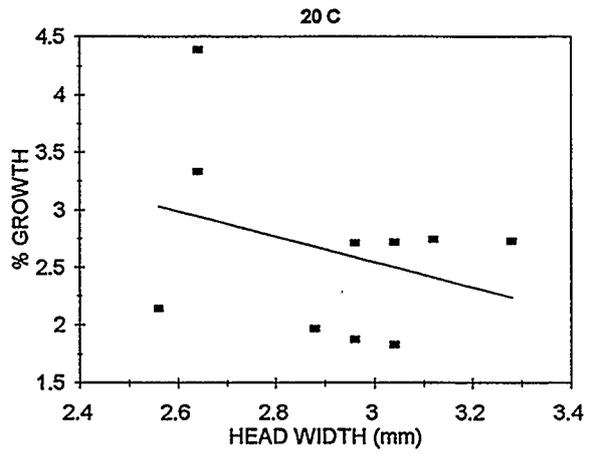


Figure 3.2 Continued.

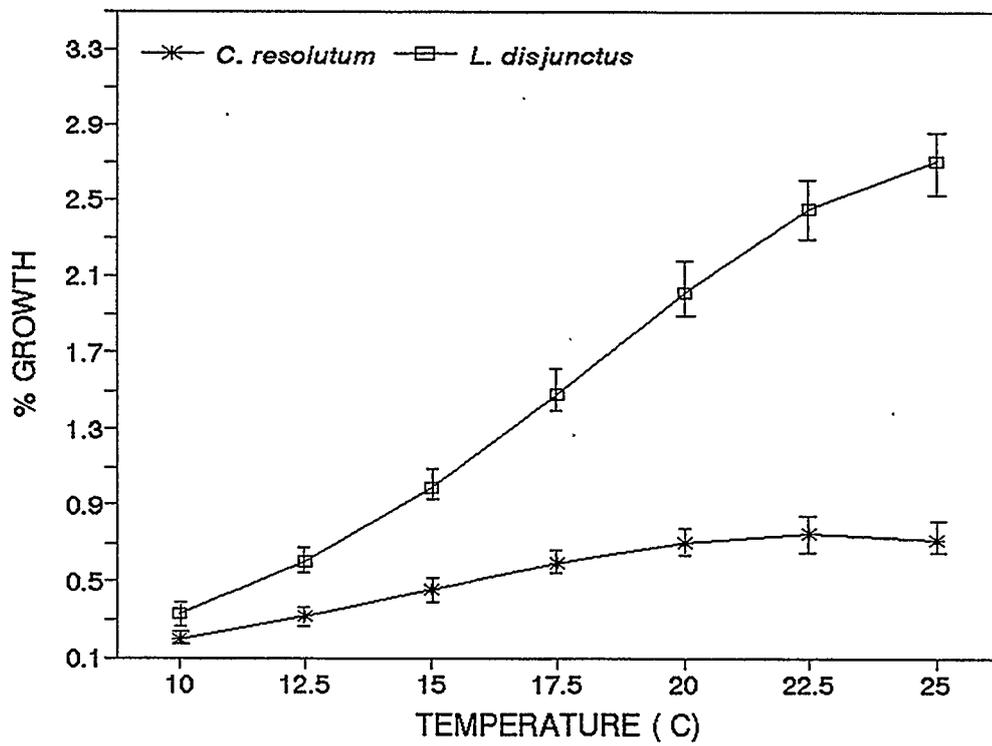


Figure 3.3 Predicted mean % growth rates ( $\pm$  Std.Err) of *Coenagrion resolutum* and *Lestes disjunctus* at different temperatures.

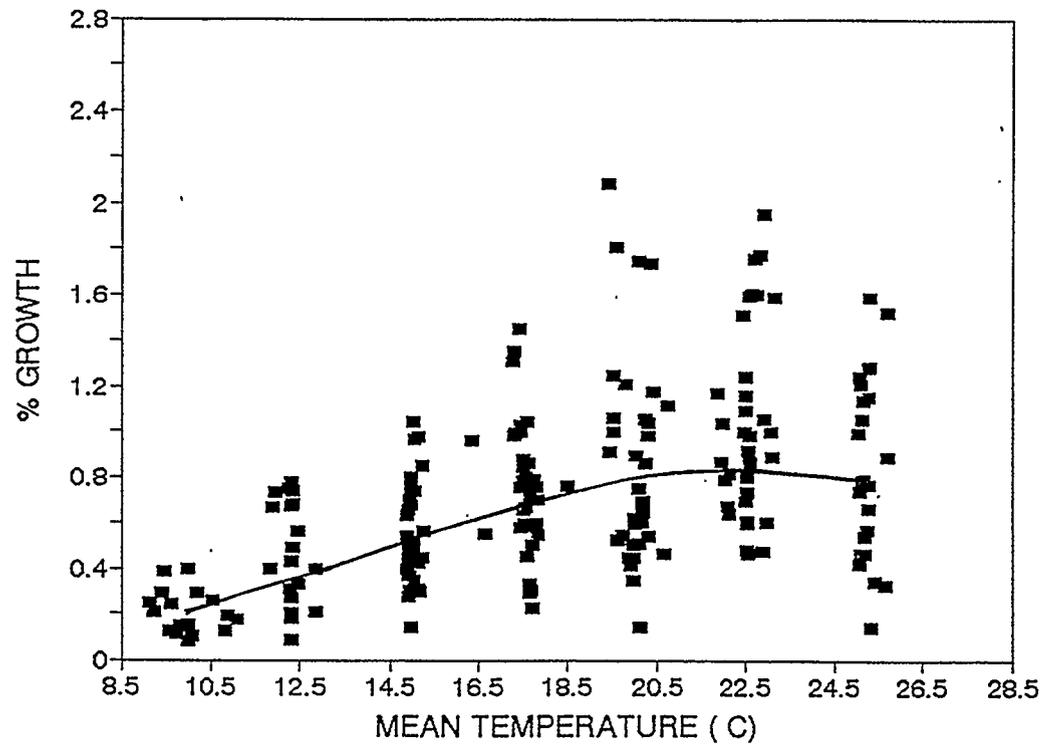


Figure 3.4 Percentage growth rates, adjusted for size, of *Coenagrion resolutum* at different temperatures. Solid line shows the mean growth rates predicted from Equation 3.2.

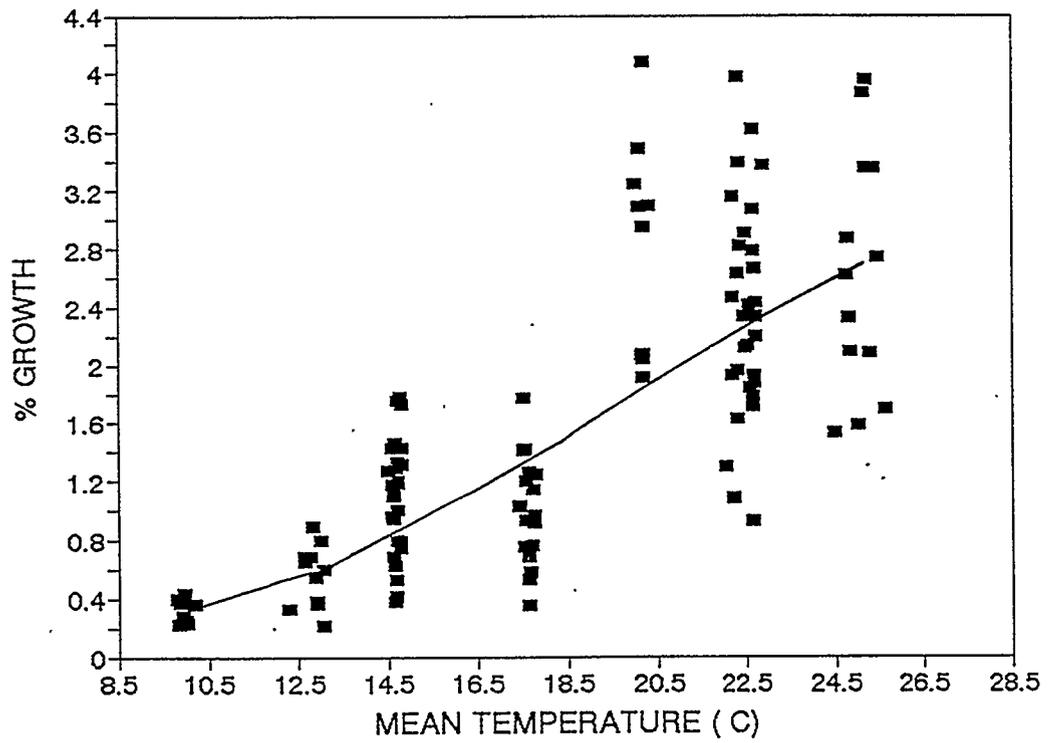


Figure 3.5 Percentage growth rates, adjusted for size, of *Lestes disjunctus* at different temperatures. Solid line shows the mean growth rates predicted from Equation 3.2.

## CHAPTER 4

FUNCTIONAL RESPONSES OF *COENAGRION RESOLUTUM* AND  
*LESTES DISJUNCTUS*

## 4.1 INTRODUCTION

The feeding rate of dragonflies can be measured in terms of their functional response to prey density. The functional response is the change in the rate of consumption of prey by individual predators in response to changes in prey density, and is defined by two parameters - the attack coefficient and the handling time (Holling, 1959). Dragonflies show a 'Type II' functional response (feeding rate decreases with increased prey density reaching a plateau) to single prey species (Lawton et al., 1974; Thompson, 1975 & 1978b; Akre and Johnson, 1979; Cothran and Thorp, 1985). Some studies have shown that odonate larvae also have a Type II response to a prey species, even when an alternative prey is available in complementary densities, implying frequency independent prey selection (Colton, 1987; Chowdhury et al., 1989). However, Lawton et al., (1974) in their studies with *Ischnura elegans*, and Akre and Johnson (1979) in their studies with *Anomalagrion hastulatum* (Say), showed frequency-dependent prey selection (prey switching leading to a sigmoidal or Type III response) when alternative prey were available in complementary densities.

My aim was to determine how the attack coefficient and handling time differ between *L. disjunctus* and *C. resolutum* when they were offered the same type of prey

at different densities and whether there were differences that might explain their differential growth rates. The null hypothesis was that the attack coefficient ( $a$ ) and handling time ( $h$ ) were the same for both species.

## 4.2 METHODS

### 4.2.1 Collection and maintenance of *C. resolutum* and *L. disjunctus* larvae

The larvae required for the functional response experiment were collected from the University of Calgary Research Pond during summer 1993, and larvae in three size classes (1.3-1.4, 2.2-2.3 and 2.7-2.8 mm) were held individually in the laboratory in small plastic containers filled with 50 mL of dechlorinated water. Different size classes of larvae were collected at different times and the experiments were conducted at different periods accordingly. Larvae were housed in a controlled environment chamber at 23°C and a photoperiod of 16:8 light:dark condition. The larvae were fed with appropriately sized *Aedes aegypti* (L.) larvae until they moulted. Two to four days after the moult, head widths of larvae that were feeding normally were again recorded (Table 4.1) and these larvae were used in the experiments which were conducted in the same environmental chamber where the larvae were initially housed. A larva was used only once during the experiment.

### 4.2.2 Prey species

Because species of *Daphnia* are the most commonly used prey in functional response experiments involving dragonflies, I selected *Daphnia magna* as the prey

species in this experiment (see Chapter 3 for culturing procedure). The *D. magna* cultures were maintained under the same conditions of temperature and photoperiod described for the maintenance of the dragonflies. Three size classes of *D. magna* (Table 4.2) were used with each species of dragonfly, *D. magna* belonging to size classes A, B and C being used with small, medium and large size classes of dragonfly, respectively.

#### 4.2.3 Experimental procedure

The procedure outlined by Houck and Strauss (1985) was followed. Prior to each experiment, the dragonfly larvae were fed *ad libitum* with *A. aegypti* larvae and then were starved for 48 h to achieve a standard level of hunger at the beginning of the experiment. Pyrex crystallizing dishes (9.8 cm diameter x 5 cm deep) containing 250 mL of dechlorinated water were used as experimental arenas. Twelve prey densities (1, 3, 5, 7, 9, 11, 13, 15, 17, 19, 25 and 35 per 250 ml) were offered to each size class of dragonfly (although, in large *C. resolutum*, only the first 8 densities, with 3-6 replications, were eventually used). A further container at each density was used without a predator as a control for natural *D. magna* mortality; in fact, no mortality of *Daphnia* was observed during the 15 min experiments. Prey of the required sizes were collected by passing the *D. magna* culture through appropriate sieves and individuals were counted into the arenas using a Pasteur pipette. They were allowed to distribute evenly through the arena prior to the experiment and about 1 ml of thick *Chlamydomonas* solution was added to each arena as food for the *D. magna*.

One dragonfly larva was introduced to each arena and was allowed to feed for 15 min. Prey were replaced as they were captured. Captures were of two types: prey that were more than 50% consumed were considered as eaten; otherwise they were considered as 'wasteful killing' (Johnson et al., 1975). The total number of prey in each arena was also counted at the end of the experiment to check for natural death and for counting error.

#### 4.2.4 Statistical analysis

To see whether the size of dragonfly larvae affected the number of *D. magna* eaten at each prey density, I plotted the residuals against size of individual dragonflies used in each experiment. Except for the large *C. resolutum*, all size classes of dragonflies showed no relationship between the residuals and size. In the case of large *C. resolutum*, the residuals fell into two groups with different variability. To remove this size effect, these larvae were divided into those with head widths of 2.9-3.12 mm and those with head widths of 3.12-3.36 mm. As it turned out, larvae in the first group had not been tested against the lower prey densities and so had to be eliminated from the analysis. To test the data on number of prey eaten at each prey density for normality, Hartley's  $F_{\max}$  test was performed. The results of the test were non-significant for all three size classes of each dragonfly species.

Holling's Type II functional response model

$$E = \frac{anT}{1 + ahn}, \quad (4.1)$$

where  $E$  = number of prey eaten

$a$  = attack coefficient

$n$  = prey density

$T$  = total time of exposure

$h$  = handling time

was fitted to the data by the non-linear regression procedure with SYSTAT (1990) for each size class. A two-factor ANOVA was performed to test the effect of species and prey density on number of prey eaten. Parameter estimates for each species were compared within size classes by Student's  $t$  test at  $\alpha = 0.05$ . Comparison of parameter values among size classes within species also used Student's  $t$  test, but significance was based on  $\alpha = 0.017$ , obtained from Sidak's equation for multiplicative inequality (Zar, 1984).

#### 4.2.5 Labial length

Dragonflies capture prey by protrusion of a prehensile labium and a longer labium should increase the predator's reactive distance, an important component of the attack coefficient. Therefore, I measured the length of the prementum in 60 individuals, from second to final instar, in each species.

### 4.3 RESULTS

#### 4.3.1 Predation by *Coenagrion resolutum*

*Coenagrion resolutum* killed more *Daphnia magna* at a decelerating rate as

prey density increased in all three size classes. The mean predation rate of small, medium and large size classes *C. resolutum* over 15 min exposure ranged from 0 to 2.83, 0.33 to 3.5 and 0.6 to 5.2 *D. magna*, respectively. Based on non-linear regression and examination of the residuals and  $r^2$  values, Holling's type II model seems to fit the data well for all size classes of *C. resolutum* (Figs. 4.1, 4.2 & 4.3).

Comparison of attack coefficients and handling times within the species showed no significant differences among the three size classes (Table 4.3; Figs. 4.4 & 4.5).

#### 4.3.2 Predation by *Lestes disjunctus*

Holling's type II functional response model also fits the data for all three size classes of *L. disjunctus*. The mean predation rates of small, medium and large *L. disjunctus* were higher than those of *C. resolutum*, ranging from 0.5 to 4.5, 1 to 5.2 and 0.8 to 6.2 *Daphnia*/15-min, respectively, and the functional response curves were higher for small and medium larvae (Figs. 4.1, 4.2 & 4.3). Comparison of the attack coefficients and handling times within the species showed a non-significant relationship between the size classes for attack coefficient, but a significant difference was seen between the handling times of small and large larvae (Table 4.3; Figs. 4.4 & 4.5).

#### 4.3.3 Comparison between species

ANOVA showed a significant difference in the number of prey eaten by small ( $F_{1,120} = 57.78$ ;  $P < 0.001$ ; Fig. 4.1) and medium ( $F_{1,120} = 47.25$ ;  $P < 0.001$ ; Fig. 4.2) *C. resolutum* and *L. disjunctus*. However, large *C. resolutum* and *L. disjunctus* fed at the

same ( $F_{1,94} = 1.69$ ;  $P > 0.20$ ).

Comparison of mean attack coefficients for the same size class between species showed that only the small *L. disjunctus* attacked significantly more *D. magna* than did *C. resolutum* in the same amount of time. Handling times were significantly longer for medium *C. resolutum* than for *L. disjunctus*, but small and large larvae handled the prey in the same time in both species (Table 4.3).

#### 4.3.4 Labial length

The equation for the relationship between length of the prementum (LP) and head width (HW) in *C. resolutum* was:

$$LP_C = 0.0676 + 0.6834 HW \quad (4.2)$$

and for *L. disjunctus* was:

$$LP_L = -0.3421 + 1.2927 HW \quad (4.3)$$

Based on a test of heterogeneous slopes, labial length increased with head width more rapidly for *L. disjunctus* than for *C. resolutum* ( $F_{1,116} = 705.13$ ;  $P < 0.001$ ). Thus, except at very small size, the labium of *L. disjunctus* is longer than that of *C. resolutum*, the difference increasing with increasing larval size.

#### 4.3.5 Wasteful Killing

Total wasteful killing ranged from 7.6 to 16.9% in *Coenagrion* (Table 4.4) and 14.4 to 20.6% in *L. disjunctus* (Table 4.5). I assessed the effect of this killing by modifying Holling's Disc equation to partition the time involved in handling prey into that spent in wasteful killing and that spent handling prey that were killed and eaten (see Appendix I). The equation was:

$$E = \frac{anTf}{(1 + an[fh + (1-f)w])} \quad (4.4)$$

where

- $E$  = number of prey killed and eaten
- $T$  = total time of exposure
- $f$  = fraction of prey killed and eaten
- $a$  = attack coefficient
- $n$  = prey density
- $h$  = handling time for prey killed and eaten
- $w$  = handling time for wasteful killing

The equation was fitted using the Marquardt method of the SAS (1988) non-linear regression program.

The iteration process would not converge on a solution to the equation for *C. resolutum*. For medium and large *L. disjunctus* the values for  $w$  were not different from zero, and none of the values for  $a$  and  $h$  were significantly different from the values obtained from Holling's disc equation (Table 4.6; also see Table 4.3). Thus,

this particular model does not successfully incorporate wasteful killing.

#### 4.4 DISCUSSION

The results of the present study show that both *Coenagrion resolutum* and *Lestes disjunctus* exhibit a Type II functional response to varying densities of *Daphnia magna*, as also shown by earlier studies on functional response of dragonflies involving single prey species (Thompson, 1975 & 1978b; Akre and Johnson, 1979; Cothran and Thorp, 1985; Colton, 1987; Chowdhury et al., 1989; Crowley and Martin, 1989). Small and medium size classes of *L. disjunctus* feed at a greater rate than the same size classes of *C. resolutum* over the whole range of prey density. However, the attack coefficient for *L. disjunctus* was significantly greater only for small larvae and the handling time significantly shorter only for medium larvae. Pickup and Thompson (1990), in their studies with *Coenagrion puella* and *Lestes sponsa*, reported similar results, where the functional responses of *L. sponsa* were higher than those obtained for *C. puella* for all instars studied and for all prey densities tested, except for the lower prey densities at which the responses were similar. The values for the attack coefficient of *L. sponsa* were almost twice those for *C. puella*.

Factors contributing to the attack coefficient include: capture success; speed of movement of the predator; speed of movement of the prey; and maximum distance at which the predator responds to prey (the reactive distance) (Holling, 1963). My observations suggest that the higher attack coefficient of small *L. disjunctus* at low prey densities (Fig. 4.1) was achieved possibly by three related factors: 1) a greater

reactive distance; 2) a longer labial length; 3) a different hunting strategy. During the experiments, *L. disjunctus* attacked *D. magna* from about 3 to 5 mm, whereas *Coenagrion* attacked only when the prey was within 1 to 2 mm. This was possibly due in part to the longer labia of *L. disjunctus* (Table 4.1), but does not explain why only small larvae should show a significant difference. Both species are primarily sit and wait predators and attack their prey from ambush, but *L. disjunctus* was frequently observed to follow a swimming mode, especially when the prey density was low. This increase in predator movement relative to that of the prey should increase the chance of capturing prey.

There are three components of handling time: time involved in orienting to, pursuing and subduing the prey; time involved in eating; and time involved in the digestive pause (Holling, 1963). Although none of these components was measured, a difference in handling times could be due to faster movement of the predator relative to the prey, thereby reducing the time spent orienting towards and pursuing prey. But why this should apply only to the medium size-class comparison between *C. resolutum* and *L. disjunctus* is unknown.

Thompson (1978b) and Pickup and Thompson (1990) observed a significant increase in attack coefficients and decrease in handling times with predator size within species. The same trend was also shown in my experiments, but because I used different sized prey for each predator size, I cannot be sure whether the changes in the estimated values are only due to predator efficiency. The estimates could also have been influenced by prey size.

My attempts to show that the functional response of *L. disjunctus* was higher than that of *C. resolutum* was limited by the fact that the standard errors of the estimates were quite large, especially for *L. disjunctus*. However, the trend shown by the values certainly indicate that *L. disjunctus* is capable of feeding at higher rates than *C. resolutum*.

Table 4.1 Sizes of *Coenagrion resolutum* and *Lestes disjunctus* larvae used in the functional response experiment.

Species	Size class	Mean Head width ± Std.Err <sup>1</sup>	Mean Labial length ± Std.Err <sup>2</sup>
<i>C. resolutum</i>	Small	1.783 ± 0.008	1.235 ± 0.018
	Medium	2.546 ± 0.010	1.898 ± 0.020
	Large	3.278 ± 0.009	2.354 ± 0.017
<i>L. disjunctus</i>	Small	1.806 ± 0.006	2.024 ± 0.024
	Medium	2.596 ± 0.010	3.285 ± 0.025
	Large	3.066 ± 0.008	3.625 ± 0.019

<sup>1</sup> n = 72 in each size class for each species except for large *C. resolutum* where n = 42;

<sup>2</sup> n = 25 individuals in each size class, selected from larvae used in the functional response experiments.

Table 4.2 Size classes of *Daphnia magna* used in the functional response experiments (n = 50 in each class).

Size class	Mean length (mm)	± Std. Err
A	1.097	0.005
B	2.070	0.018
C	2.897	0.022

Table 4.3 Mean ( $\pm$  Std. Err) estimates of attack coefficient ( $a$ ) and handling times ( $h$ ) for *Coenagrion resolutum* and *Lestes disjunctus* from non-linear regression of Holling's (1959) type II functional response model.

Species	Size class	$a \pm$ Std.Err	$h \pm$ Std.Err
<i>Coenagrion resolutum</i>	Small	0.396 $\pm$ 0.101**	0.278 $\pm$ 0.101
	Medium	0.771 $\pm$ 0.221	0.278 $\pm$ 0.030*
	Large	1.173 $\pm$ 0.350	0.156 $\pm$ 0.034
<i>Lestes disjunctus</i>	Small	1.623 $\pm$ 0.459**	0.247 $\pm$ 0.018
	Medium	1.711 $\pm$ 0.465	0.201 $\pm$ 0.015*
	Large	1.373 $\pm$ 0.320	0.168 $\pm$ 0.014

\* values are significantly different at  $p < 0.05$ ; \*\* values are significantly different at  $p < 0.01$ .

Table 4.4 Percentage wasteful killing (WK) by larvae of *Coenagrion resolutum* at different prey densities.

	Prey density												All densities
	1	3	5	7	9	11	13	15	17	19	25	35	
<i>Small larvae</i>													
No. Killed	0	5	7	12	9	13	13	16	16	24	14	15	
No. eaten	0	5	7	11	8	10	12	15	15	23	13	14	
% WK	0	0	0	8.3	11.1	23.1	7.7	6.2	6.3	4.2	7.1	6.7	7.6
<i>Medium larvae</i>													
No. Killed	2	6	14	16	20	18	16	20	20	17	21	20	
No. eaten	2	6	11	15	17	17	14	17	17	14	21	17	
% WK	0	0	21.4	6.3	15	5.6	12.6	15.0	15.0	17.6	0.0	15.0	11.6
<i>Large larvae</i>													
No. Killed	3	16	24	12	32	39	24	21	-	-	-	-	
No. eaten	3	12	20	9	27	31	19	21	-	-	-	-	
% WK	0	25.0	16.7	25.0	15.6	20.5	20.8	0.0	-	-	-	-	16.9

Table 4.5 Percentage wasteful killing (WK) by larvae of *Lestes disjunctus* at different prey densities.

	Prey density												All
	1	3	5	7	9	11	13	15	17	19	25	35	Densities
<i>Small larvae</i>													
No. Killed	3	15	16	27	22	27	31	21	26	17	25	27	
No. eaten	3	13	15	23	18	21	27	17	25	16	21	20	
% WK	0	13.4	6.3	14.8	18.2	22.2	12.9	19.1	3.9	5.9	16.0	25.9	14.4
<i>Medium larvae</i>													
No. Killed	6	19	18	28	28	23	26	35	30	29	33	31	
No. eaten	6	17	16	23	24	19	24	31	27	25	25	26	
% WK	0	10.5	11.1	17.9	14.3	17.4	7.7	11.4	10.0	13.8	24.2	16.1	14.4
<i>Large larvae</i>													
No. Killed	5	10	24	25	27	41	45	43	38	29	35	37	
No. eaten	5	10	21	20	20	30	35	36	30	23	27	28	
% WK	0	0	12.5	20.0	25.9	26.8	22.2	16.3	21.1	20.7	22.9	24.2	20.6

Table 4.6 Mean ( $\pm$  Std. Err) estimates of attack coefficient ( $a$ ), handling time ( $h$ ) for prey killed and eaten, and handling time for wasteful killing ( $w$ ), for *Lestes disjunctus* obtained from modified Holling's Type II functional response model.

Size class	Parameters	Mean $\pm$ Std. Err.
Small	$a$	2.612 $\pm$ 0.638
	$h$	0.242 $\pm$ 0.012
	$w$	0.088 $\pm$ 0.028
Medium	$a$	1.952 $\pm$ 0.481
	$h$	0.196 $\pm$ 0.015
	$w$	0.021 $\pm$ 0.034
Large	$a$	1.626 $\pm$ 0.333
	$h$	0.147 $\pm$ 0.016
	$w$	0.064 $\pm$ 0.037

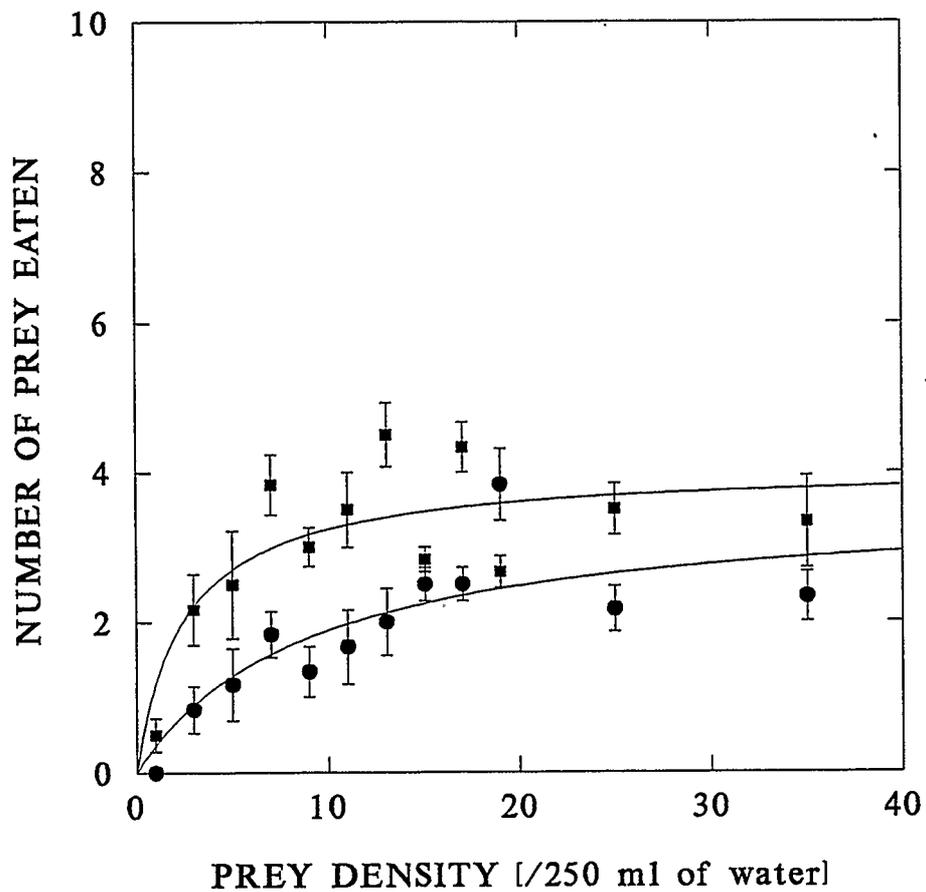


Figure 4.1 Functional responses of small *Coenagrion resolutum* (●) and *Lestes disjunctus* (■) to varying densities of *Daphnia magna* of size class 'A', fitted by Holling's disc equation. Means and standard errors of numbers of *D. magna* eaten at each density are shown.

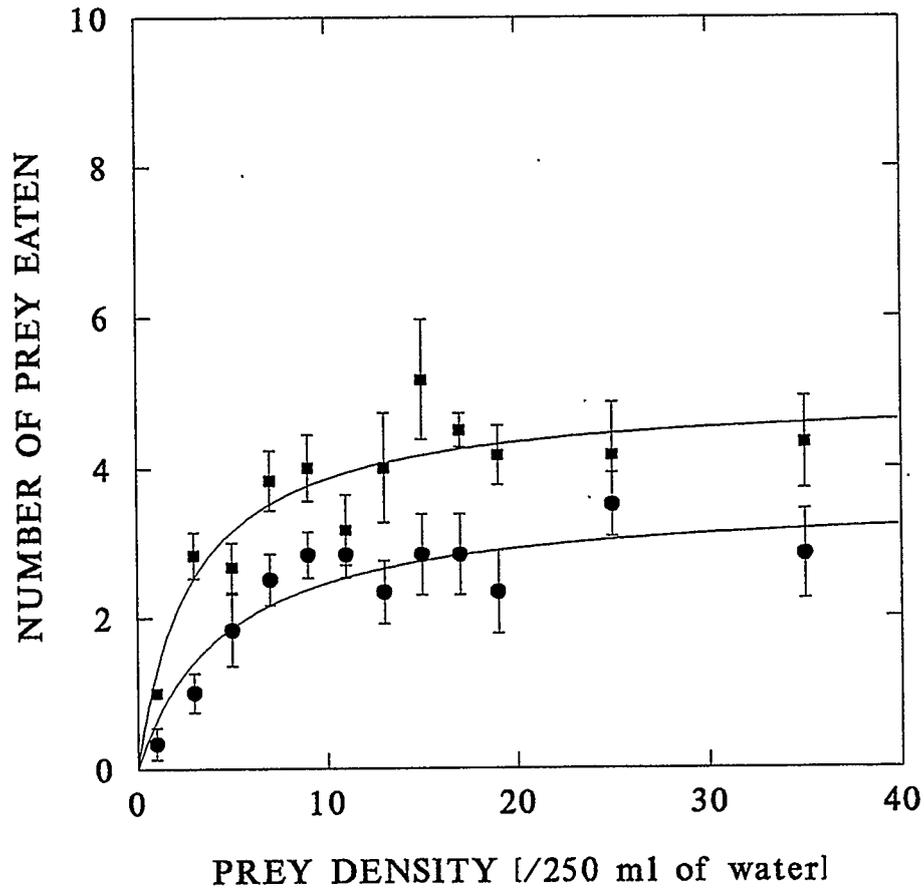


Figure 4.2 Functional responses of medium *Coenagrion resolutum* (●) and *Lestes disjunctus* (■) to varying densities of *Daphnia magna* of size class 'B', fitted by Holling's disc equation. Means and standard errors of numbers of *Daphnia* eaten at each density are shown.

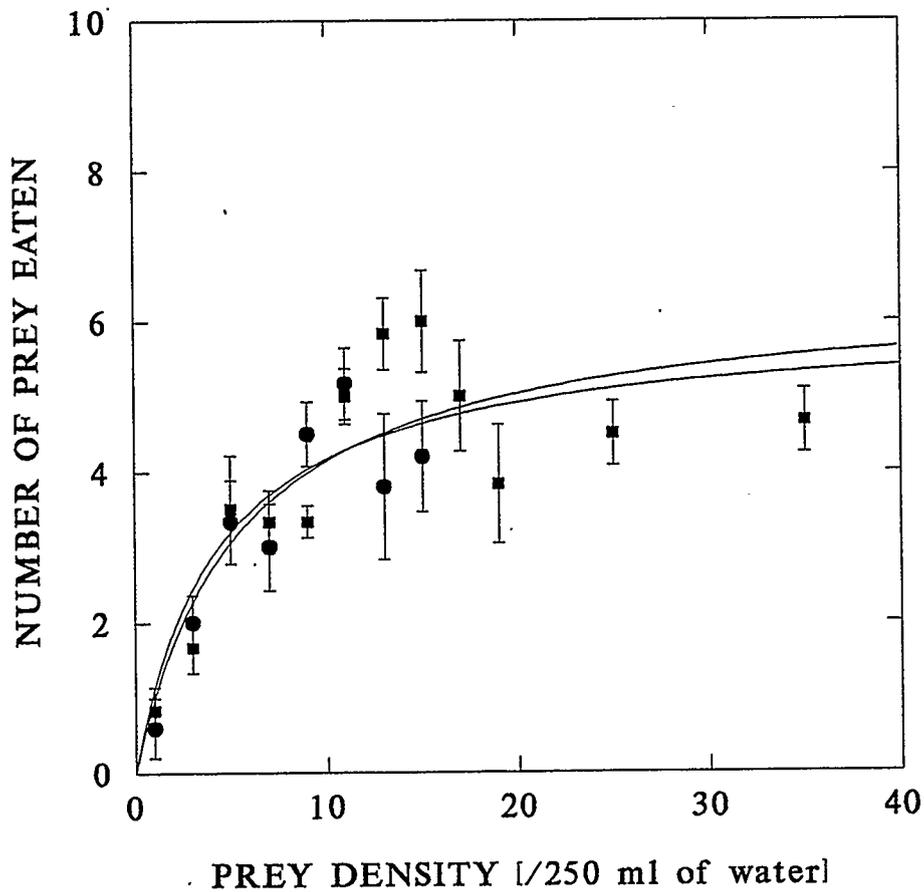


Figure 4.3 Functional responses of large *Coenagrion resolutum* (●) and *Lestes disjunctus* (■) to varying densities of *Daphnia magna* of size class 'C', fitted by Holling's disc equation. Means and standard errors of numbers of *Daphnia* eaten at each density are shown.

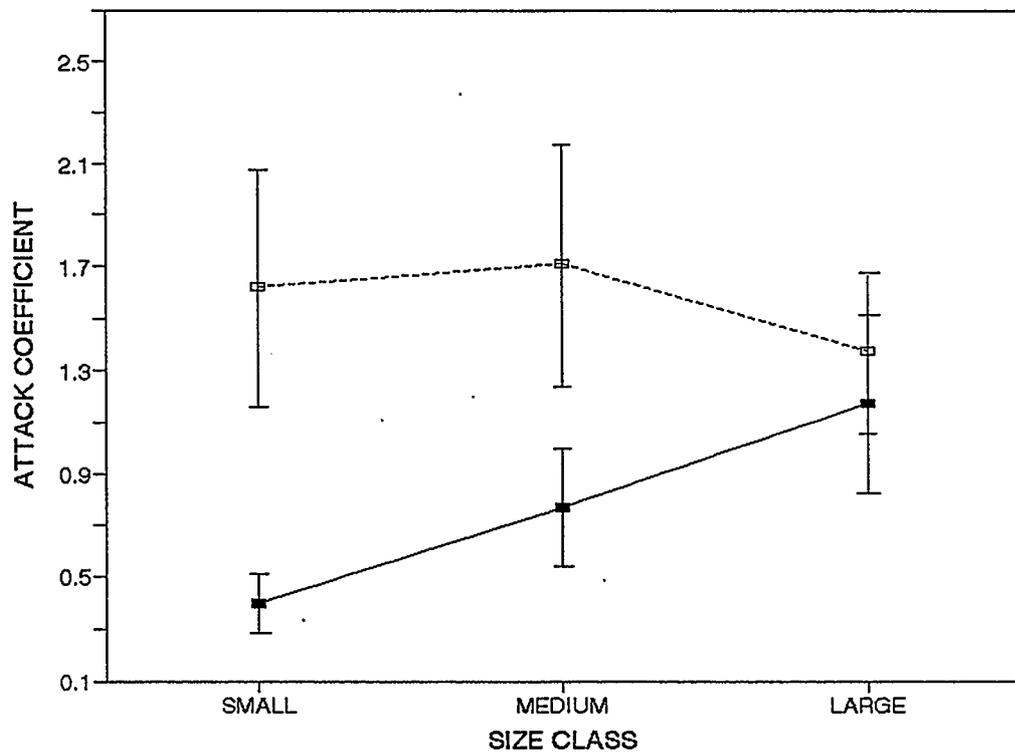


Figure 4.4 Mean ( $\pm$  Std. Err) attack coefficients of *Coenagrion resolutum* (■) and *Lestes disjunctus* (□).

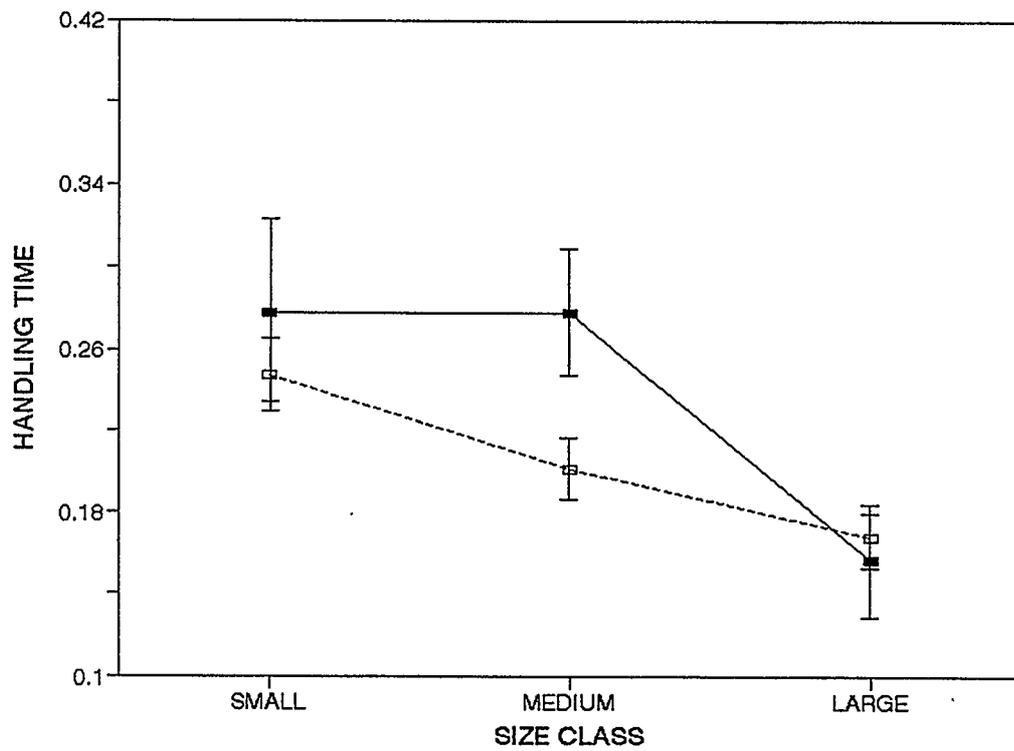


Figure 4.5 Mean ( $\pm$  Std. Err) handling times of *Coenagrion resolutum* (■) and *Lestes disjunctus* (□).

## CHAPTER 5

### GENERAL CONCLUSIONS

The present study was conducted with the aim of elucidating some of the factors contributing to the different life histories of two commonly occurring dragonflies, *Coenagrion resolutum* and *Lestes disjunctus*, at the University of Calgary Research Pond. *L. disjunctus* follows an obligatory univoltine life cycle with an eight month egg diapause, whereas *C. resolutum* follows a mixed univoltine and semivoltine life cycle without an egg diapause (Chapter 1). Thus, even though larvae of both species coexist in the same habitat, larval growth rates are very different. My specific objective was to determine why *L. disjunctus* larvae grow faster than *C. resolutum* larvae. To fulfil this objective, I followed the life cycles of the two species (Chapter 2) and determined their growth rates in their natural habitat. The results of the study confirmed that *L. disjunctus* indeed grew faster than *C. resolutum* at the University Pond. I then showed that *L. disjunctus* grows faster than *C. resolutum* in the laboratory at all temperatures experienced in the field.

My second experiment tested the hypothesis that these higher growth rates of *L. disjunctus* resulted from a faster feeding rate embodied in the functional response of larvae to prey density (Chapter 4). Higher feeding rates should be translated into higher growth rates. Although the experimental results showed an increased functional response by the larvae of *L. disjunctus* (in terms of number of prey attacked), comparisons of attack coefficients and handling times were generally non-significant

because of high sampling errors. However, mean attack coefficients were consistently higher for *L. disjunctus*, that for small larvae significantly so, and, with one exception, mean handling times were shorter, significantly so in medium sized larvae. Therefore, the data suggest that *L. disjunctus*' feeding rate contributes to its faster growth rate. Future studies focussing on the sub-components of the functional response parameters such as reactive volume, capture success, hunting strategy, time spent orienting to, pursuing, subduing, and eating prey, and in wasteful killing, would perhaps refine the conclusions obtained in this study. Use of visual aids like video-taping experiments under both light and dark (red light) conditions would facilitate access to this sort of information. Studies on energy assimilation and allocation would also be necessary to develop a complete explanation for the contribution of feeding to the faster growth rate of *L. disjunctus*.

Other factors could contribute to the faster growth of *L. disjunctus* in the field. One is the lack of spacing behaviour (Baker, 1981b) which, if present (as in *C. resolutum* in the laboratory), decreases the average feeding rate due to exclusion of individuals from prime feeding sites. Another is the tendency of *L. disjunctus* larvae to occupy the shallow, warmer parts of the pond, in which feeding rates would be higher as long as prey is not limiting. A detailed survey of the distribution of the two species in the field and the temperature regimes in different parts of the pond would be necessary to address this question.

To summarize, in terms of fulfilling my objective I make the following conclusions from the study:

- 1) *Coenagrion resolutum* follows a mixed univoltine and semivoltine life cycle which allows it to extend the life cycle from 1 to 2 years under unfavourable conditions. Univoltine individuals of *C. resolutum* grow at a rate of 0.004 mm/mm/day, whereas the semivoltine individuals grow at slower rate of 0.005 mm/mm/day.
- 2) *Lestes disjunctus* follows an obligatory univoltine life cycle taking exactly one year to complete the life cycle from egg to adult stage. Larvae complete their development in approximately 90 days at a rate of 0.02 mm/mm/day, 5 times faster than that of the univoltine individuals of *C. resolutum*.
- 3) Growth experiments conducted under constant laboratory conditions revealed that *L. disjunctus* grows 1.4 to 3.3 times faster than *C. resolutum*, the differential increasing with increases in temperature (i.e. *L. disjunctus* has a higher temperature coefficient for growth).
- 4) The functional response experiment showed significant differences between species only in the attack coefficients of small larvae and in the handling times of medium larvae.
- 5) Wasteful killing was found to be a common phenomenon in both species, but the model developed to incorporate it into Holling's functional response equation did not change the parameter estimations.

Finally, the characters shown by *L. disjunctus* (such as faster growth rate and higher feeding rate compared to *C. resolutum*) are quite promising for it to be used as a biocontrol agent of mosquitoes and prompts a study of their biological control potential.

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## APPENDIX I

To incorporate the time involved in wasteful killing into the total handling time, I modified Holling's Type II functional response model. If the total number of prey eaten ( $E$ ) is the product of the total number of prey killed ( $K$ ) and the fraction of prey killed that are eaten ( $f$ ), then

$$E = fK. \quad (1)$$

Following Holling (1959), the number of prey killed can be expressed as

$$K = aT_s n, \quad (2)$$

where,  $a$  = attack coefficient, which is a constant equal to the rate of searching multiplied by the probability of finding a prey

$T_s$  = time available for searching

$n$  = prey density

If an experiment is conducted for a fixed period ( $T$ ), then  $T_s$  will vary with the handling time per prey ( $T_h$ ), as handling time decreases the time available for searching, so that

$$T_s = T - T_h K. \quad (3)$$

Handling time ( $T_h$ ) can be partitioned as time spent in handling the prey killed and eaten and time spent in wasteful killing:

$$T_h = fKh + (1-f)Kw \quad (4)$$

where,  $h$  = handling time for each prey killed and eaten and  
 $w$  = handling time for each prey killed and wasted.

Substituting equations (3) and (4) in equation (2) yields

$$K = a (T - fKh - Kw + fKw)n. \quad (5)$$

Simplifying equation (5), gives

$$K = aTn - afKh - aKw + afKw \quad (6)$$

Isolating terms with  $K$  on the left gives

$$K + afKh + aKw - afKw = aTn, \quad (7)$$

so that the number of prey killed is

$$K = \frac{anT}{(1 + an[fh + (1-f)w])}. \quad (8)$$

The number of prey eaten is found by substituting equation (8) in equation (1), or

$$E = \frac{anTf}{(1 + an[fh + (1-f)w])}. \quad (9)$$