

AN ABSTRACT OF THE THESIS OF

Robert W. Wisseman for the degree of Master of Science in
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Title: Biology and Distribution of the Dicosmoecinae
(Trichoptera: Limnephilidae) in Western North
America

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N. H. Anderson

Literature and museum records have been reviewed to provide a summary on the distribution, habitat associations and biology of six western North American Dicosmoecinae genera and the single eastern North American genus, Ironoquia. Results of this survey are presented and discussed for Allocosmoecus, Amphicosmoecus and Ecclisomyia.

Field studies were conducted in western Oregon on the life-histories of four species, Dicosmoecus atripes, D. gilvipes, Onocosmoecus unicolor and Ecclisocosmoecus scylla.

Although there are similarities between genera in the general habitat requirements, the differences or variability is such that we cannot generalize to a "typical" dicosmoecine life-history strategy. A common thread for the subfamily is the association with cool, montane streams. However, within this stream category habitat associations range from semi-aquatic, through

first-order specialists, to river inhabitants. In feeding habits most species are omnivorous, but they range from being primarily detritivorous to algal grazers. The seasonal occurrence of the various life stages and voltinism patterns are also variable.

Larvae show inter- and intraspecific segregation in the utilization of food resources and microhabitats in streams. Larval life-history patterns appear to be closely linked to seasonal regimes in stream discharge. A functional role for the various types of case architecture seen between and within species is examined. Manipulation of case architecture appears to enable efficient utilization of a changing seasonal pattern of microhabitats and food resources.

Biology and Distribution of the Dicosmoecinae
(Trichoptera: Limnephilidae) in Western North America

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Robert William Wisseman

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Head of Department of Entomology

Redacted for privacy

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**BIOLOGY AND DISTRIBUTION OF THE DICOSMOECINAE
(TRICHOPTERA: LIMNEPHILIDAE) IN WESTERN NORTH AMERICA**

INTRODUCTION

**Distribution and Systematics of the World Fauna of
Dicosmoecinae**

The subfamily Dicosmoecinae is thought to contain the most primitive extant members of the Limnephilidae (Schmid 1955, Wiggins 1977). Adult characters are outlined by Schmid (1955, 1980). Wiggins (1977) has described the larvae of North American genera. Flint (1960, 1982) described the larvae of many of the South American genera and the Australian genus Archaeophylax.

The Dicosmoecinae occur throughout the Nearctic and eastern Palaearctic regions (Table 1). It is the only subfamily of the Limnephilidae in the Neotropical region, where it is represented by a number of genera in the austral portions of the Chilean subregion. Archaeophylax is the only genus of the Limnephilidae known from the Australian region. The sole representative of this subfamily in the western Palaearctic is Ironoquia dubia which is considered by some to be of dubious placement into the Dicosmoecinae (Svensson and Tjeder 1975).

Flint and Wiggins (in prep.) are currently reviewing the systematics of the subfamily at the world level. Although Schmid (1955, 1980) has tentatively placed three isolated western North American genera (Allomyia-Imania, Pedomoecus, and Rossiana) in the Dicosmoecinae, Wiggins

TABLE 1. Genera of the Dicosmoecinae (Trichoptera: Limnephilidae) of the world, their distribution and number of known species.

REGION	GENERA	#SPP.	REFERENCES
Western Nearctic	<u>Allocosmoecus</u>	1	Wiggins 1977
	<u>Amphicosmoecus</u>	1	Wiggins 1977
	<u>Cryptochia</u>	7	Wisseman & Anderson 1987
	<u>Dicosmoecus</u>	4	Wiggins & Richardson 1982
	<u>Ecclisocosmoecus</u>	1	Wiggins 1977
	<u>Ecclisomyia</u>	3	Wiggins 1977
	<u>Onocosmoecus</u>	4	Wiggins & Richardson 1987
Eastern Nearctic	<u>Ironoquia</u>	4	Wiggins 1977
Western Palaeartic	<u>Ironoquia</u> (incertum)	1	Svensson & Tjeder 1975 Malicky 1983
Eastern Palaeartic	<u>Dicosmoecus</u>	3	Wiggins & Richardson 1982
	<u>Ecclisocosmoecus</u>	1	Schmid 1964, Wiggins 1977
	<u>Ecclisomyia</u>	2	Schmid 1955
	<u>Evanophanes</u>	1	Schmid 1955
	<u>Nothopsyche</u>	9	Schmid 1955
	<u>Onocosmoecus</u>	?4	Wiggins & Richardson 1987
Australian	<u>Archaeophylax</u>	3	Flint 1960, Neboiss 1983
Neotropical (Austral)	<u>Anomalocosmoecus</u>	3	Flint 1982, 1983
	<u>Antarctoecia</u>	1	Schmid 1955, Flint 1982
	<u>Austrocosmoecus</u>	1	Schmid 1955, Flint 1982
	<u>Magellomyia</u>	16	Schmid 1955, Flint 1982
	<u>Metacosmoecus</u>	1	Schmid 1955, Flint 1982
	<u>Monocosmoecus</u>	6	Schmid 1955, Flint 1982
	<u>Platykosmoecus</u>	1	Schmid 1964, Flint 1982

(pers. comm.) believes that these genera may belong in other limnephilid subfamilies. The western North American fauna thus consists of about 21 species distributed among 7 genera (Table 1), which are believed to be monophyletic with the Siberian fauna (Wiggins, pers. comm.). Relationship of this branch of the dicosmoecines with other world genera is obscure at present.

Biology of the World Fauna

Though the subfamily contains members that are among the largest of all Trichoptera and many species are conspicuous components of the western North American montane stream fauna, it is only in recent years that a basic understanding of their biology, distribution and systematics has begun to emerge. Wiggins (1977) and Anderson (1976) have published summaries of habitat associations, case architecture and trophic status.

An array of putative species in the Holarctic Dicosmoecus and Onocosmoecus genera were united by Wiggins and Richardson (1982, 1987) into several variable species within each genus. General life history features of a few of these species were inferred from random collections made throughout their ranges. Voltinism patterns were obscured in this regional analysis, and appeared to display high inter- and intraspecific variation regarding univoltine versus biennial

development patterns. Subsequent data collected from local populations have confirmed some of Wiggins and Richardson's basic conclusions on voltinism and developmental patterns for two species of Dicosmoecus (Gotceitas and Clifford 1983, Hauer and Stanford 1982), but conclusive data from other populations are required to support suggested variation in life history parameters.

Wisseman and Anderson (1987) examined the life history of Cryptochia pilosa in an Oregon Coast Range watershed, and summarized the distributional records of the seven Cryptochia species. Published information on the remaining western North American genera consists largely of scattered distributional records with occasional notes on larval habitat associations or feeding habits.

Published data on the life cycles of Dicosmoecinae species other than those in western North America are minimal. Williams and Williams (1975), Clifford (1966) and Flint (1958) have examined some aspects of the life history of Ironoquia spp. in eastern North America. Flint (1982) provides notes on habitat associations for the South American genera, and Turcotte and Harper (1982) have published the only seasonal size-frequency analysis of larvae for a Neotropical species (Anomalocosmoecus

illiesi). Lepneva (1966) provides habitat associations and distribution for Siberian species.

Objectives

Life history studies of western caddisflies have been a focus of research at Oregon State University for over 20 years. In particular, several sites in the Oregon Coast Range and western Cascade Mountains have been examined in terms of trichopteran community composition and population dynamics, along with studies in the life histories of selected species (Anderson 1976; Anderson and Grafius 1975; Grafius and Anderson 1979, 1980; Anderson et al. 1982, 1984).

As part of this larger project, we examined the life histories of species of the Dicosmoecinae at several sites in the Pacific Northwest and collated the data from published, personal and museum records. Objectives of this study are:

1. To provide detailed life history data on dicosmoecine species at selected field sites in western Oregon, with emphasis on the seasonality and habitat associations of all life stages, voltinism and growth patterns, feeding habits, case architecture, egg biology, quiescent periods, and larval and adult behavior.
2. To elucidate the regional patterns of distribution, habitat association, and life histories based on characteristics of western North American physiographic provinces.

Studies on the western North American genera are presented as separate chapters. A synopsis of published

distributional and biological information available on Ironoquia spp. in eastern North America is included.

STUDY REGION

Provinces and Regions of Western North America

Nearctic dicosmoecine species are found throughout montane western North America, from the Rocky Mountain cordillera westward to the Pacific Coast ranges. It is instructive to discuss distributional patterns and variability in life history characteristics in the context of the spectrum of landforms and climatic conditions present in this large geographic area.

Physiographic provinces are depicted in Figure 1 with general characteristics provided in Table 2. This classification system has been assembled from various sources for this review (Bird 1972; Donley et al. 1979; Franklin and Dyrness 1969; Hunt 1967, 1974; Kimerling and Jackson 1985). The level of resolution for regional units in our intensive study area (the northwest states of the Pacific Coastal Province) is given in greater detail than for other physiographic provinces.

The diverse topography of western North America produces localized altitudinal gradients. Over short distances there are marked changes in climatic conditions, in aquatic habitats, and in the associated fauna and flora. Provinces and regions can be contrasted between those composed of mountain systems and those which are principally lowlands, broad basins or plateaus (Figure 1).

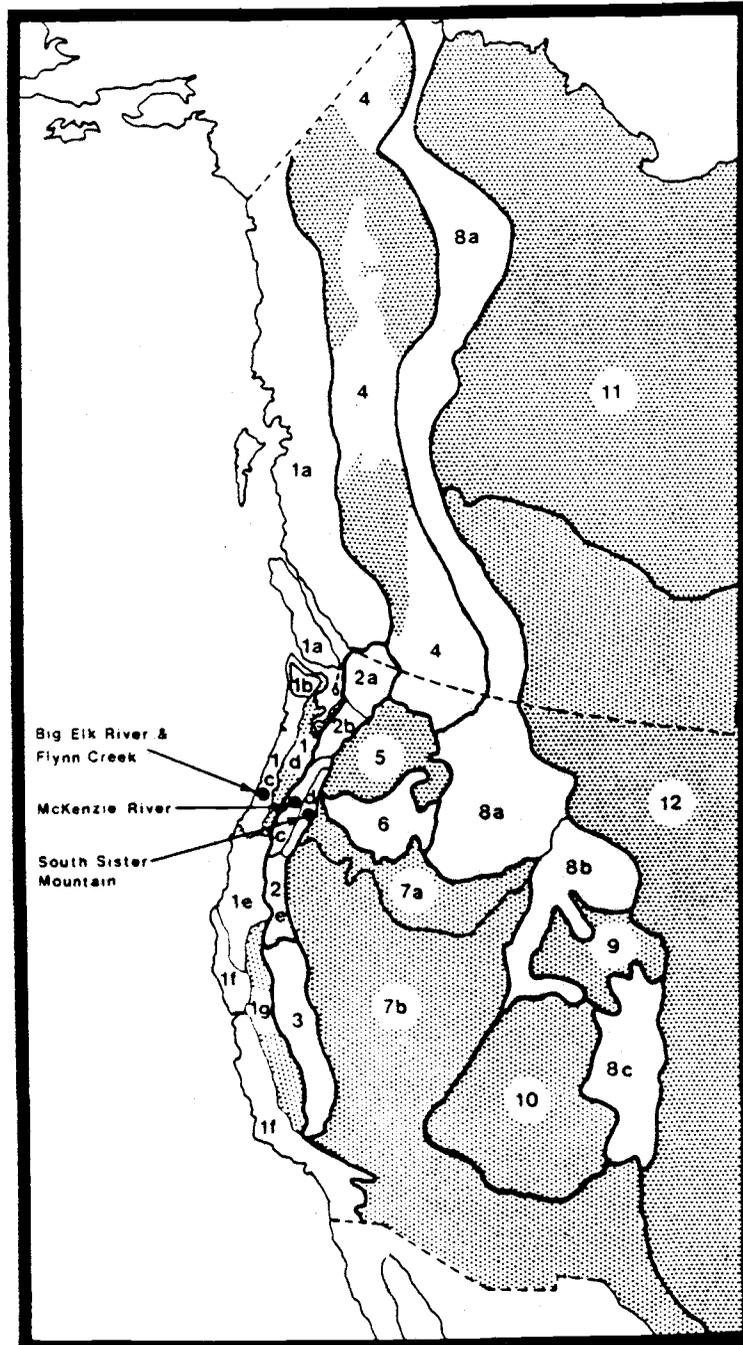


Figure 1. Physiographic provinces and regions of montane western North America. See Table 2 for explanation. Shaded areas represent provinces and regions composed primarily of lowlands, basins, plains and plateaus.

TABLE 2. Physiographic provinces and regions of western North America. A synopsis of the general topography, elevations, climates and natural vegetation types provided. See text for references.

	PROVINCES (1-12) Regions (a-g)	CHARACTERISTICS
1	PACIFIC BORDER	
a	Southeast Alaska and British Columbia Coast Ranges	High mountains, 0 to >3000m elevation; precipitation >250 cm/year; moist maritime, montane, alpine climates; dense coniferous forest and isolated alpine vegetation.
b	Olympic Mountains	High mountains with continuous crests; 1000-2500 m elevation; 200 to >300 cm/year precipitation; moist maritime & isolated alpine climates; dense coniferous forest & alpine vegetation.
c	Oregon-Washington Coast Range	Low mountains; mostly <500 m elevation; 150-250 cm/year precipitation; mild, moist maritime climate; dense coniferous forest vegetation.
d	Willamette-Puget Lowland	Plains with low ridges; 0-300 m elevation; 100-150 cm precipitation; mild, moist maritime climate; dense coniferous forest & steppe vegetation.
e	Klamath Mountains	High mountains, complex system of crests; 0-2500 m elevation; 100 to >200 cm/year precipitation; mediterranean, montane & maritime climates; mixed broadleaf & coniferous forest vegetation with isolated scrub pockets.
f	California Coast Range	Open, low mountains with isolated crests; mostly <500 m, isolated peaks to 2500 m; precipitation >150 cm/year in north to mostly 25-75 cm/year in the south; mediterranean climate with pockets of steppe; complex vegetation, with steppe, scrub & mixed forest; generally divisible into northern and southern subregions.
g	Great Valley	Flat plains; 100-300 m elevation; 10-50 cm/year precipitation; mediterranean in north, steppe and desert climates in south; grassland & scrub vegetation.

TABLE 2 cont.

2	CASCADES	
a	North Cascades	High mountains, complex interlocking crests; mostly > 1500 m elevation; >250 cm/year precipitation; moist maritime & isolated alpine climates; dense coniferous forests & isolated alpine vegetation.
b	Washington Cascades	Low to moderate elevation mountains with isolated high volcanic peaks; mostly 1000-2000 m elevation; >250 cm/year precipitation; moist maritime & isolated alpine climates; dense coniferous forests and isolated alpine vegetation.
c	Western Oregon Cascades	Low mountains with complex crests; <1500 m elevation; 100-200 cm/year precipitation; moist, maritime climate; dense coniferous forests.
d	Oregon High Cascades	High mountain system with isolated volcanic peaks; >1500 m elevation; 100-200 cm/year precipitation; montane and isolated alpine climates; open coniferous forest with isolated vegetation.
e	Southern Cascades	Open low mountains with isolated volcanic peaks; mostly <1000 m elevation, peaks to >3000 m; mostly >150 cm/year precipitation; montane with isolated mediterranean and alpine climates; mostly open coniferous forest with isolated alpine and scrub.
3	SIERRA NEVADA MOUNTAINS	High mountains with continuous crests; 1000 to >3000 m elevation; >100 cm/year precipitation; at high elevations, 75-100 cm at low; montane and alpine climates; open coniferous forests and alpine vegetation.
4	NORTHERN INTERIOR RANGES AND PLATEAUS	Intermediate elevation mountains separated by broad plateaus with low ridges; plateaus ca. 1000 m, mountains <2000 m elevation; 100-150 cm/year precipitation; montane climate; dense coniferous forests.
5	COLUMBIA BASIN	Plains & low ridges; 300-600 m elevation; <40 cm/year precipitation; steppe and desert climates; grassland and scrub vegetation.
6	CENTRAL OREGON MOUNTAINS	Open moderate to high mountains; >1000 m to peaks of 2900 m; 40-80 cm/year precipitation; steppe, montane and alpine climates; open coniferous forest and isolated alpine vegetation higher, scrub vegetation lower.

TABLE 2 cont.

7	BASIN AND RANGE	
a	High Lava Plains	High plains with isolated ridges; mostly 1200 m elevation; <40 cm precipitation; steppe and desert climates; scrub vegetation.
b	Basin and Range	Arid mountains broadly separated by desert basins; basins 0-1500 m, ranges 1500-3000 m elevation; <50 cm precipitation; steppe and desert climates; scrub vegetation.
8	ROCKY MOUNTAINS	
a	Northern Rockies	High mountains with continuous crests; 1500 to >3000 m elevation; 25-125 cm/year precipitation; montane and alpine climates; open coniferous forests mostly with isolated alpine vegetation, scrub at lower elevations.
b	Middle Rockies	Complex mountain system of moderate to high elevation with intervening plateaus; elevation of most ranges 2000-2500 m, some to 3500 m; <50 cm/year precipitation; steppe, montane and alpine climates; alpine (>3500m), coniferous forest (>3000 m), scrub (<3000 m) vegetation.
c	Southern Rockies	Continuous system of high mountains; extensive portion >3000 m elevation; 35-50 cm/year precipitation; montane and alpine climates; alpine (>3500 m), open coniferous forest (>2250 m), scrub (<2000 m) vegetation.
9	WYOMING BASIN	High basin with low ridges; 1800-2400 m elevation; <50 cm/year precipitation; steppe climate; scrub and grassland vegetation.
10	COLORADO PLATEAU	Complex high plateaus, canyons, and ridges; 1500-3000 m elevation; < 50 cm/year precipitation; steppe and desert climates; desert scrub, grassland vegetation, with isolated open coniferous forest at higher elevations.
11	PEACE-SLAVE-MACKENZIE LOWLANDS	Eastern border of montane western North America; low to mid- elevation plains; cold, humid climate; Boreal coniferous forest.
12	GREAT PLAINS	Eastern border of montane western North America; upland plain with low ridges; 500-1500 m elevation; semiarid to arid steppe climate; grassland & scrub vegetation.

In the western United States the areas occupied by humid coniferous forest generally reflect areas where the annual precipitation exceeds the evapo-transpiration rate, and consequently where small perennial streams are likely to occur (Figure 2). Embedded in this coniferous matrix are riparian zones having in some cases mixed conifer and deciduous trees supplying a diverse quality of litter substrates. Small perennial streams are abundant in the moist, coastal climates of the maritime northwest states, western Canada, and Alaska. Stream abundance decreases markedly, and is increasingly confined to higher elevations, in the more xeric interior regions of the western United States.

The western Dicosmoecinae are almost exclusively confined to the montane provinces and regions as shown in Figure 1. We believe that their preferred habitats, and consequently their relative abundances, within these areas are strongly correlated with the occurrence of humid coniferous forests.

Sites of Intensive Study

The life history information reported here is based primarily on studies and observations of populations in the Pacific northwest states. All western dicosmoecine genera and most species are found in this area. Principal study sites are labeled in Figure 1. Intensive studies on the

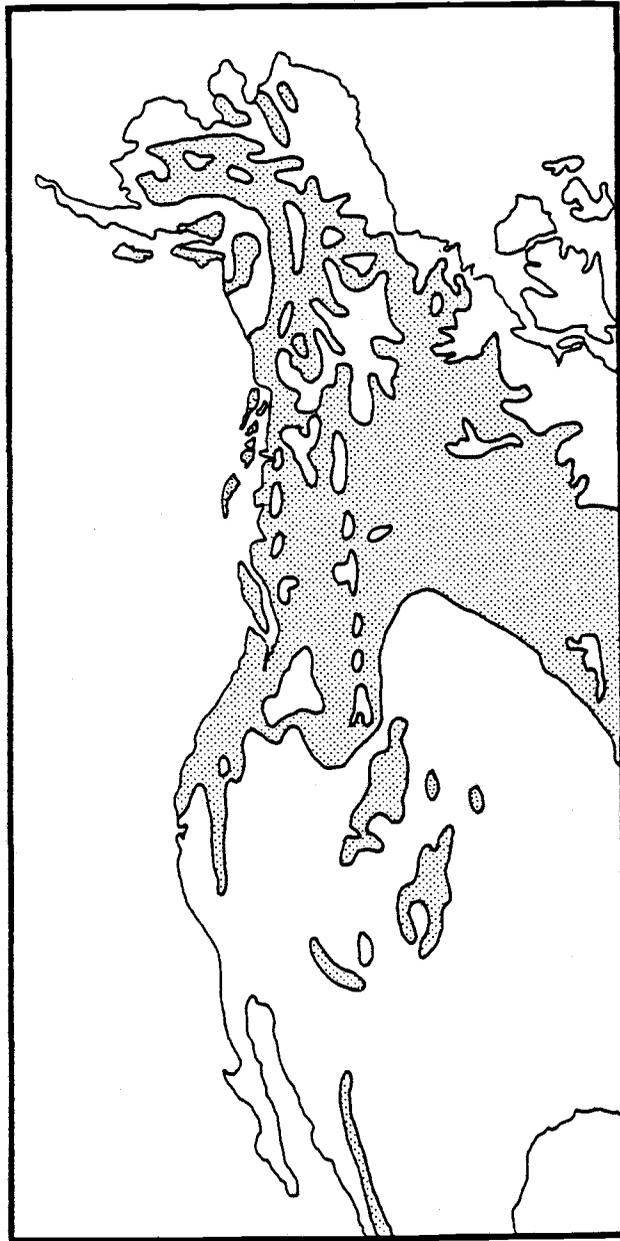


Figure 2. The distribution of humid coniferous forests in western North America (shaded). Redrawn from Anonymous (1953).

bionomics of a number of species have been conducted in Oregon at Flynn Creek and Big Elk River in the Coast Range, tributaries of the McKenzie River in the western Cascades, and streams on South Sister Mountain in the Oregon High Cascades (Table 3). These sites are representative of low, mid-, and high elevation areas in the maritime Northwest. Figures 3 & 4 provide representative data on seasonal discharge patterns and thermal regimes present in these watersheds or in comparable watersheds near the study sites (USGS 1971-1984).

The seasonal discharge pattern seen for the high-elevation Cascade site is generally reflective of higher elevation streams throughout western North America. Peak discharge coincides with spring-summer snowmelt.

In the low mountains of the Oregon-Washington Coast Range, precipitation occurs mostly as winter rain, which maintains high stream discharge from November to April. The McKenzie River (Western Cascades) maintains high water levels from November to June, being recharged by both winter rains on lower elevation watersheds and spring snowmelt from higher ones.

Mean monthly temperatures vary from 7.5-12.5 °C at Flynn Creek, a small, densely shaded stream in the Oregon Coast Range (Figure 4), while a larger, open river in the same vicinity displays a high annual temperature range of 6.0-21.5 °C (Siuslaw River near Big Elk River). Cool

TABLE 3. Watershed characteristics of four study sites in western Oregon, U.S.A.

PARAMETER	FLYNN CREEK	BIG ELK RIVER	MCKENZIE RIVER	SOUTH SISTER MOUNTAIN
Province	Pacific Border	Pacific Border	Cascades	Cascades
Region	Oregon-Wash- ington Coast Range	Oregon-Wash- ington Coast Range	Western Oregon Cascades	Oregon High Cascades
County	Lincoln	Lincoln	Lane	Deschutes
Lat./Long.	44° 32'N 123° 52'W	44° 33'N 123° 42'W	44° 15'N 122° 15'W	44° 02'N 121° 46'W
Elevation	150-300 m	125 m	300-800 m	1800-2000 m
Watersheds	Flynn Creek	Big Elk River	Tributaries of McKenzie River	Tyee, Goose & Todd Creeks
Stream order	1-3	5	1-6	1-3
\bar{X} stream width	0.3-3 m	7-10 m	2 to >20 m	0.3-3 m
Riparian vegetation	Closed canopy, coniferous & broadleaf forest	Open canopy, coniferous & broadleaf forest	Closed & open, coniferous & broadleaf forest	Open canopy, coniferous for- est & alpine meadow

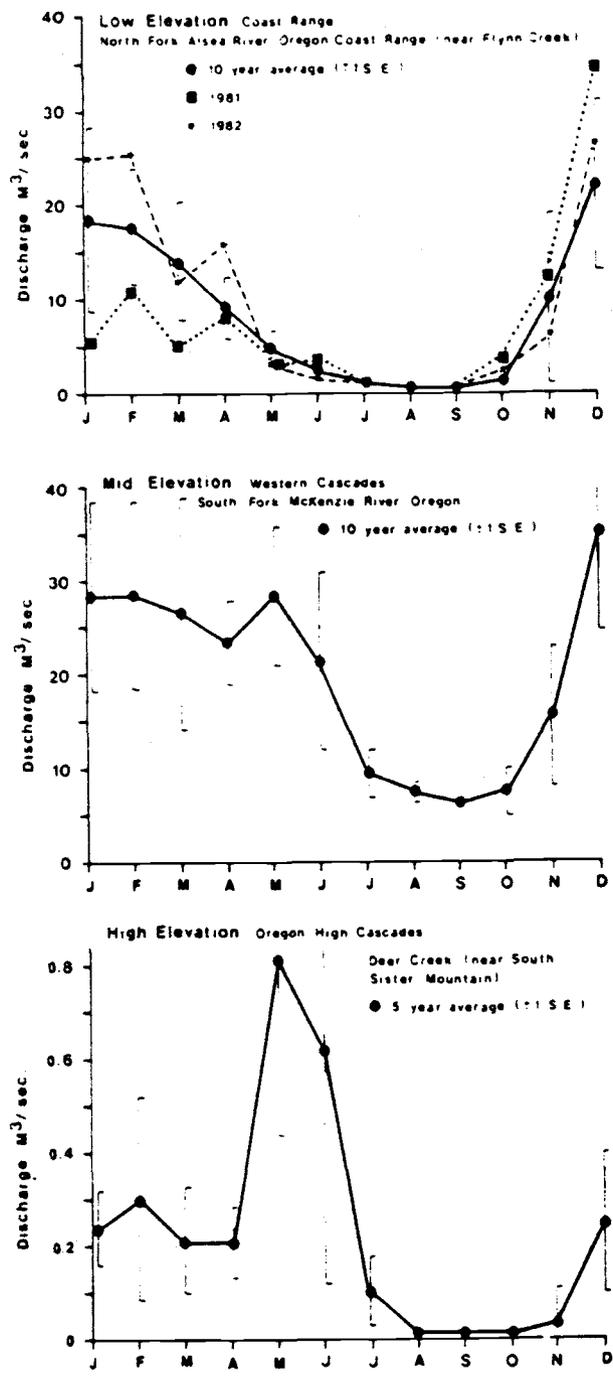
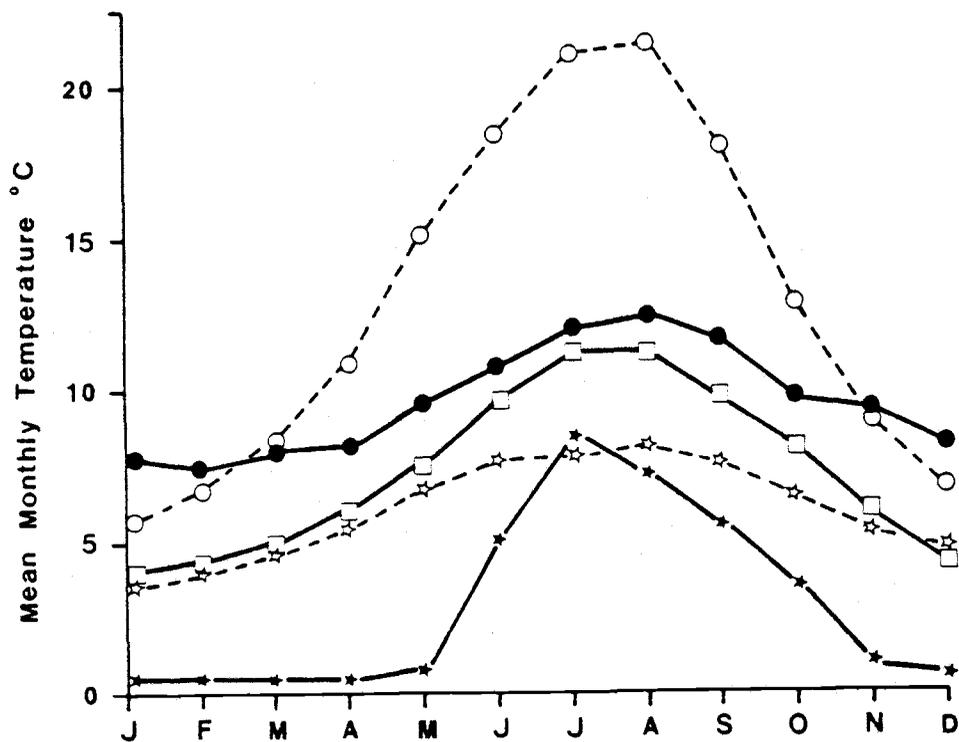


Figure 3. Stream discharge patterns from forested, montane watersheds at low, mid- and high elevation sites in the maritime Northwest. Mean monthly discharge provided (USGS 1971-1984).



Low Elevation: Oregon Coast Range

● Flynn Creek (USGS 5 year average)

○ Siuslaw River: near Big Elk River (USGS 6 year average)

Mid Elevation: Western Cascades

□ South Fork McKenzie River (USGS 7 year average)

High Elevation: Oregon High Cascades

★ Metolius River: near South Sister Mountain (USGS 3 year average)

High Elevation: Northern Rocky Mountains

★ Dyson Creek, Alberta (Gotceitas and Clifford 1983)

Figure 4. Stream water temperatures from forested, montane watersheds at low, mid- and high elevation sites in the maritime Northwest. Mean monthly temperature provided.

temperatures, without a high summer maxima, are found in the McKenzie River drainage. More uniformly low temperatures are found in the Metolius River, a spring-fed river in the Oregon High Cascades (similar to the spring-fed streams examined on South Sister Mountain).

METHODS

Material Examined

Information on the biology and distribution of the species discussed was obtained from published and unpublished sources. Museum collections are abbreviated as follows: OSU= Oregon State University; ROM= Royal Ontario Museum; CWU= Central Washington University; USNM= U.S. National Museum; UCB= University of California, Berkeley.

Adults from the field study were obtained by laboratory rearing or collections made by ultraviolet light trap, sticky traps, sweeping, and hand picking. Forewing length was used as an index of size. Measurements were taken from the anterior edge of the tegula to the wing tip with either an ocular micrometer or calipers (accuracy 0.1 mm).

Ovarian Development

Abdomens of pupae and adults were dissected and examined to determine the relative stage of egg development. The classification system of Novak and Sehnal (1963) was modified as follows:

Stage A: Ovaries small; ovarioles compressed; individual eggs not visible in ovarioles; fat body voluminous.

Stage B: Ovaries enlarged; ovarioles expanded; developing eggs up to ca. 75% of mature size contained within ovarioles; fat body in process of being exhausted.

Stage C: Mature eggs, many free of the ovarioles, fill ca. anterior two-thirds of the abdomen; fat body largely exhausted; oviposition has not occurred.

Stage C-D: Oviposition of an initial egg mass has occurred; however the female possesses sufficient developing eggs and reserves to produce a second mass.

Stage D: female spent; all fat body exhausted; remaining embryonic and ovarian tissue degenerated.

Eggs

Egg counts, predator infection, and larval emergence counts were made on over 1000 trichopteran egg masses collected in the Oregon Coast Range (Wisseman and Anderson 1984). These included about 23 species, primarily limnephilids. Laboratory rearing of larvae derived from the masses was conducted to identify the species. Egg masses from three of the western dicosmoecine genera are described in this report.

Egg masses collected both above and below the waterline were reared in the laboratory at 12°C on wetted filter paper in petri dishes. Egg masses contain up to 600 eggs, so it is difficult to perform direct counts. Summing the number of larvae eclosing from a mass with the number of nonviable eggs remaining, provides a method whereby the total egg count can be accurately determined.

Larvae

All Dicosmoecinae examined had five clearly differentiated larval instars as determined from frequency distributions of head-capsule widths. Instars are designated by the Roman numerals I to V. Actively foraging or feeding fifth-instar larvae are designated as VF, while

those that had achieved their final mass, had ceased feeding and had attached or burrowed into stream bottom substrates are designated as resting fifths or VR (Wiggins and Richardson 1982). This category includes the prepupal stage and may also incorporate larvae which have entered some form of dormancy prior to pupation.

Measurements were taken at the widest part of the head capsule, when viewed dorsally, with an ocular micrometer at 25 or 50X magnification (accuracy of 0.04 or 0.02 mm, respectively). Interocular width, as used by Wiggins and Richardson (1982) for *Dicosmoecus* is about 5-10% less than the maximum head capsule width as used in this study.

Biomass determined by drying to constant weight at 60 °C, is based on weights of individual larvae. Balances used, Mettler H16 and Cahn 4100, had an accuracy of 0.05 and 0.005 mg, respectively. Specimens collected were placed into 70% ethanol and usually were stored for less than one month before weighing.

Growth

A major focus of the field work was to examine the pattern of growth in the *Dicosmoecinae* for seasonal timing, rates, and instar-specific biomass accumulation. Growth is discussed in terms of biomass gain per unit time. Specific Growth Rate is labeled as SGR, and calculated as (Kaufman 1981):

$$\text{SGR} = (\log_e M_t - \log_e M_0) / t$$

M_t = mean dry mass at end of time t
 M_0 = mean dry mass at beginning of time t

The percentage contribution of each instar to the total final larval biomass was determined for some species. The total range in larval mass, from eclosing first-instar larvae (or mean eclosion mass= MEM) to fifth-instar larvae that have recently ceased growth (mean final or total mass= MTM), was estimated from weights of field-collected larvae. For some species, a MEM could be derived from larvae freshly emerged from egg masses. Each larval instar was then assumed to consist of a population having a "mean initial mass" (MIM), which then grows and molts at a "mean molting mass" (MMM). To normalize the percentage (i.e. summation= 100%) contribution to the total mass range (MTM - MEM) of each instar, an adjusted biomass range was calculated as follows:

Instar I: Adjusted mass range is MEM to MMM I, where

$$\frac{(\text{greatest instar I mass}) + (\text{least instar II mass})}{2} = \text{MMM I \& MIM II}$$

Instar II: Adjusted mass range is MIM II to MMM II,
 where

$$\frac{(\text{greatest instar II mass} + \text{least instar III mass})}{2} = \text{MMM II \& MIM III}$$

Instar III and IV: Similar to instar II.

Instar V: Adjusted mass range is MMM instar IV to MTM.

Larval growth curves (biomass gain per unit time) for dicosmoecine populations examined in western Oregon appear to conform to a logistic model (Kaufman 1981). This curve

is characterized as being sigmoid in shape, to be somewhat symmetrical about the inflection point, and to rapidly approach an asymptote with time. The asymptote for our data would be the point in time that most of the population enters the resting V stage (MMM). After this point, biomass decreases because of loss due to respiratory costs of the resting V stage.

Habitat Association

Habitat association records specify the number of separate locales where collection data indicate a verified species association of larvae or pupae with a particular habitat type. Adult records are also included when data indicated that collections were made adjacent to a habitat type. Habitats are defined as follows (streams at mean summer discharge):

TS= temporary stream
SS= small streams of less than 1 m mean width.
MS= mid-size streams of 1-4 m mean width.
LS= large streams of 4- 10 m mean width.
SR= small rivers of 10-20 m mean width
RI= rivers of greater than 20 m mean width
LK= lake
PD= pond
TP= temporary pool
MA= marsh

Sampling Methodology

Qualitative population samples of several species were taken about twice a month at a number of study sites. Extensive preliminary surveys were made to obtain sites within a watershed where a given species was most abundant.

Within these habitats, study reaches varying from hundreds of meters to over a kilometer in length were established. At each sampling date, all microhabitats were examined to determine the relative proportion of the population in each type. Representative larval samples were hand-picked from substrates. The number of specimens collected is reported for each species. Sample size was limited for several species in some habitats to prevent local extinction.

LIFE HISTORIES OF THE GENUS DICOSMOECUS IN WESTERN OREGON,
USA, WITH A REVIEW OF LIFE HISTORY PARAMETERS

Introduction

Dicosmoecus spp. are large, common caddisflies inhabiting western North America and northeastern Asia. Recent advances in systematics have clarified the species status of adults and larvae within the genus and elucidated the life history patterns of D. atripes and D. gilvipes (Wiggins and Richardson 1982). Wiggins and Richardson demonstrated broad differences between the two species in terms of diet, habitat, elevational and geographic range, voltinism patterns, and seasonal timing of various life stages. They proposed that D. atripes represented the generalized condition for the genus with a 2-year life cycle and omnivorous trophic behavior, while the univoltine cycle and herbivory of late-instar D. gilvipes larvae was a remarkable shift to a specialized condition.

Although the existence of univoltine populations of both species has been suggested (Gotceitas and Clifford 1983, Hauer and Stanford 1982, Wiggins and Richardson 1982), no site-specific life-history data are available to confirm this. We report here on studies in low elevation, maritime watersheds (Flynn Creek and Big Elk River) of the Oregon Coast Range (Figures 1, 3 and 4; Table 3), where both D. atripes and D. gilvipes have obligate univoltine life cycles.

Methods

Site characteristics for the Flynn Creek and Big Elk River watersheds are provided in the introductory chapter of this series. D. atripes was found in low to moderate numbers at Flynn Creek but was absent at the Big Elk site. It occurred where Flynn Creek had moderate gradient, sand-gravel substrates and was shaded by a dense riparian canopy. Life cycle information was derived from qualitative samples taken from December 1980 through October 1982. Larval and pupal collections were made by a thorough search of microhabitats over a 0.5 km stretch of the stream. The numbers of larvae and pupae collected per month ranged from 6 to 33. Care had to be exercised in limiting the numbers collected, so as not to cause local extinction.

D. gilvipes was abundant at the Big Elk River site, and 20-100 larvae or pupae were collected monthly from May 1981 to September 1982. Several population samples were taken from other sites in western Oregon on different dates to illustrate variability in the development rate of different populations.

Results and Discussion

Life Cycle, Trophic and Case Building Behavior of Dicosmoecus atripes at Flynn Creek

D. atripes had a univoltine life cycle in Flynn Creek (Figure 5). First and second instars appeared in the stream in December-January. Larvae proceeded through all larval

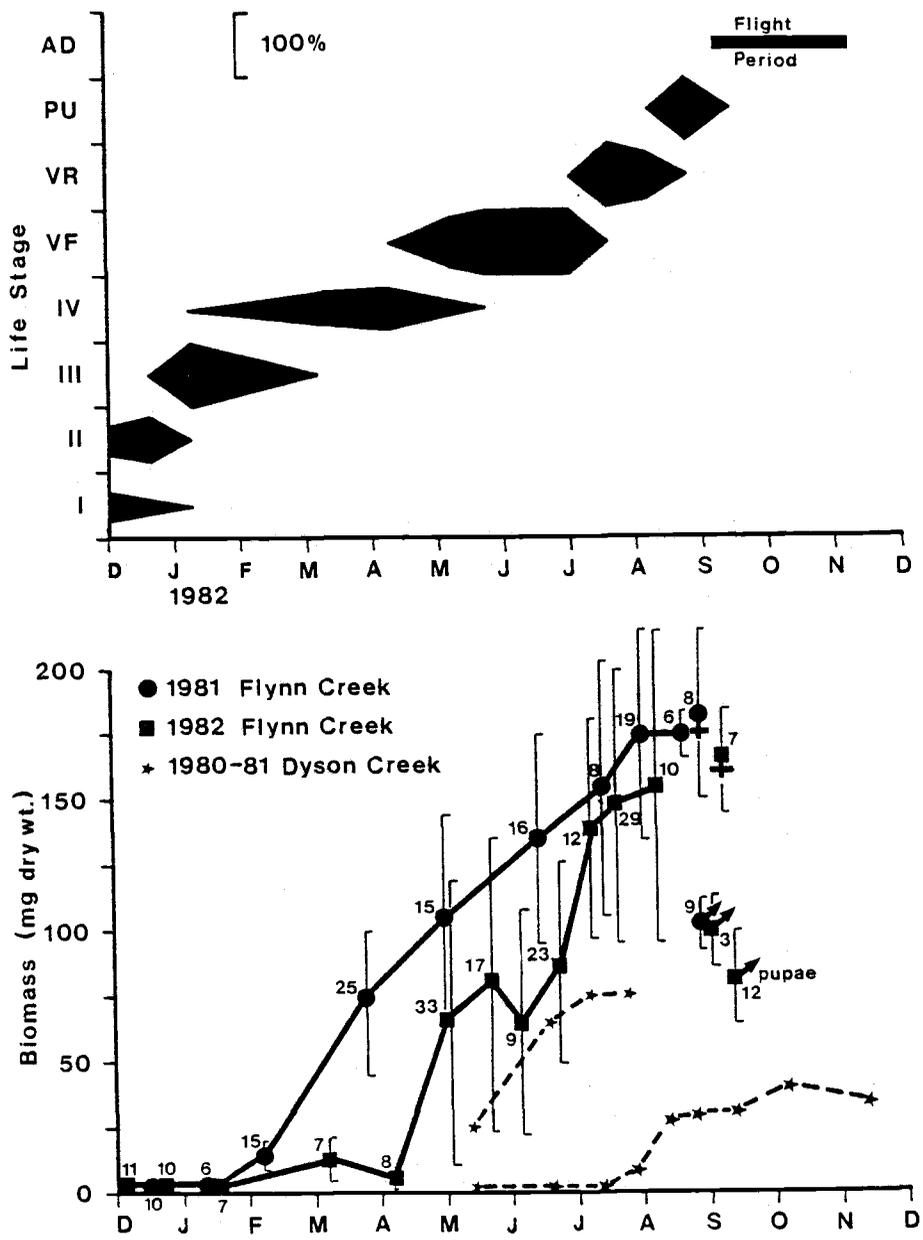


Figure 5. Growth and development of *Dicosmoecus atripes* at Flynn Creek, Oregon Coast Range. Mean larval biomass (n, + S.E.) are shown. Mean male and female pupal biomass also provided. Life stage data is for 1982, Flynn Creek. Comparative biomass data from Dyson Creek, Alberta is also shown (Gotceitas and Clifford 1983).

stages rapidly, with the entire population achieving the final instar by mid-May. Growth of instar V proceeded rapidly from mid-May to early July. By mid-July most larvae had ceased feeding and tied their cases to large woody debris or on the occasional large cobble present in the stream. These resting V larvae were often found in aggregations, as is typical for the genus (Anderson 1976, Gotceitas 1985).

The resting stage of instar V was short, with transformation to the pupal stage occurring in late-July and early August. Pupae were found throughout August and into early September. Adults appeared by August 25, with flight continuing to November 9. Adults captured in UV- light traps placed near the stream were mostly males.

Gut-content analysis indicated that late-instar larvae were predaceous (Table 4). Larvae also have been observed feeding on patches of filamentous algae, leaves and catkins, fish carcasses, and breaking into sealed cases of caddis including those of other D. atripes. Trichoptera fragments were dominant items in the guts examined. The most common prey items were Apatania sorex (39%) and Lepidostoma spp. (23%). One caddis egg mass was also recorded in a gut. Vagile taxa, such as Plecoptera and Ephemeroptera, were rarely found.

Classification of D. atripes as an opportunistic omnivore in the later instars agrees with the results

TABLE 4. Gut contents of instar IV and V larvae of Dicosmoecus atripes at Flynn Creek, Oregon Coast Range. Insect fragments were dominant in 25 of 26 guts examined.

CONTENTS	# CONSUMED	FAMILIES (decreasing order of abundance)
Trichoptera larvae-pupae	119	Limnephilidae, Lepidostomatidae, Uenoidae, Calamoceratidae, Psychomyiidae, Glossosomatidae, Brachycentridae
Diptera larvae-pupae	23	Chironomidae, possibly Simuliidae, Tipulidae
Terrestrial Insects	2	Coleoptera, Formicidae
Ephemeroptera	1	unknown
Plecoptera	1	unknown
Wood fragments	abundant	Probably caddis case material
Sand grains	common	Probably caddis case material

reported by Wiggins and Richardson (1982). Guts of instars I-III were not examined, but Gotceitas and Clifford (1983) found a shift in diet from diatoms to animal tissue between early and late instars in an Alberta stream.

A shift from predominantly organic cases to mineral cases was observed for the Flynn Creek population as has been reported by Wiggins and Richardson (1982) and Gotceitas and Clifford (1983). This shift occurred in instars IV and V during April-May. Larvae with predominantly mineral cases had enough ballast to be able to cross fine gravel substrate in moderate currents without being dislodged, but they were not able to withstand higher current velocities.

No eggs of D. atripes have been recovered from any western Oregon site. It is presumed that oviposition occurred between September and November (adult flight period), and that incubation was direct. First- and second-instar larvae were found as early as mid-December.

Life Cycle, Trophic Behavior and Habitat Association of Dicosmoecus gilvipes

The D. gilvipes population had a univoltine life cycle in both 1981 and 1982 (Figure 6, Table 5). First-instar larvae were present in the river by mid-January (1982 data), the earliest date sampled. By mid-March, larvae of instars I-IV were present, and by mid-May the population consisted mostly of final-instar larvae. By July 6, virtually the entire population had tied up and entered the resting phase.

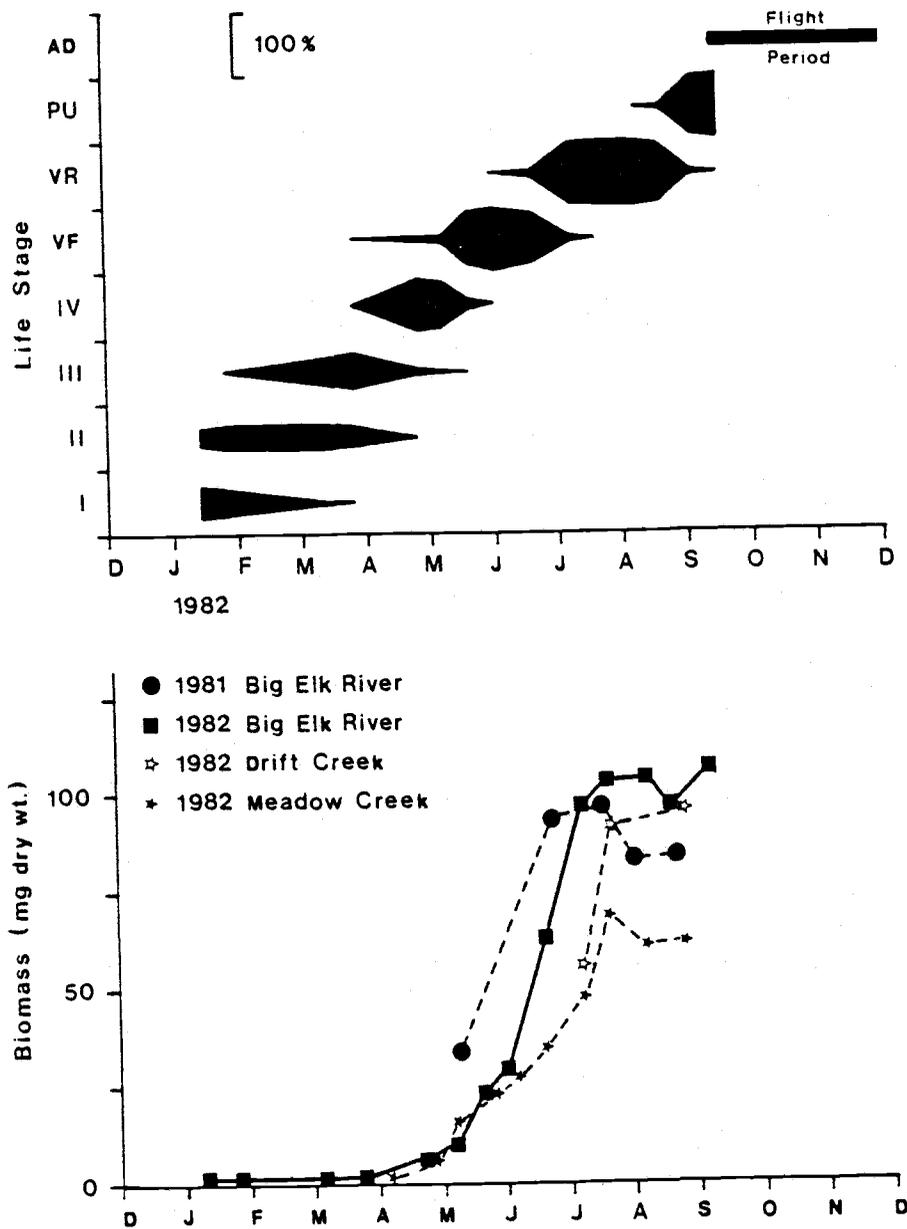


Figure 6. Growth and development of Dicosmoecus gilvipes in the Oregon Coast Range. Mean larval biomass at three sites is shown. Life stage data is for the Big Elk River population in 1982.

This interval lasted from early July to about the end of August. The first pupae appeared in the August 19 samples, but it was not until September 2 that most of the population had molted to pupae. Pupae could be found until the end of September. Adults were observed at the river from mid-September to the end of November. Eggs of *D. gilvipes* have not been recovered at field sites in western Oregon.

During the winter and early spring, larvae at the Big Elk occurred along the stream edge and in backwaters associated with detritus, moss, and mineral substrates. These larvae had cases constructed of organic matter, and presumably fed chiefly on detritus. A similar type of case and feeding behavior were found by Hauer and Stanford (1982) in the Flathead River, Montana population.

As spring progressed, late-instar larvae were found increasingly on mineral substrates towards mid-stream, and to have incorporated more mineral particles into their cases. This shift in microhabitat preference and the associated diet change from detritivory to herbivory (scraping of rock surfaces) occurred in April and May. Increase in migration appeared to be directly correlated with decrease in stream discharge and consequent lower mid-stream current velocities (Figure 3). The onset of this migration differed in the springs of 1981 and 1982 (Figure 6), with an earlier start in 1981 due to an unusually low-discharge pattern in the winter (Figure 3). Migration to

mid-stream microhabitats was complete in both study years by mid-May.

Variation in Larval Growth Patterns in the Oregon Coast Range

Differences in the timing of rapid growth periods between years for both Dicosmoecus atripes and D. gilvipes appear to be better explained by flow conditions rather than by temperature differences. The 1981 water year was characterized by early peak flows from late November to mid-January. After that time there were no spates significant enough to cause major redistributions of benthic substrates (Figure 3). In contrast, in 1982 both the Big Elk River and Flynn Creek were impacted by several high-water events that caused redistribution of many substrate types from December through April. The interval of rapid growth in 1982 was delayed about 4 weeks compared with 1981. This delay, for cohorts of both species, can be attributed to the disruptive effects of spates on foraging efficiency.

Growth patterns of D. gilvipes at other Coast Range sites are compared with those at Big Elk in Figure 6 and Table 5. Meadow and Drift Creek (4th and 5th order sites, respectively) are downstream of the Flynn Creek watershed. The open, low-gradient, Meadow Creek site had few large, mineral substrates for scraping, and contained a population stressed by high summer maximum temperatures. The growth rate was similar to that of the Big Elk population until

early June. Thereafter the growth rate fell off considerably. Though some larvae at Meadow Creek did complete growth, their final biomass was low and mortality was high, both as resting fifth instars and as pupae. The shift in timing of growth at the Drift Creek site cannot be explained because no site-specific temperature nor discharge data are available.

In addition to riverine habitats, D. gilvipes females sometimes oviposit in small, temporary lentic bodies of water. Larvae were found at Flynn Creek in several ditches and temporary pools near the stream from February to May 1982. Substrates in these pools were exclusively detrital. Mineral substrates supporting algal growth were not found. Here, larvae grew and developed up to the final instar by early May, with a biomass as great as 15.3 mg (dry weight). No larvae were found after this, and the populations in these temporary habitats died out. The occurrence of final instars in these habitats illustrates the capacity of larvae to grow and molt to instar V on a detrital diet (Hauer and Stanford 1982, Wiggins and Richardson 1982).

Body Size Differences Between Populations

Head-capsule widths of Dicosmoecus atripes at Flynn Creek are substantially greater than those reported elsewhere (Table 6). The final biomass of instar V larvae at Flynn Creek is more than twice that reported by Gotceitas and Clifford (1983) for an Alberta population (Figure 5).

TABLE 6. Head capsule widths (mm) of Dicosmoecus atripes larvae. Flynn Creek, Oregon Coast Range larvae are compared to widths found by Gotceitas and Clifford (1983) for an Alberta population, and those reported by Wiggins and Richardson (1982) from larvae taken throughout western North America.

INSTAR	FLYNN			ALBERTA		W. NORTH AMERICA	
	n	\bar{X}^*	RANGE	\bar{X}	RANGE	\bar{X}	RANGE
I	9	0.56	0.58-0.60	0.51	0.48-0.55	-	-
II	13	0.79	0.78-0.86	0.73	0.67-0.81	-	-
III	8	1.15	1.16-1.28	1.11	0.90-1.22	1.0	0.85-1.2
IV	27	1.75	1.76-2.00	1.48	1.31-1.64	1.5	1.2- 1.7
V	172	2.53	2.40-2.88	1.99	1.76-2.19	-	1.7- 2.5
V-male	-	-	-	-	-	1.9	
V-female	-	-	-	-	-	2.1	

X* Flynn Creek larvae were measured across the widest part of the head capsule when viewed dorsally, in contrast to across the eyes by the other authors. An adjustment factor of ca. -5% was applied to the Flynn Creek data.

TABLE 7. Head capsule widths (mm) of Dicosmoecus gilvipes larvae. Big Elk River, Oregon Coast Range larvae are compared to widths found by Hauer and Stanford (1982) for a Montana population and those reported by Wiggins and Richardson (1982) for larvae taken throughout western North America.

INSTAR	BIG ELK RIVER			MONTANA		W. NORTH AMERICA	
	n	\bar{X} *	RANGE	\bar{X}	RANGE	\bar{X}	RANGE
I	71	0.41	0.42-0.46	0.46	0.40-0.57		
II	75	0.56	0.56-0.66	0.72	0.64-0.82		
III	84	0.82	0.78-1.00	1.04	0.89-1.17	0.85	0.75-1.0
IV	88	1.19	1.16-1.40	1.37	1.31-1.47	1.3	1.1-1.5
V	189	1.78	1.68-2.16	1.68	1.57-1.74	1.8	1.5-2.2

X* Big Elk River larvae were measured across the widest part of the head capsule when viewed dorsally, in contrast to across the eyes (Wiggins and Richardson 1982). An adjustment factor of -7.2% was applied to the Big Elk data.

Populations of D. gilvipes are more similar in head capsule width throughout its range (Table 7).

Comparisons of Adult Phenology Between Coast Range and Other Western Populations

When the phenology of D. atripes and D. gilvipes ovarian development was compared, it was evident that egg maturation and oviposition is more rapid in the former species. Pharate females of D. atripes (n= 4) were found to have nearly mature eggs (Stage C), and 56 field collected females from various locales had either mature eggs, or had deposited an initial mass (Table 8).

Pharate females of D. gilvipes (n=2) were in stage B of ovarian development, while early season females were predominantly stage B or C. It was not until somewhat later in the flight season that dissections revealed that most females had deposited an initial egg mass. This may indicate that in D. gilvipes the pre-oviposition period is longer than in D. atripes.

In high elevation, interior and northern regions, peak flight activity of D. atripes occurs about a month prior to that of D. gilvipes (Table 9). Earlier emergence combined with rapid egg maturation and oviposition would appear to be an appropriate response to short-season situations found at high elevations and in colder climates.

An extension of the flight and oviposition period of both species in the Coast Ranges is evident (Tables 8, 9).

TABLE 8. Ovarian development stage of Dicosmoecus atripes and D. gilvipes. Females are from Oregon and Washington, derived primarily from UV light traps. See methods for description of stages.

OVARIAN STAGE	WEEK																
	JULY	AUGUST				SEPTEMBER				OCTOBER				NOVEMBER			
	4	1	2	3	4	1	2	3	4	1	2	3	4	1			
<u>D. atripes</u> C	3	1*	4*	5	2	8											
C-D		2*	1*	9*	1	10	6	2		2							
<u>D. gilvipes</u> B								3	5	3							
C								2*	4		2			1			
C-D								1*	3	6	8	3	27				

* Indicates records obtained from >1000 m elevation. The remaining records are from <1000 m elevation in the Oregon Coast Range and Western Cascades.

TABLE 9. Seasonal distribution of adult records of Dicosmoecus atripes and D. gilvipes in western North America. A single record is for one locale at one date.

PROVINCE	JUN	JUL	AUG	SEP	OCT	NOV
NW Coastal Ranges						
<u>D. atripes</u>	1	3	7	6	7	2
<u>D. gilvipes</u>		2	1	16	39	16
Interior & Northern						
<u>D. atripes</u>	1	28	105	52	6	
<u>D. gilvipes</u>		2	26	63	22	

Mature larvae have a long summer quiescence in coastal rivers and streams, thus it would seem that emergence and flight could occur much earlier. An explanation may be that it is advantageous to delay egg deposition in this region until late in the fall. The consequences of a delay would be to slow embryo development and larval eclosion from the egg mass, which may reduce mortality of early-instar larvae during a period when peak spates are most likely to occur.

Voltinism and Growth Patterns in Low and High Elevation Populations

Based on the data from the Oregon Coast Range, it appears that the seasonal discharge pattern is a primary factor in determining the growth pattern of univoltine populations of both species. Stream discharge may control foraging efficacy. The importance of stream discharge has not been recognized in areas where Dicosmoecus has a 2-year life cycle. The indirect effect of temperature in regulating snow melt (and thus discharge) may be as important in extending the life cycle as is its direct effect on growth.

In the Oregon Coast Range, D. gilvipes instar VF larvae accumulated approximately 90% of their final biomass during a 2.5 month period of low stream discharge and high water temperature in the late spring and early summer (Figures 3, 4 and 6).

From written descriptions and seasonal instar-histograms provided by Haeur and Stanford (1982), the biennial population of D. gilvipes present in the Flathead River, Montana (Northern Rocky Mountains) does not achieve instar VF until fall of its first year, just prior to low winter temperature regimes which induce quiescence. Larval migration to midstream habitats occurs in the summer of the second year after snow melt waters recede. It appears that instar VF larvae accumulate most of their final biomass in a similar 2.5 month period as the Oregon Coast Range population, but under a considerably cooler temperature regime. This indicates that the specific growth rate (SGR) of instar VF larvae in both populations may be similar. Attenuation to a biennial life cycle in the Flathead River would then appear to be due to a low SGR of instars I-IV during the first year, which places instar VF larvae past the window of favorable growth conditions for a univoltine life cycle.

In contrast, larvae of the biennial population of D. atripes in Dyson Creek, Alberta (Northern Rocky Mountains) achieve instar VF by early August of its first year and accumulate a significant portion of their final biomass before winter quiescence (Figure 5). Instar VF (period of most biomass accrual) spans a period of approximately 4 months, split about equally between years 1 and 2. The SGR of the biennial instar VF D. atripes would then appear to be

lower than for D. gilvipes. However progression from instar II to VF by D. atripes at Dyson Creek requires about 1.5 months in the first summer, as opposed to approximately 5 to 6 months for D. gilvipes in the Flathead River.

D. atripes instar VF larvae at Flynn Creek required approximately 4 to 5 months to achieve their final biomass, similar to the biennial populations at Dyson Creek (Figure 5). However, larvae at Flynn Creek had significant growth in the late winter and early spring of the first year, about 6 months prior to the Dyson Creek population. Delay in development for the Rocky Mountain population appears to be primarily due to an extension of the instar I stage, possibly in some form of quiescent state, until snowmelt waters recede in the first summer.

Geographical Ranges, Habitats, and Competition

Wiggins and Richardson (1982) provide an outline of the ranges of these two common western species. They note that D. gilvipes appears to be restricted to lower elevations than D. atripes, and that the latter species is much more widely distributed.

D. atripes is widely distributed in western North America up to the Alaskan-Yukon border (Wiggins and Richardson 1982). Within this region, the records are closely correlated with the montane provinces outlined in Figure 1, except that no records are available from the California coast ranges. When locale records are compared

with the distribution of coniferous forests in western North America we obtain nearly an exact fit. As stated in the introduction, the presence of coniferous forests in the western United States is indicative of where smaller perennial streams occur. This is the preferred habitat of the species, although it is also found in the littoral zone of high elevation oligotrophic lakes.

The northern extension of D. gilvipes is truncated (Wiggins and Richardson 1982). It is presumed that a thermal barrier even for biennial populations occurs in southern Canada. The lack of southerly extension into the Middle and Southern Rockies is curious, and may indicate a lack of suitable habitat or even the existence of geographical barriers to range extension for this species. D. gilvipes is principally a large-stream and small river species, particularly in the moist, maritime regions where dense overstory vegetation shades small and mid-size streams. In the more xeric regions of the western United States, it is commonly found in mid-size streams having light to moderate shading by vegetation. It appears to be excluded from lowland and basin areas of the western United States (Figure 1) where open streams and rivers reach high temperatures in the summer.

Dependence of late instar D. gilvipes larvae on herbivory may place constraints on range extension into northerly and high elevation regions, where low winter

temperatures inducing quiescence, combined with a snow melt hydrograph limit grazing efficacy and reduce algal production. Omnivory, as displayed by D. atripes, may be less subject to limitations induced by low temperature regimes and snow melt hydrographs. High quality food for predators and omnivores may be concentrated in backwaters and pools of small to mid-size streams during periods of moderate to high flow, while access to high quality algal resources on large mineral substrates in mid-channel riverine microhabitats is restricted.

Though D. atripes is not a competitor with D. gilvipes, Allocosmoecus partitus may be (Wiggins and Richardson 1982). D. gilvipes and A. partitus have similar life cycles, size, feeding habits, microhabitat use, and have nearly identical geographical and elevational distributions.

ALLOCOSMOECCUS PARTITUS IN WESTERN NORTH AMERICA

Introduction

Allocosmoecus Banks, 1943 is a monotypic genus which is sympatric with Dicosmoecus gilvipes. There exist similarities in size, larval morphology, case architecture, feeding behavior, and larval habitat use in these two species (Anderson 1976, Wiggins 1977, Wiggins and Richardson 1982). Adults bear a superficial resemblance to Dicosmoecus (Flint 1966; Schmid 1955, 1980), but characteristics of the genitalia suggest that the two genera are clearly distinct. Records are reviewed to further elucidate distributional patterns, habitat affinity, and life-history characteristics for A. partitus, and to compare these with patterns for D. gilvipes.

Results and Discussion

Geographical Distribution

Allocosmoecus partitus is largely confined to the Pacific Coast mountain ranges, from southern British Columbia to northern California, and in the Cascade-Sierra Nevada Ranges, from southern British Columbia to Lake Tahoe in California (Figure 1, Table 10). It is commonly encountered in the Coast and Cascade Ranges of Oregon and Washington. In the north it has penetrated the Rocky Mountains of Idaho and eastern Washington, but has not been found in the bulk of the Rocky Mountain Cordillera or in the

TABLE 10. Distribution and habitat associations of Allocosmoecus partitus in western North America. A summary of collection data. Adult (AD) and larval (LA) records are indicated by "+". Multiple records for a habitat class are indicated by numbers. SS= small stream (< 1m wide) MS= mid-size stream (1-4 m wide) LS= large stream (4-10 m wide).

STATE: County (# locales)	PROVINCE Region	AD	LA	HABITAT	REFERENCE
BC: (2)	1a	-	+	SS,MS	OSU-ROM
WA:Jefferson (2)	1b	-	+	MS2	ROM
OR:Clatsop (1)	1c	+	-	-	OSU
OR:Lincoln (4)	1c	+	+	MS4	OSU-ROM
OR:Benton (5)	1c	+	+	SS,MS4	OSU-ROM
OR:Curry (1)	1c	-	+	MS	OSU
CA:Siskiyou (1)	1e	-	+	LS	OSU
CA:Humboldt (1)	1e	-	+	-	HUM
WA:King (3)	2a	-	+	MS3	OSU-ROM
WA:Pierce (2)	2b	-	+	MS2	ROM
WA:Skamania (3)	2b	+	+	MS2,LS	OSU
OR:Hood River (2)	2c	+	+	MS,LS	OSU-ROM
OR:Clackamas (3)	2c	+	+	MS,LS	OSU-ROM
OR:Jefferson (3)	2c	+	+	LS2	OSU
OR:Linn (3)	2c	-	+	SS,MS2	OSU-ROM
OR:Lane (5)	2c	+	+	MS3,LS2	OSU
OR:Douglas (2)	2c	-	+	MS	ROM
OR:Jackson (1)	2c	+	-	-	OSU
CA:Siskiyou (1)	3	-	+	LS	OSU
CA:Shasta (4)	3	+	+	MS3,LS	OSU-ROM
CA:Plumas (1)	3	-	+	MS	ROM
CA:Nevada (1)	3	-	+	MS	ROM-UCB
WA:Ferry (1)	4	-	+	LS	OSU
ID:Kootenai (2)	8a	-	+	-	ROM
ID:Shoshone (1)	8a	+	-	-	CWU

Great Basin. It occupies a low to intermediate elevation range as does D. gilvipes.

A. partitus and D. gilvipes are sympatric, but the latter is somewhat more broadly distributed. D. gilvipes occupies more of the Rocky Mountain cordillera (Wiggins and Richardson 1982) and can be found in streams and rivers in more xeric areas, while A. partitus is confined to cool, forested, headwater drainages.

Larval Habitats and Microhabitats

Wiggins (1977) suggests that A. partitus is found in smaller streams than D. gilvipes. We found this to be the case in several stream systems examined in the Oregon and Washington Coast and Cascade Ranges. A. partitus occurred most abundantly in the mid-size stream class as defined here (68% of the records, Table 10), while D. gilvipes was dominant in large streams and small rivers. A zone of overlap was frequently observed between A. partitus and D. gilvipes populations in the same drainage.

In the Cascade Mountains we found A. partitus larvae associated with stream margin habitats during high water in late winter and early spring. In the late spring and early summer, when water velocities are more moderate, larvae migrate towards glides and runs in mid-channel where they scrape periphyton from larger cobble, boulder and bedrock surfaces. They are not associated with shallow riffle or cascade habitats. When growth is completed in mid-summer,

the larvae attach their cases to the underside of stones, often in aggregations, and aestivate through the remainder of the summer.

Preliminary observations indicate that there are no substantial differences between A. partitus and D. gilvipes in early- and late-instar seasonal partitioning of microhabitats.

Life Cycle

The developmental sequence for A. partitus, as assembled from records from throughout its range (Figure 7), is nearly identical to that of D. gilvipes as reported by Wiggins and Richardson (1982). We believe that environmental parameters such as discharge and temperature, as discussed for Dicosmoecus, operate in a similar manner on Allocosmoecus in determining growth and developmental patterns.

A. partitus appears to have a univoltine life cycle, with maximum growth occurring in the late spring and early summer, followed by a resting stage of variable length during the summer. Pupation occurs in the late summer or early fall, followed immediately by emergence. There appears to be a pre-oviposition period of a week or two, with adult flight continuing to mid-November. Oviposition and eggs have not been observed, though it is believed that incubation proceeds slowly over the late fall and winter.

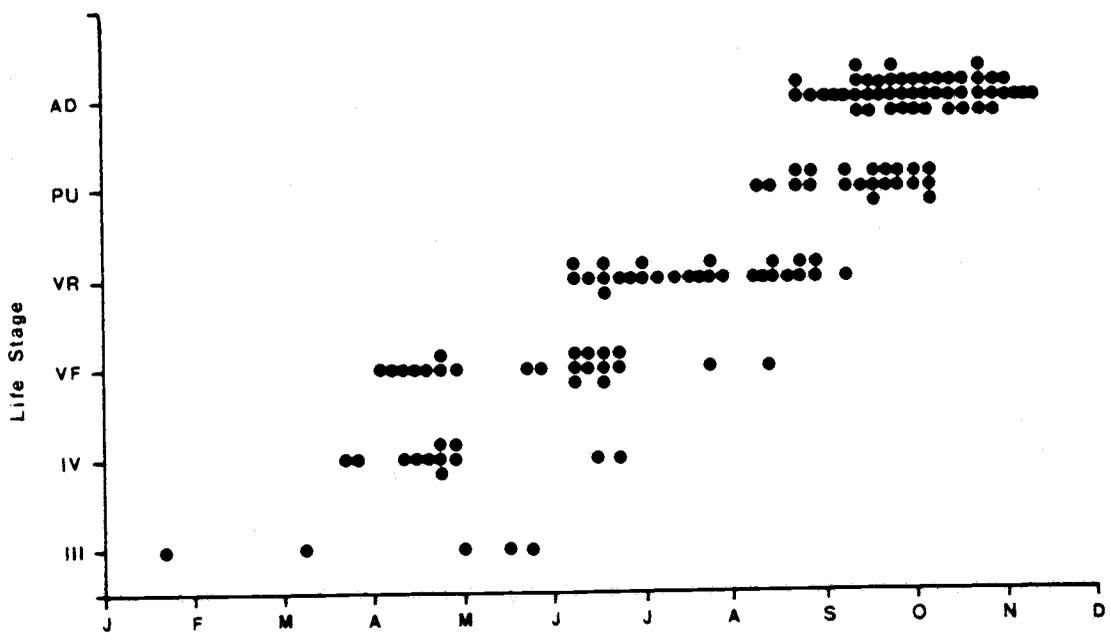


Figure 7. The seasonality of collection records for *Allocosmoecus partitus* life stages in western North America. Each dot represents one site at one date.

Early instar larvae have been collected in March from stream margin habitats in the western Cascades Mountains.

Conclusive evidence of a 2-year life cycle for any A. partitus populations has not been documented, in contrast to both univoltine and biennial populations having been reported for D. gilvipes (Hauer & Stanford 1982).

Ecological Segregation of A. partitus and D. gilvipes

Longitudinal zonation appears to be the primary parameter determining separation in these two ecologically equivalent species. Allocosmoecus is the largest invertebrate herbivore found in smaller, forested streams of western Oregon. Investigation into the mechanisms determining its successful occupation of this habitat where D. gilvipes fails would be of interest.

LIFE HISTORY OF ONOCOSMOECUS UNICOLOR IN A WESTERN OREGON
COAST RANGE STREAM

Introduction

Onocosmoecus is the most widely distributed genus in the subfamily Dicosmoecinae. It is found throughout the western and northern Nearctic and also in Siberia. Wiggins and Richardson (1987) have recently provided a review of the systematics of Onocosmoecus. Seven putative species were collapsed into two. The highly variable species, Q. unicolor, occupies the entire range of the genus, and Q. sequoia is found in the Sierra Nevada Mountains of California. Two additional species formerly placed into this genus, Q. frontalis and Q. schmidi, are not considered to be monophyletic and have been placed into genus incertum within the Dicosmoecinae (G.B. Wiggins, pers. comm.).

Wiggins and Richardson (1987) provide a synopsis of the range, seasonality of some life stages, habitat association, and trophic status for Q. unicolor, as determined from examination of specimens and records from throughout its range. Winterbourn (1971) provides limited life history information for Q. unicolor from Marion Lake, British Columbia, which appears to show a univoltine life cycle. Q. unicolor is an abundant detritivore in the Flynn Creek watershed of the Oregon Coast Range. It was studied as part of a larger project on the caddisfly community associated with woody debris in streams (Anderson 1978). In this

chapter, the life history of O. unicolor is described, with emphasis on larval growth and feeding behavior for comparison with other genera in the subfamily Dicosmoecinae.

Methods

Flynn Creek, Third-Order Site Description

A general site description for Flynn Creek is given in the introductory chapter (Table 3) and details of habitat conditions in the first-order tributaries are provided later in the Ecclisocosmoecus chapter.

Most research was conducted in the upper watershed of the third-order reach of Flynn Creek, which has a moderate gradient, and coarse sand to fine gravel as the dominant substrates. Large bole-wood is abundant and is important to the formation of various microhabitats as well as in the retention of allochthonous detritus. The annual hydrograph and temperature regime are depicted in Figures 3 and 4.

The hillslope vegetation is primarily 75-150 year old Douglas-fir (Pseudotsuga menziesii), with deciduous trees (primarily alder, Alnus rubra) and shrubs (primarily salmonberry, Rubus spectabilis) providing a dense canopy along the stream. Detrital inputs are derived principally from the deciduous leaf litter, but conifer needles and small woody debris are also abundant.

The lower watershed has regrowth vegetation following clear-cutting of the forest. Only occasional samples were obtained from this area.

Detrital Microhabitats

Preliminary surveys in 1980 suggested that substrate type and the distribution of detrital accumulations were major factors governing the occurrence of many species of caddisfly larvae. To assess the microhabitat associations of the detritus-associated taxa, and especially *O. unicolor*, 8 categories of substrates were defined:

1. Sand-gravel. No overlying detritus present. This was the major substrate type during most of the year.
2. Large bole-wood. Stable logs and larger branches occurred in areas with slow to fast current velocities.
3. Debris jams. These usually formed behind, and on top of, large bole-wood spanning the channel. The composition was seasonal in nature, with branch wood found throughout the year, and leafy detritus abundant in fall and early winter.
4. Floating debris. Patches that formed in pools behind debris jams or in backwaters were composed mainly of twigs of salmonberry (see Wisseman and Anderson 1987).
5. Floating leaves. Freshly fallen leaves covered a high proportion of the stream surface in the fall before the rainy season commenced.
6. Stream edge leaves. These are single leaves or small leaf masses caught on the stream margin. This substrate was abundant throughout the fall.
7. Benthic leaves. Leaves that had become conditioned (Anderson and Sedell 1979) and waterlogged sank to the bottom of pools. Increasing stream flow in the late fall shifted the floating and stream edge leaves into this microhabitat. The quantity of benthic leaves steadily declined throughout late fall and winter.
8. Particulate drop zones (PDZ). Accumulations of particulate organic matter are concentrated by the current in pools and backwaters. Detrital composition varied spatially and temporally. Coarse wood, bark chips, twigs and conifer needles persist throughout the year, whereas leaf veins, leaf fragments, and catkins

are more ephemeral. PDZ materials were divided into fine (<1 mm), medium (1-10 mm), and large (>10 mm) fractions. The fines were present during summer low-flow, whereas the medium category was important in late fall and the larger fraction persisted throughout the year.

As general categories these microhabitats are predictable and occur from year to year in a seasonal pattern and with the same relative abundance. The actual residence period of a given microhabitat or substrate class depends on the timing and amount of winter rains. The number of storm events causing spates of sufficient magnitude to destabilize and redistribute the PDZ category is highly variable from year to year (Beschta et al. 1981).

Three 10 m reaches in the upper Flynn Creek watershed were established as study plots. The area covered by each substrate type was mapped using a 0.25 m quadrat with a 10 X 10 cm grid, on six occasions in the late summer, fall, and early winter. This was the approximate residence period of the leaf detritus microhabitats. Quantitative samples of each microhabitat-substrate type were taken monthly between July 29, 1981 and July 7, 1982. Q. unicolor larvae were sorted from the samples and head-capsule widths were obtained prior to their being dried and weighed. Detritus was thoroughly washed of all adherent mineral particles, dried and weighed. Data are expressed as numbers of larvae, or milligrams (dry weight) of larvae, per gram (dry weight) of detritus. Supplementary qualitative samples of the Q. unicolor population were taken throughout the Flynn Creek

basin and downstream watersheds along with the study plot sampling.

Results and Discussion

Flight Period and Eggs

O. unicolor adults are late-season fliers and a dominant component of light-trap collections in the west. In the Clearwater Valley, near Mt. St. Helens, Washington, they accounted for over 50% of all Trichoptera in a UV light-trap from mid-July to mid-September in 1985 (Anderson and Wisseman 1987). Wiggins and Richardson (1987) reported that the flight period over its entire range was from the end of June to late October, and Nimmo (1971) reports flight in Alberta starting in early May. We collected adults at Flynn Creek from late August to the end of November, which extends the total flight period to about 7 months.

Egg masses were collected at Flynn Creek from August 25 to the end of November. Several hundred masses were collected in the forested upper watershed, but only two in the downstream clearcut. They were on the undersides of branches and logs from 10 cm to 2 m above the stream surface. Masses were cylindrical, about 2 cm long and 0.75 cm wide. They were firmly attached to the substrate along their entire length. The mass was a clear gelatinous matrix with no surficial skin, containing straw-colored eggs (0.6-0.7 mm diameter) embedded in the matrix. The mean number of eggs per mass was 204 (n=22, range= 63-390). The masses

began to liquify after hatching, and first-instar larvae were "dripped" into the stream.

Since Q. unicolor egg masses occur out of the water, they are vulnerable to predation by Megaselia alsea, a phorid fly (Wisseman and Anderson 1984).

Larval Instars and Habitats

The five larval instars of Q. unicolor are clearly defined by head-capsule measurements (\bar{X} , range in mm): I 0.34, 0.32-0.36; II 0.52, 0.48-0.58; III 0.80, 0.68-0.90; IV 1.24, 1.04-1.44; V 1.84, 1.60-2.08; with n= 9, 21, 72, 133, 197 respectively. Larval development is asynchronous, resulting in several stages being present in a given interval at Flynn Creek. Wiggins and Richardson (1987) indicate that instars III to V occur in all months when records are combined over the entire range. At Flynn Creek, the residence period ranged from 4 months for instar I, to 9 months for instar V. Variability in development rates attributed to food and habitat conditions is discussed below under Growth Patterns. Despite the asynchrony in development, or the absence of a clearly defined progression of cohorts, there is no indication from the Flynn Creek data for other than a univoltine life cycle.

Q. unicolor was one of the most abundant caddisflies in the third-order segment of Flynn Creek. Larval density was less in the higher gradient, second-order reaches, and they were absent in the first-order tributaries. Larvae were

also common in the fourth-order downstream reaches. Based on the absence of egg masses in this area it appears that winter floods disperse the population from the third-order sections into the downstream reaches.

Figure 8 illustrates the seasonal occurrence of larvae in several detrital substrate classes. Data are presented as biomass and numbers of larvae per gram of organic substrate. Feeding larvae were almost exclusively associated with these detritus substrates. The relative proportion of instars present at each sampling date is depicted in Figure 9.

A seasonal progression in the types of detrital microhabitats occupied was evident. Larvae preferred leafy substrates when they were available. Larval abundance in debris-jam leaves was low because these leaf packs were on protruding wood in swift water. Refractory detritus (CPDZ) was continuously present but *Q. unicolor* larvae did not forage in this habitat until leaf material had been exhausted or flushed from the stream. Numbers and biomass of *Q. unicolor* rose steadily in the CPDZ over winter.

Egg hatch and the appearance of early instars coincides with autumn leaf drop. Instars I-IV were found almost exclusively in leafy microhabitats, while foraging fifth instars were most abundant in the drop zones. This apparent partitioning of habitat is explained by the ephemeral nature

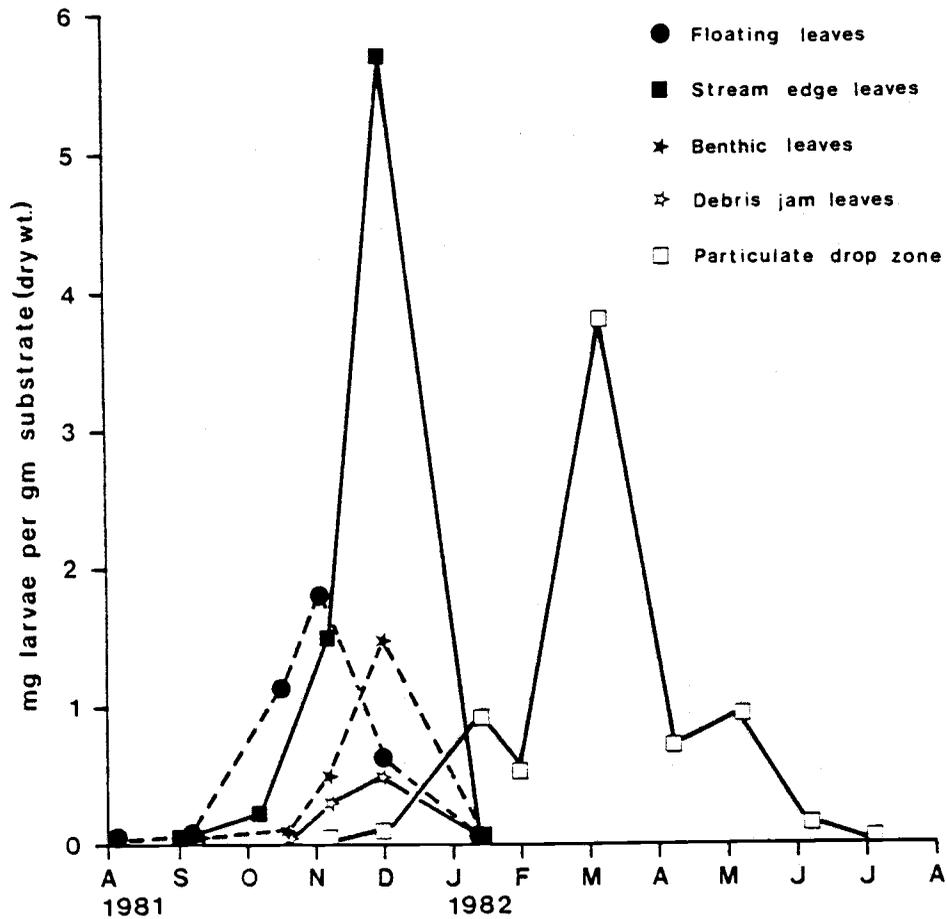


Figure 8. Biomass of *Onocosmoecus unicolor* larvae per gram of substrate derived from five detrital microhabitats at Flynn Creek, Oregon Coast Range.

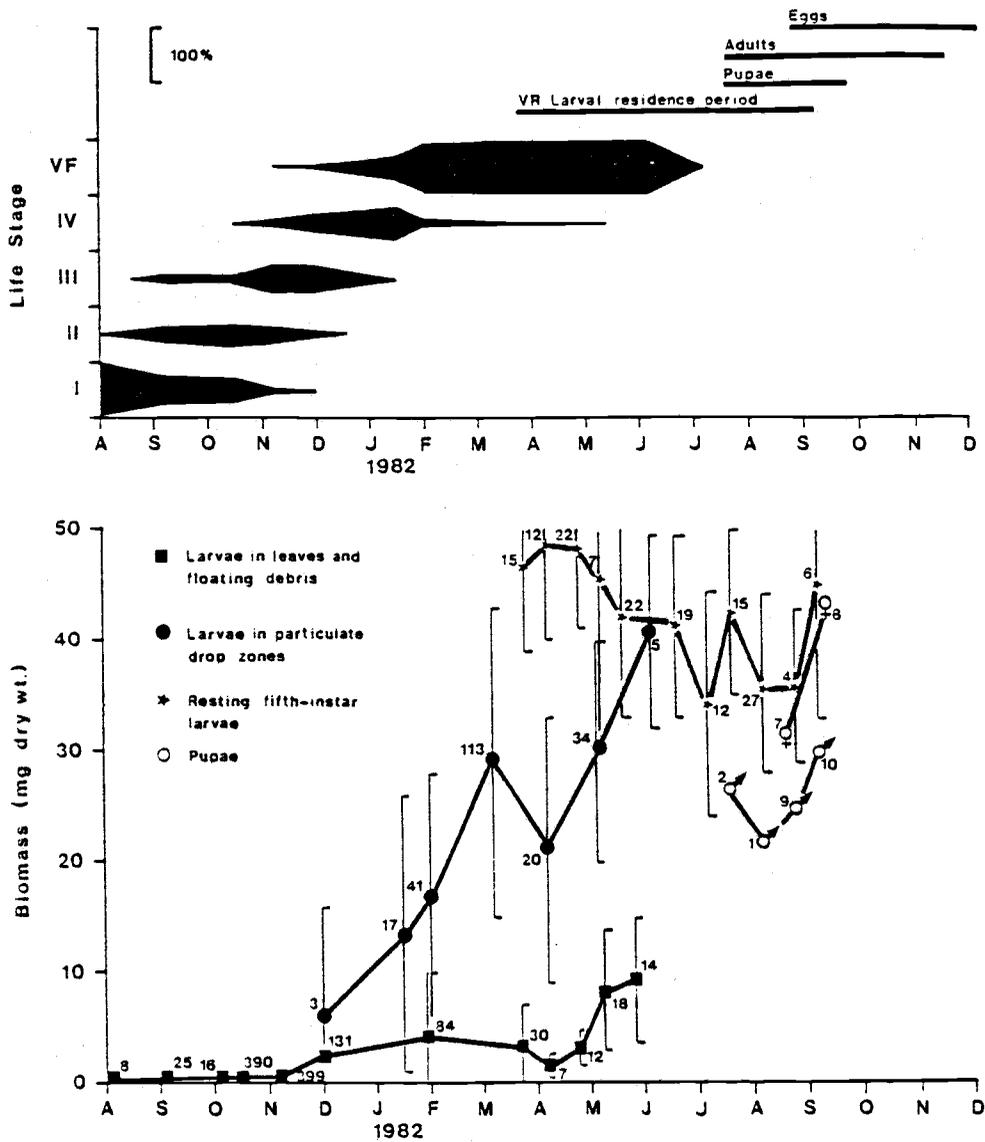


Figure 9. Growth and development of *Onocosmoecus unicolor* at Flynn Creek, Oregon Coast Range. Mean biomass (n, + S.E.) of larvae in different microhabitats is shown. Percent composition of the five larval instars (feeding larvae) at each date, and residence period of instar VR, pupae, adults and eggs is shown above.

of leafy substrates, and the persistence of drop zones throughout the year.

Larval Case Architecture

Case architecture and composition may be manipulated by some detritivore caddis larvae to change case size, form, and specific gravity to facilitate larval ability to track food resources that are seasonally ephemeral and patchily distributed. At Flynn Creek detrital inputs occur as seasonal pulses (e.g. leaves in the autumn and catkins in the spring). Detrital accumulations are seasonally unstable, and subject to intermittent disruption by spates, entry into bedload transport, and subsequent deposition in drop zones after the water recedes. These patches may be widely separated in space by sand or gravel in areas of moderate current. Observations on the caddis community at Flynn Creek indicate that only large larvae with robust cases, as found in several limnephilid species, were able to crawl on the bottom in areas of moderate current.

Q. unicolor case architecture changes in concordance with the shifting seasonal detrital microhabitats and the progression of instars. Larvae construct cases of two styles with transitional forms linking the two. The buoyant-drifting case is a random patchwork of detritus surrounding a central tube. Materials used are highly variable, and include leaf fragments, bits of bark or wood, twigs arranged as vanes, and small amounts of other types of

debris. The smooth-crawling case is found in larger, instar VF larvae. It is a smooth, slightly tapered and curved tube of flat chips of wood and bark (Wiggins 1977).

Early instar larvae in floating or stream-edge leafy microhabitats construct buoyant-drifting cases, often incorporating vanes of salmonberry twigs into their cases. These twigs are pithy, and float for months before sinking upon becoming waterlogged. As was found for Cryptochia pilosa, incorporation of salmonberry stems into the case allows larvae to float at the surface (Wisseman and Anderson 1987). Buoyant cases allow larvae to be passively transported by the current to detrital patches containing food resources, especially during high-water conditions. Cases mimic detrital particles used as food, drifting and settling into detrital depositional areas in a similar manner.

Water levels moderate in late winter or spring. Late instar larvae construct smooth-crawling cases to facilitate active foraging. These larvae, in heavier, smooth cases, can search by crawling for rare and patchily distributed food items of high quality during intervals of lower discharge.

Feeding Behavior

Wiggins and Richardson (1987) classify O. unicolor as a shredder, but they note that some larvae examined were exceptions. Winterbourn (1971) examined 33 O. unicolor

larvae at Marion Lake, British Columbia, and found sediment and animal fragments in the guts. Cowan et al. (1983) found plant detritus, with traces of animal fragments and diatoms in guts of larvae examined from interior streams in Alaska.

Guts of early instar larvae from leafy microhabitats at Flynn Creek contained nearly 100% leaf fragments, with traces of mineral particles and occasional animal fragments. These larvae were detritivores or leaf shredders. Guts of larvae taken from particulate drop zones most often contained vascular plant tissue derived from either leafy or woody substrates. Animal fragments were present in a significant proportion of the guts examined.

In the fall aggregations of O. unicolor larvae were observed feeding on salmon carcasses stranded in the stream. Similar concentrations of larvae were found on alder catkins in the spring, patches of filamentous algae, drowned terrestrial arthropods, senescent skunk cabbage leaves, and even luncheon meat thrown into the stream by moss gatherers.

At Flynn Creek, O. unicolor is predominantly a detritivore when high quality leafy substrates are abundant and accessible in the fall. They become increasingly omnivorous in the fifth instar and when leaves become scarce in the winter and spring. The change in foraging strategy mentioned above reflects a change in the food resources consumed. The shift from detritus feeding to higher quality

foods in the final instar is characteristic of many caddisflies (Anderson and Cargill 1987).

Larval Growth Patterns

Seasonal cohort progression was highly uneven in the Flynn Creek population of *Q. unicolor* (Figure 9). The residence period of instars in the stream varied from about 4 months for instar I to over 9 months for instar V. The increase in mean biomass from October to May of a group of larvae collected in detrital substrates was 30 mg. The mean biomass of larvae that had achieved their final mass and burrowed into the stream bottom ranged from 35-45 mg. Resting larvae were common from late March until early September. In the lower watershed larvae of instars III to IV were present in floating debris through May, at which time they disappeared from this microhabitat, and all remaining larvae in the stream were instar VF in drop zones or VR larvae.

Quiescent Larvae, Prepupae and Pupae

The residence period of instar VR larvae in Flynn Creek was from mid-March to September. These larvae were mostly found burrowed several cm in coarse-sand and fine-gravel areas of the stream bottom. They also were found wedged in crevices of bole wood in the stream. Resting larvae in streams with rocky substrates have been found attached to the underside of cobble.

Burrowed larvae were inactive, but did not seal their cases. A garden rake was used to stir the top 10 cm of sediments, and this allowed the current to lift larvae in their organic cases up to the surface. These larvae became active after several minutes and reburrowed into the stream bottom. Quiescent larvae can thus regain suitable pupation microhabitats if the stream bottom is disturbed.

Burrowed larvae and resting larvae wedged in wood do not seal their cases until just prior to pupation. They then tie a silk faceplate across the anterior opening, adopt a prepupal pose, and molt to the pupal stage within several days. The burrowed and wedged larvae shown in Figure 8 are resting instar V. They have attained their maximum weight, have ceased feeding, and have moved to a microhabitat where they remain inactive until pupation. True diapause is not evident in O. unicolor instar VR larvae at Flynn Creek. The quiescent phase may be important in synchronizing adult emergence in local populations.

Pupae were collected from late-July to early-September at Flynn Creek, in the same microhabitats as instar VR larvae.

Life History Strategy of Onocosmoecus unicolor

O. unicolor is the most widely distributed dicosmoecine in North America and within a single watershed it is the most variable species with respect to rate of larval development. The exceptional expansion in the residence

periods of all life stages compared with other univoltine limnephilids fits with the concept of "spreading the risk" as an adaptive strategy in a changing environment (Andrewartha and Birch 1984).

The life history pattern displayed by Q. unicolor at Flynn Creek can be viewed as a response to the predictable pattern of leaf inputs (late summer through fall) but whose duration in the system is unpredictable. The annual hydrograph at Flynn Creek is characterized by fall-winter peaks. However the onset, frequency and magnitude of individual storm events that will cause major redistribution of the substrates and flush leafy debris from the system is highly variable.

Early instar larvae are recruited to Flynn Creek over an extended period (late summer and fall). Fresh leaf detritus is abundant and accessible with little energetic cost through passive dispersal mechanisms. Spates eventually reduce the abundance and availability of food items, and deposit them in drop zones of pools or into flotsam behind debris jams. In intervals between spates, additional inputs of high quality food items (e.g. alder catkins) may be found scattered on the sandy bottom in areas of higher current.

Q. unicolor is one of a half-dozen abundant detritivorous or omnivorous species with cohorts of rapidly growing larvae moving into a period of winter-spring

resource limitation, or "crunch" period (Wiens 1976, 1977). Q. unicolor is unique in having a highly uneven cohort which is capable of efficient utilization of all remaining detrital microhabitats present. This is analogous to uneven cohorts present in some aquatic predator species, which is thought to be advantageous in allowing the exploitation of heterogeneous prey sizes (Hynes 1961, Wevers and Wisseman 1987).

AMPHICOSMOECUS CANAX IN WESTERN NORTH AMERICA

Introduction

Amphicosmoecus canax (Ross) 1947 is a monotypic genus known only from western North America. Originally placed into Dicosmoecus, Schmid (1955) later elevated it to generic rank on the basis of specialized male genitalia. Schmid (1980) described the female and Wiggins (1977) provided the first larval association. The larvae resemble those of Onocosmoecus (sensu stricto after Wiggins and Richardson 1987), and construct a case of wood fragments as does Onocosmoecus. Wiggins (1977) summarizes the limited amount of biological information available on Amphicosmoecus canax. The pupa remains to be associated and described.

Published accounts and unpublished museum records were reviewed to provide a synopsis of data on distribution, flight period, and larval habitat for this uncommon genus.

Results and Discussion

Table 11 summarizes distributional and biological information available for Amphicosmoecus canax. The species is most common in the Rocky Mountains from northern New Mexico to southern British Columbia and Alberta. Larvae have also been collected from lakes in Saskatchewan. In the central portion of its range, the species exists in isolated pockets to the west of the Rockies in the Great Basin and in the Central Mountains of Oregon. As discussed by Wiggins

TABLE 11. Distribution and habitat associations of Amphicosmoecus canax in western North America. A summary of collection data. Adult (AD) and larval (LA) records are indicated by "+". Multiple records for a habitat class are indicated by numbers. MS= mid-size stream (1-4 m wide) LS= large stream (4-10 m wide) SR= small river (10-20 m wide) LK= Lake.

STATE:County (# sites)	PROVINCE Region	AD	LA	HABITAT	REFERENCE
CA:Plumas (1)	3	-	+	-	ROM
CA:Nevada (2)	3	+	-	MS	OSU-ROM
CA:*Yosemite (1)	3	-	+	SR	ROM
CA:*Sequoia (1)	3	-	+	-	ROM
OR:Grant (1)	6	+	-	-	Anderson 1976
OR:Baker (1)	6	-	+	MS	OSU
OR:Klamath (1)	7b	-	+	LS	Anderson 1976
OR:Harney (1)	7b	-	+	LS	Anderson 1976
BC:*Yoho & vic. (3)	8a	+	+	MS2,LS	ROM
BC:**southern (7)	8a	+	+	MS,LS,SR	Nimmo & Scudder 1978, 1983
ALTA: (2)	8a	+	-	-	ROM,Nimmo 1965
ALTA:Waterton (2)	8a	+	-	-	Nimmo et al. 1976
MT:Lincoln (1)	8a	+	-	LS	OSU
MT:Lake (2)	8a	+	-	LS	ROM
MT:Gallatin (1)	8a	-	-	SR	ROM
ID:Bingham (1)	8a	+	-	MS to	Newell &
ID:Bonneville (1)	8a			SR	Minshall 1977,
ID:Custer (4)	8a				1979
ID:Fremont (2)	8a				LaFontaine
ID:Kootenai (1)	8a				1981
ID:Lemhi (2)	8a	+	-	-	CWU
ID:**southeast	8a				Smith 1965,CWU
WY:Teton (1)	8b	-	+	SR	ROM
UT:Cache (1)	8b	+	-	-	Ross 1947
UT:Salt Lake (1)	8b	+	-	LS	CWU
CO:Lake (1)	8c	-	+	SR	Hermann 1985
NM:Santa Fe (2+)	8c	-	+	MS	Molles 1982
SASK (2)	11	-	+	LK	Wiggins 1977

*= National Park

**= Region of state or province, county unknown.

(1977), the species appears to be very local in distribution with larvae never being found in great abundance.

Except for two lake records, all collections are associated with cold, moderate gradient, montane streams and small rivers (Table 10). Larval and adult records are about equally distributed between small stream, large stream, and small river habitats. A. canax is listed as a detritivore (shredder) by Wiggins and Mackay (1978), however no published accounts of gut contents are available. Wiggins (1977) has suggested a univoltine life cycle based on collection records, but this remains to be confirmed. An unusual case form, consisting of a hollowed-out twig, was reported for some larvae collected (Wiggins 1977). Like other large western dicosmoecines, this species is a late season flier, with flight records from September 13 to November 4. There are questionable records of adults in July, August, and February.

The basic biology of A. canax remains to be elucidated. Larval and case morphology, plus habitat association suggests a life history pattern similar to Onocosmoecus unicolor. The two species are sympatric, though O. unicolor is much more widely distributed.

DISTRIBUTION, POPULATION VARIATION AND LIFE HISTORY PATTERNS
OF ECCLISOCOSMOECCUS SCYLLA IN WESTERN NORTH AMERICA

Introduction

Ecclisocosmoecus Schmid, 1964 is a genus of two species in the subfamily Dicosmoecinae: E. spinosus Schmid, 1964 is known from Sakhalin (Siberia), and E. scylla (Milne) 1935 from western North America (Wiggins 1975, 1977). No previous life history information is available on either species.

The life history of E. scylla at Flynn Creek in the Oregon Coast Range is outlined. Observations made on other populations in the Pacific Northwest are included to highlight intraspecific variability in life history patterns within this montane region.

Divergence in life history patterns, habitat and size of E. scylla is apparent when Coast Range and Cascade Range populations are compared from the southern portion of the species range. These montane populations appear to have become isolated from each other since the last glacial retreat by the presence of a broad, intervening valley lowland (Willamette-Puget Lowland).

Study Areas

Oregon Coast Range

Ecclisocosmoecus scylla is abundant in the first-order tributaries of the upper Flynn Creek watershed (Table 3, Figure 1). The drainage network consists of 50-75 annual

and perennial channels descending steep ridge sides to form the mainstem of Flynn Creek. Streambed substrates are derived from soft, porous sandstone. Gravel-cobble substrates predominate in the tributaries, but are interspersed with bedrock reaches on the ridge slopes, and sandy outwash areas in the mainstem valley floor.

Ridge tops bear an overstory of Douglas-fir (Pseudotsuga menziesii) in 75-150 year-old stands. The valley bottom overstory is dominated by red alder (Alnus rubra). Understory vegetation is dense, with salmonberry (Rubus spectabilis) being the predominant shrub.

Oregon Cascade Range

Populations of E. scylla were also examined at sites in the High Cascades between 1800-2000 m elevation (Table 3, Figure 1). The species is found in cold springs and streams of this recent volcanic terrain. Annual precipitation ranges from 150-200 cm, and falls mostly as snow between November and May. Heavy snowpack covers the area for about half of the year.

Tyee, Goose and Todd Creeks, 20-30 km west of Bend, Deschutes County, were examined on seven dates in the summers of 1982, 1983, and 1985. Tyee Creek, the principal site examined, emerges as a large, diffuse spring from porous volcanic rocks to form a 3-4 m wide stream of steep gradient. Riparian overstory is lodgepole pine (Pinus contorta), and understory vegetation is sparse. Moss is

abundant in and near the stream, particularly at the springhead.

Methods

Distribution and flight period data were obtained from published records (Anderson 1976; Denning 1951; Ellis 1978; Milne 1935; Nimmo 1986; Nimmo and Scudder 1978, 1983; Ross 1950; Ross and Spencer 1952; Vineyard 1982). These records were extended by collecting and examination of material in museum collections.

Monthly collections of larvae were made in several Flynn Creek tributaries from July 1981 to January 1983. At each site, larvae were hand-picked from the substrate, and sample size was usually limited to 20-40 larvae monthly to avoid depleting local populations.

Results and Discussion

Geographical Distribution and Population Variation

Ecclisocosmoecus scylla occurs in the Pacific Border Province from southeast Alaska to Oregon and in the Cascade Range from British Columbia to Oregon (Figure 10). It is not known from the drier interior regions of the western United States. This species is confined to cool headwater montane streams. It occurs from near sea level to at least 2000 m elevation.

The Oregon Coast Range adults were larger than those in the Cascade Range or more northerly populations (Table 12). Forewing lengths varied from 10.72 to 16.00 mm for males and

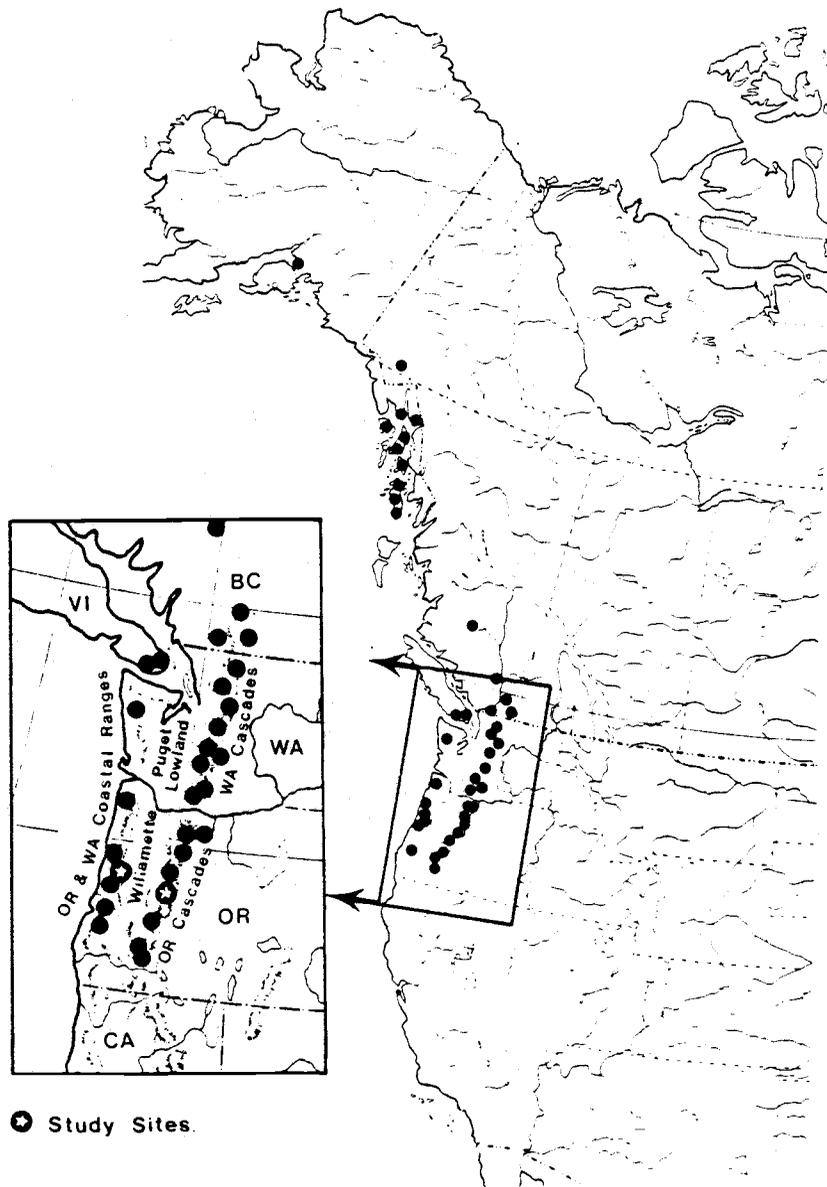


Figure 10. The distribution of Ecclisocosmoecus scylla in western North America.

TABLE 12. Forewing length and flight period of *Ecclisocosmoecus scylla* adults from different physiographic regions. Mean forewing length (n, + S.E.), range in wing length and first and last flight dates provided.

REGION		\bar{X} (mm)	RANGE (mm)	FLIGHT PERIOD
Southeast Alaska Coast Range	♂	12.57 (12, +0.53)	11.84-13.44	Jun. 7-Oct. 5
	♀	11.68 (4, +1.42)	10.08-12.80	
North Cascades and Washington Cascades	♂	12.61 (60, +0.58)	10.72-14.24	Jul. 24-Sep. 30
	♀	13.09 (11, +0.59)	11.84-14.24	
Western Cascades and High Cascades	♂	13.39 (60, +0.62)	12.00-15.20	Jul. 13-Sep. 28
	♀	13.28 (22, +0.63)	11.84-14.72	
Oregon-Washington Coast Range	♂	15.15 (22, +0.39)	14.56-16.00	Mar. 7-Jun. 1
	♀	15.43 (12, +0.40)	14.88-16.16	

from 10.08 to 16.16 mm for females over the entire geographical range. Degree of melanization varied geographically, with Oregon Coast Range adults being darkest, and Cascade Range specimens being the lightest. The presence and degree of development of the preapical spurs of the hind legs varied between populations. All Cascade Range individuals possessed two strongly developed preapical spurs. This character was unstable in Coast Range individuals, varying from preapicals absent, to one present, or with the spurs very weakly developed (less than one-half the length of the apicals). No differences in genitalic structure or other external morphological features were evident.

The flight period of northern (Southeast Alaska and British Columbia Coast Ranges) and inland (Cascades) populations extends from early June to October. In contrast, adults in the Oregon-Washington Coast Range were on the wing from March to early June (Table 12).

Larval Habitats of the Coast and Cascade Range

Coast Range populations of E. scylla are restricted to very small streams and usually to those with a dense canopy of deciduous trees and shrubs. Substantial populations of larvae occurred in all forested sites examined in the Flynn Creek basin, whereas in five first-order tributaries in recent clearcuts (no tree overstory) no E. scylla were found. In the Flynn Creek watershed, populations are

largely confined to 100-150 m reaches of first-order streams in the ridge-foot and valley outwash areas (Figure 11), where mineral substrates grade from cobble-gravel to gravel-sand. Very few eggs, larvae or pupae were found above the ridge-foot or in the main channel of Flynn Creek.

In contrast to their occurrence at low elevations in the Coast Range, larvae or adults have only been recovered from streams between 500-2000 m in the Oregon and Washington Cascades. They occur in cold spring streams from springheads and small channels (ca. 0.5 m wide) to larger reaches of 3-5 m width. The Cascade Range sites are markedly different from the Coast Range habitats described above. They are cold, almost constant temperature spring streams (3-6°C) with long periods of snow cover and with peak discharge in late spring and early summer resulting from snowmelt. Also, the riparian vegetation is composed of a coniferous overstory, with detrital inputs principally from moss and conifers, as opposed to the autumnal pulse of deciduous leaves in the Coast Range sites.

Life Cycle in the Oregon Coast Range

Adults

Peak flight activity of *E. scylla* at Flynn Creek occurred early, with about two-thirds of the specimens being taken before April 7th. Females were captured near the oviposition sites by sticky traps or by sweeping streamside vegetation. Most males were caught at night in UV light

traps placed in the mainstem valley. Flight activity was commonly observed at dusk and both males and females occasionally were seen flying during the afternoon. Oviposition under logs was observed on two occasions at sunset. It is presumed that most of the mating and oviposition activity occurs at sunset or shortly afterwards.

Males were considerably lighter in weight than females (Figure 14), with a mean dry weight of 5.34 ± 0.82 mg (n=44) compared to pre-oviposition female weights of 9.86 ± 0.98 mg (n=4). Forewing length was not significantly different between the sexes.

Eggs, Ovarian Development and Fecundity

Females oviposit from early April to early June along a limited section of the first-order tributaries at Flynn Creek (Figure 11). Egg masses are usually suspended on the underside of large deadfall logs which span the stream in the ridge-foot reach or, less frequently, in moss on wetted rock faces 10 to 100 cm above the stream. Oviposition sites are aggregated with most masses occurring on only a few logs at each stream.

The pre-oviposition period is short for E. scylla. The ovaries in mature pupae contain developing eggs of about 0.20 mm dia. (Stage B). Reared females contained mature eggs (Stage C) after two days. At that time the abdomen was packed with eggs and the fat body had largely disintegrated.

Masses range from 0.5 to 1.5 cm in diameter when swollen with moisture. Eggs occur in rough rows within the clear, tacky, gelatinous matrix. They are 0.40-0.45 mm in diameter, oblong, have a clear chorion, and contain a yellow-orange colored embryo. Masses contain 50-600 eggs (n=68).

The incubation period in the laboratory at 12 °C, and of marked masses in the field, was approximately three weeks. Larvae remain in the mass for 3-5 days while tanning of body sclerites is completed. Masses then begin to liquify and larvae are "dripped" to the stream or onto its banks. Frequent rains at this time of year appear to facilitate the escape of larvae from the gelatinous matrix.

Egg mass size decreases over the oviposition season (Figure 12). This is interpreted as deposition of an initial egg mass and then a smaller mass later in the flight period. Early season egg masses had a mean of 333 (n=20, S.E.=115) eggs, while mid- and late-season counts were 203 (n=40, S.E.=108) and 127 (n=44, S.E.=44), respectively.

Egg counts obtained by dissection of field-collected females verified production of multiple masses. Six early-season females averaged 365 (S.E.=48) mature eggs, and the ovaries still contained developing eggs. By contrast, in nine females taken later in the flight season, the number of mature eggs ranged from 31-204 (\bar{x} =106), and all the eggs were in the posterior half of the abdomen.

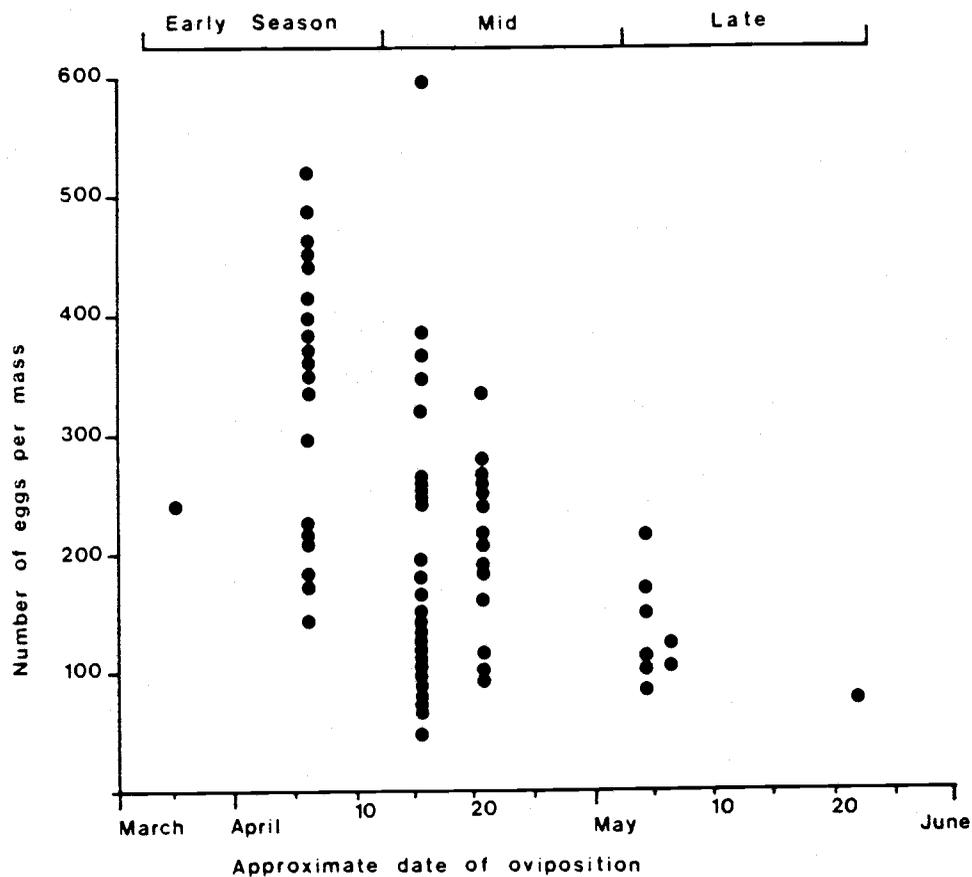


Figure 12. The number of eggs per mass for Ecclisocosmoecus scylla at Flynn Creek, Oregon Coast Range, as a function of approximate oviposition date. Only recently laid masses as evidenced by lack of embryo development are plotted.

Our estimate of mean fecundity, based on doubling the mean of eggs per mass from Figure 12, is 461 eggs per female. This assumes that females lay two egg masses and that the regular censusing over the course of the oviposition period has sampled the first and second egg masses about equally.

Egg mortality due to the phorid predator, Megaselia alsea Robinson (Diptera: Phoridae) was estimated as 38.3 % (Wisseman and Anderson 1984).

Larvae and Larval Development

The larva and case of E. scylla are illustrated by Wiggins (1977). The head is wide and bulbous, effectively sealing the anterior opening when the body is withdrawn into the case. The mandibles are stout and apically toothed, typical of the Dicosmoecinae (Wiggins 1977). The larvae construct a slightly curved, cylindrical case, using sand grains in all instars. Additional material is added when the larva is actively growing, resulting in a long, tapered case. The final instar cuts off the tapered posterior portion prior to pupation.

The five larval instars are readily distinguished by head-capsule width (Figure 13). Final instars from the High Cascade Range population were smaller than those at Flynn Creek.

E. scylla is a univoltine species with a clearly defined progression of larval instars in the Coast Range

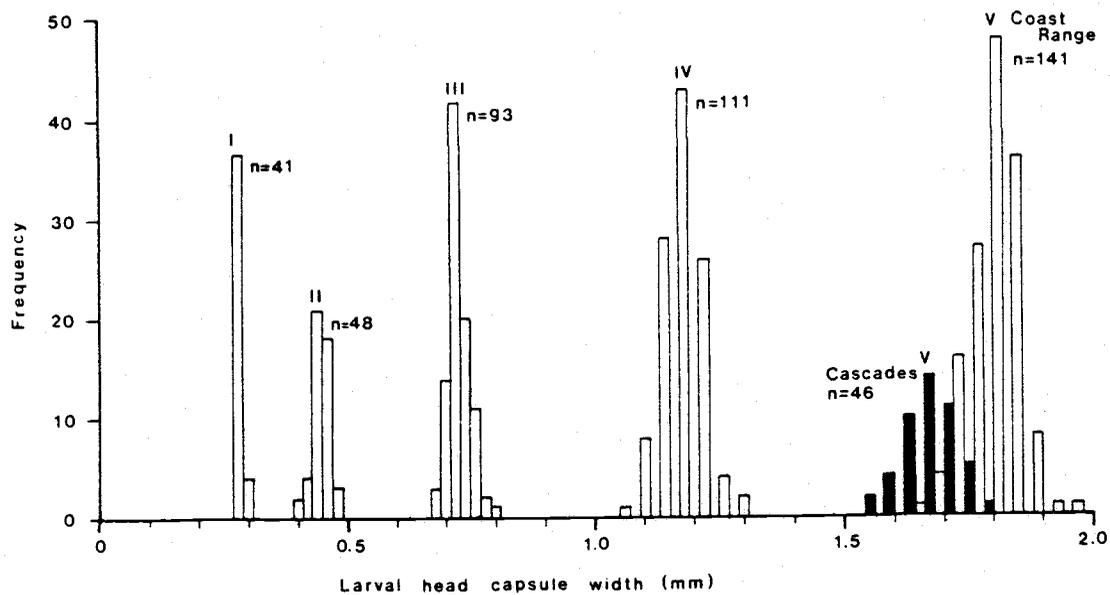


Figure 13. Frequency distribution of larval head capsule widths of *Ecclisocosmoecus scylla* form Flynn Creek, Oregon Coast Range (unshaded), and for instar V larvae from the Oregon High Cascades (shaded).

streams (Figure 14). First-instar larvae began appearing in late April or May and were concentrated near oviposition sites in the ridge-foot (Figure 11). Early-instar larvae were usually found near the water line on mineral substrates or newly fallen alder leaves. Guts contained finely divided detrital material and some diatoms. During the summer, biomass of larvae is low, but a rapid succession of instars occurred. During late summer, many of the first-order streams were intermittent and larvae aggregated in the remaining open pools or aestivated in damp stream bed substrates.

Most of the *E. scylla* population reached the final instar by mid-October. A period of rapid growth at this time (Figure 14) coincided with several changes in the physical environment, including decreasing temperature, leaf drop and increased discharge caused by the onset of fall rains. Rapid growth occurred from early October to mid-December when alder leaves were abundant and rising water levels made leaf packs accessible. All late instar larvae were found in leaf packs or associated with alder leaves. All guts examined ($n > 50$) contained leafy detritus exclusively.

A maximum larval biomass of 19.7 mg occurred in January through February (Figure 14). Thereafter, larvae cease feeding and aestivate in bottom substrates.

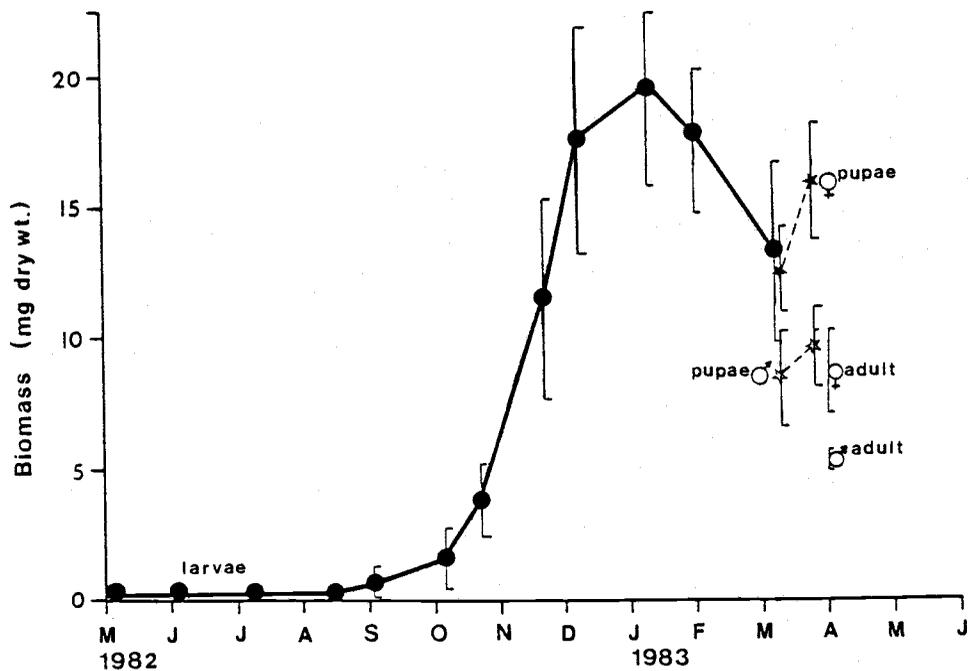
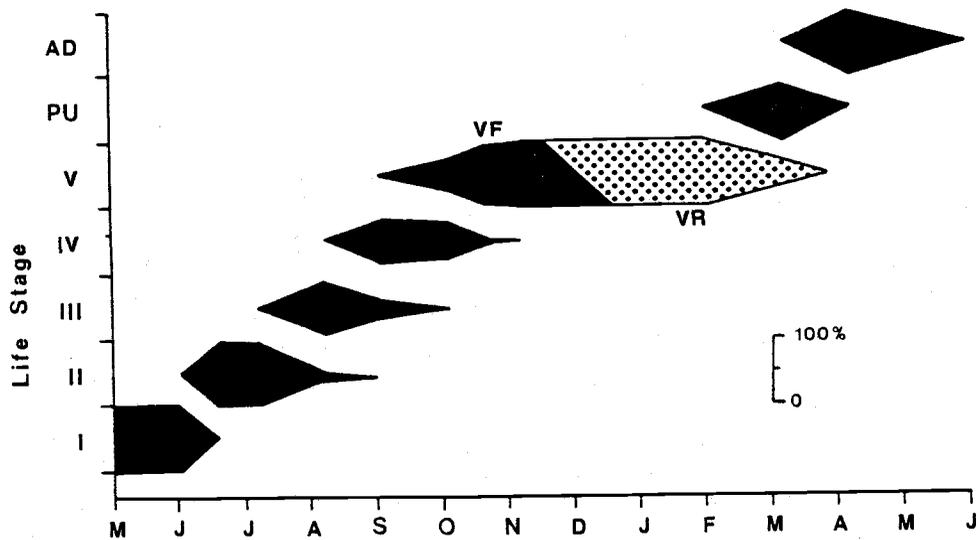


Figure 14. Growth and development of *Ecclisocosmoecus scylla* at Flynn Creek, Oregon Coast Range. Mean biomass (+ S.E.) is shown, and proportion of total population in each life stage.

Difference in growth patterns from adjacent tributaries (Figure 15), reflected a difference in timing of groundwater recharge and increased flow in each tributary watershed. Tributary A was more perennial in nature and generally responded with increased discharge earlier than did tributaries B, C, and D. Populations appeared to respond immediately to improved foraging conditions afforded by higher flow and flooding of stream margins.

All larvae were final instars from late fall until about March. In permanent channels and where leaves had been abundant, some larvae completed their growth by December. Winter spates transported substrates and larvae downstream. By January most larvae occurred in the outwash area, about 50-100 m downstream from the hatching sites (Figure 11).

Larvae burrowed several cm into the loosely consolidated substrates after completion of growth. By mid-February no larvae were found on substrate surfaces or feeding in leaf packs. Burrowed larvae were quiescent but did not tie down nor seal their cases until shortly before pupation. When dislodged manually from benthic substrates, larvae reburrowed after several minutes. Since substrates in the valley outwash region are subject to resorting by flooding in the late winter, abbreviating the immobile "prepupal" stage would be advantageous.

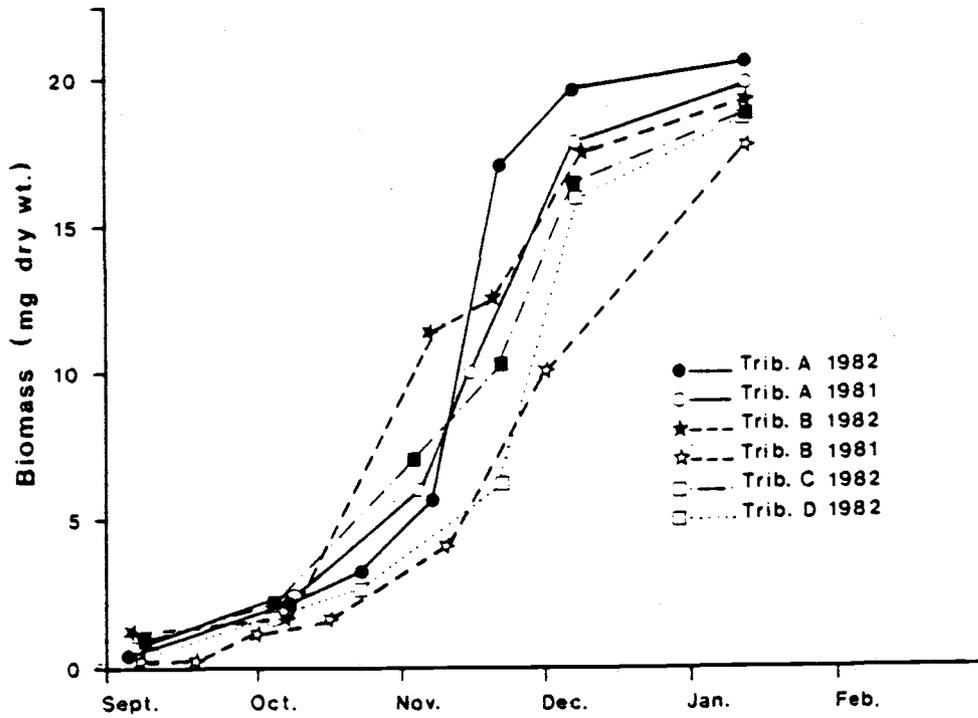


Figure 15. Mean biomass of *Ecclisocosmoecus scylla* larval populations in four tributaries of Flynn Creek, Oregon Coast Range.

Pupae

Pupation occurred throughout March at Flynn Creek. On March 7, 1982, 10 of 14 sealed cases contained pupae, while four were prepupae. By March 22, no prepupae remained. Thirty-two percent of the cases found contained pupae, and 68% were empty with normal pupal exit holes, indicating successful emergence (n=139). On April 6, no pupae remained in the streams. Wisseman and Anderson (1984) estimated pupal mortality due to predation by Rhyacophila spp. larvae to be approximately 20%.

Life Cycle of the Cascade Range Population

Collections indicate that E. scylla has a 2-year life cycle in the High Cascades. Adults and eggs were obtained from July through September near several spring-fed streams (Table 3, Figure 10). There were also instar IV and V larvae in the streams at this time. A subsequent collection at the end of September yielded early instars from the springheads (August oviposition sites), and instar V larvae at or near maximum weight along the length of the streams. Thus, two distinct cohorts were present just before snowfall.

Instar V larvae taken from the springheads were found most often on the sides of wetted rocks. Guts (5 larvae examined) contained moss, filamentous algae, finely divided detritus, and a few insect fragments, indicating that the larvae were grazing on rock surfaces. Larvae taken

downstream from the springheads (5 examined) had guts packed with conifer needle and wood fragments.

Other than the smaller size (Figure 13) and lighter pigmentation of sclerites in the Cascade larvae, no obvious morphological differences existed between Coast and Cascade larval populations.

A total of 102 males and 35 females were collected from the Oregon Cascades from July 13 to September 28. These adults were smaller (Table 12) and less heavily pigmented than the Flynn Creek population.

Population Variation

Rapid growth and development of *E. scylla* larvae at Flynn Creek occurred in the fall when rains filled stream channels, water temperatures were mild, and detritus was abundant. At this time red alder leaves (having a high nitrogen content of 2-2.5%, Mattson 1980) were abundant and the moisture-temperature regime was suitable for its microbial conditioning. Molting to the final instar occurred prior to this brief period of most favorable foraging conditions. About 91% of the total larval biomass was accumulated in about two to three months by instar VF.

In the univoltine population at Flynn Creek there is a limited time "window" of optimal growth conditions, and the achievement of the final instar prior to this period obviates the need to suspend feeding activities for molting.

E. scylla is able to extend larval dormancy during unfavorable conditions. This results in a biennial life cycle in the High Cascades, where the snow-free growing season is brief. Early-instar larvae entered the first winter dormancy after emerging from eggs deposited in August and September. Peak growth occurred during 2-3 months of optimal conditions in the following summer. Larvae at or near their maximum biomass passed the second winter burrowed in the substrate. Pupation, emergence, and reproductive activity occurred during the second summer. Low temperatures, restriction of foraging by snow and ice cover, and detrital substrates of low quality (coniferous and moss-derived) appear to preclude a univoltine life cycle in High Cascade streams.

In the southern part of the range of E. scylla, the Coast and Cascade Mountains are separated by the Willamette-Puget Lowland (averaging ca. 50 km. in width). E. scylla is not found in the low-gradient, warm streams of these lowlands. Disjunct variation (sensu Tauber and Tauber, 1982) appears to exist between these southern populations, perhaps due to isolation by intervening lowlands.

Further study is needed to document phenotypic variation between and within populations of E. scylla. Significant divergence of genotypes in the southern range of the species since the last glaciation may also have occurred.

ECCLISOMYIA IN WESTERN NORTH AMERICA

Introduction

Three species of Ecclisomyia Banks, 1907 occur in the western Nearctic Region, and two others inhabit the Asian Palaearctic (Lepneva 1966, Schmid 1955, Wiggins 1977). E. digitata (Martynov) 1929 occurs in central Siberia and E. kamtshatica (Martynov) 1914 is known from western Siberia (Fischer 1967, Schmid 1955). The degree of affinity between the Siberian species and the species in western North America is undetermined at present. The two common and widely distributed western North American montane taxa are E. conspersa Banks, 1907 and E. maculosa Banks, 1907, while E. bilera Denning, 1951 appears to be isolated in the Sierra Nevada Mountains of California. Adult characteristics for these three species are provided by Denning (1951), Nimmo (1971), Ross (1950), and Schmid (1955, 1980). Flint (1960) and Wiggins (1977) provide details of larval morphology for E. conspersa.

The distributional records and biological notes for Ecclisomyia spp. are widely scattered in the literature. Life history information is meager and anecdotal. No detailed treatment of the bionomics of any species has been published. This chapter provides a review of the distributional and biological information available from the literature, museum collections, and personal observations on the species in western North America. E. conspersa and E.

maculosa have many similarities in their distribution and biology and are discussed together. Factors important to their ecological segregation are not evident at this time.

Results and Discussion

Distribution and Biology of Ecclisomyia bilera

E. bilera is known from only two sites (Nevada Co. and Lassen Volcanic National Park) in the high Sierra Nevada Mountains of California (Denning, 1951; G. B. Wiggins, per. comm.). Its relationship to other Ecclisomyia species remains obscure. Wiggins (1977) noted that E. bilera larvae lacked the characteristic light-colored dorsal stripe of the pro- and mesonota present in the two other western species. In addition to July and August flight records and association with small, high-elevation streams, no other biological information is available.

Distribution of Ecclisomyia conspersa and maculosa

Distributional records for both species are summarized in Table 13. E. conspersa is more widely distributed. It is found throughout the Rocky Mountain cordillera from interior Alaska to southern New Mexico, and is abundant in the northern portion of the Pacific Coastal Province (Figure 1). E. conspersa is abundant in the Cascade Mountains of Oregon and Washington, and also in the more xeric Central Mountains. As with the coastal distribution, its abundance apparently diminishes to the south, with only one record

TABLE 13. The distribution of Ecclisomyia conspersa and E. maculosa in western North America. A summary of collection data.

STATE	PROVINCE Region	NUMBER OF LOCALES		REFERENCES
		<u>E.</u> <u>conspersa</u>	<u>E.</u> <u>maculosa</u>	
AK	Interior	10		Cowan et al. 1983, Nimmo 1986b, Oswood et al. 1984, Ross 1950, Wagener & LaPerriere 1985.
AK	1a	21		CWU, Denning 1951, Ellis 1978, Nimmo 1986b, OSU, ROM, Ross 1950, Schmid & Guppy 1952, Vineyard 1982.
WA	1b	3		CWU, OSU, ROM.
WA, OR	1c	2	1	Anderson 1976, OSU, Ross 1950.
CA	1e		1	OSU.
BC, WA	2a	13	4	CWU; Nimmo & Scudder 1978, 1983; OSU; Ross 1950.
WA	2b	26	13	CWU, OSU, Ross 1950, ROM, USNM.
OR	2c	22	17	Anderson 1976, Denning 1951, OSU, ROM.
OR	2d	13	9	Anderson 1976, Denning 1951, OSU, ROM, USNM.
CA	2e		5	Denning 1951, OSU, ROM.
CA	3	1	8	CWU, Denning 1951, OSU, ROM, UCB.
BC, WA	4	8	4	CWU; Nimmo & Scudder 1978, 1983; OSU; ROM; Ross 1950; Ross & Spencer 1952.
OR	6	11	4	Anderson 1976. OSU, ROM, Ross 1941.
OR, NV	7a	4	2	Anderson 1976, OSU, ROM.
Alta, BC, ID, MT, NWT, YK	8a	43	28	CWU; Hodkinson 1975; Newell & Potter 1973; Newell & Minshall 1977, 1979; Nimmo 1971, 1986a; Nimmo et al. 1976; Nimmo & Scudder 1978, 1983; OSU; Roemhild 1982; ROM; Ross 1950.
ID, MT, UT, WY	8b	3	14	Denning 1948, 1951; Newell & Minshall 1977, 1979; OSU; Roemhild 1982; ROM; Ross 1950; Swegman & Ferrington 1980.
CO, NM	8c	4	8	Allan 1975. Dodds & Hisaw 1925, Mecom 1972, OSU, ROM, Ross 1938, 1950, Ward 1981.

available from the Sierra Nevada Mountains of California. Records from the Great Basin are few.

E. maculosa is sympatric with E. conspersa, but has a more southerly distribution. It is known from the Rocky Mountain cordillera from southern Alberta and southeast British Columbia south to Colorado. As with E. conspersa, it is common in the Cascade Mountains and the Central Mountains, but there are only isolated records in the coastal ranges of Washington, Oregon and northern California. Records indicate that it is more common in the Sierra Nevada Mountains than is E. conspersa.

Habitat Associations

Table 14 provides a synopsis of habitat associations for E. conspersa and E. maculosa as inferred from collection data. Both species occur over a range of stream sizes, from large springs to small rivers, but are more typically collected in small to mid-size streams. E. conspersa has been found more often than E. maculosa in association with large streams and small rivers. These sites are all from mountainous streams with cold water and a moderate to high gradient. Most have coniferous trees dominating the riparian vegetation, while a few records are from streams in alpine meadows. Lake records are all from the littoral zone of high elevation, oligotrophic, cold lakes.

E. conspersa and E. maculosa co-occur in streams at intermediate elevations (ca. 1000-2000 m) in the Cascade

TABLE 14. Habitat associations of *Ecclisomyia* spp. in western North America. Multiple collections from a single locale are listed as one record. See Table 13 for references used.

	<u>E. CONSPERSA</u>		<u>E. MACULOSA</u>	
	#locales	%	#locales	%
SPRINGS	3	2.2	5	4.6
SMALL-MID SIZE STREAMS (1-4 m wide)	76	55.1	72	66.7
LARGE STREAM-SMALL RIVER (4-20 m wide)	49	35.5	20	18.5
LAKE, LITTORAL ZONE	11	7.3	11	10.2
TOTAL	138 locales		108 locales	

Mountains, eastern Oregon ranges, and the northern Rockies. However, E. maculosa dominates the higher elevation (2000-3000 m) records from these regions.

Larvae in the Cascade Mountains streams were collected from stream margins, runs and glides, and pool habitats. In the littoral zone of lakes they occur on large mineral substrates, logs, and accumulations of coarse detritus. They are only occasionally taken in samples from shallow riffle habitats or from torrential waters.

Adult Flight

Flight records for E. conspersa and E. maculosa from their entire range are distributed over 7 months from April to October, but with most occurring in the summer (Figure 16). E. maculosa records are more concentrated and later in the summer than those of E. conspersa. This may be due to the dominance of the former species at higher elevations. The flight season of both species was similar in a UV light trapping study in the Washington Cascades (Anderson and Wisseman 1987). However, in emergence traps at two streams in the Oregon Cascades, Anderson et al. (1984) found that E. conspersa emerged earlier (May to early June) than did E. maculosa (late June to mid-July).

Ross (1950) observed that females of E. maculosa collected from a high elevation site in Wyoming were dimorphic. He described one morph as being decidedly brachypterous.

Larvae

Metamorphotypes and associated larvae of both species have been examined from a number of locales. No superficial anatomical features were found that would consistently allow separation of the two species. Case architecture is similar in both species (Wiggins 1977). Larvae of all instars fasten vanes, usually conifer needles, longitudinally to a central tube of coarse sand particles. Instar V larvae nearing the end of their growth have straight, cylindrical cases of coarse sand. In other dicosmoecine genera discussed, changes in case architecture and composition reflect changes in foraging patterns and feeding habits. Whether this is the case for Ecclisomyia spp. is not known.

A univoltine life cycle is postulated for populations of both species at intermediate elevations of the Cascades. Early instar larvae appear in the late summer. The larvae grow slowly over the winter, and the greatest accrual of larval biomass occurs in the spring.

Ecclisomyia spp. are broadly omnivorous, consuming any food source that is readily available. Collection notes from the Oregon Cascades indicate larval presence in accumulations of fine particulate organic matter, on rock and log surfaces, and in leaf packs. Mecom (1972) reported that the diet of E. maculosa in Colorado consisted primarily of fine organic particles with a small proportion of

vascular plant tissue fragments. Wiggins (1977) found diatoms to be dominant in the guts of Ecclisomyia (species undetermined). Small amounts of vascular plant tissue fragments and fine organic particles were also observed. Wagener and LaPerriere (1985) state that the guts of Ecclisomyia (presumably E. conspersa) larvae from some interior Alaskan streams contained 100% animal parts. In contrast, Cowan et al. (1983) report the presence of 100% plant detritus in the guts of E. conspersa larvae, while Oswood et al. (1984) reported 80% diatoms and 20% fine organic particles for larvae from other interior Alaskan streams.

SYNOPSIS OF THE DISTRIBUTIONS, FLIGHT PERIODS, AND HABITATS
OF IRONOQUIA SPP. IN EASTERN NORTH AMERICA

Introduction

In preparation for this review of the biology and distribution of the western North American genera of the trichopteran subfamily Dicosmoecinae, comparative life history and habitat data was sought from published information on other world genera. Ironoquia is the only genus of the Dicosmoecinae that is restricted to eastern North America. Data for Ironoquia was found to be considerably scattered throughout the literature. This chapter provides a synopsis of published information on the genus.

Banks (1916) erected Ironoquia to receive parvula (Flint 1958). Schmid (1951) united the four species of Caborius with Ironoquia. Presently, four species of Ironoquia (kaskaskia, lyrata, parvula and punctatissima) are known from eastern North America with a single species (dubia) being known from the western Palaearctic Region. Svensson and Tjeder (1975) present arguments for the removal of the European species (dubia) from Ironoquia. They place the species into genus incertum until larval, pupal and adult characters can be reconciled.

Flint (1958) provided larval and pupal descriptions for I. parvula, which was found to inhabit temporary pools as well as small streams. The pupae were found to be terrestrial. Williams and Williams (1975) described the

larvae, pupae and biology of I. punctatissima in temporary streams in Ontario. Wiggins (1977) provided detailed characters for the larvae along with a synopsis of the known biological information.

A tabular summary of distributional and biological information on Ironoquia in eastern North America is presented here, with a synopsis by state or province, county or physiographic region, recorded adult flight dates, and larval presence data. Habitat associations were assigned on the basis of either larval or pupal collections or by close association of adult records with a particular habitat type.

Results and Discussion

Distribution

The distributional and biological information for the species of Ironoquia is provided in Tables 15-18. Collectively, the four species occupy much of eastern North America, from the Great Plains to the Atlantic Coastal Plain, and from the Boreal Forest of southern Canada to semi-tropical regions of the southeast United States. I. punctatissima occupies this entire geographic area. I. kaskaskia is more southern in distribution, while I. lyrata and I. parvula are more northern species. Each species inhabits more than one physiographic region. Ironoquia punctatissima displays exceptional adaptation to a wide range of climatic and physiographic regions.

TABLE 15. Distribution, flight period and habitat associations of Ironoquia kaskaskia in eastern North America. A summary of published collection data. Adult (AD) records as month-day. Larval (LA) records are indicated by "+". SS= small stream RI= river MA= marsh TP= temporary pool.

STATE:County	AD	LA	HABITAT	REFERENCE
IL:Clinton	IX-25	-	RI	Ross 1944
DL:Sussex	IX, X	-	-	Lake 1984
WV:Randolph	-	-	-	Hill & Tarter 1978
WV:Wayne	-	-	-	Tarter & Hill 1980
TN:Cumberland	IX-10 to	-	-	Etnier & Schuster 1979,
Hardin-Madison	X-27	-	-	Etnier & Way 1973
NC and SC:	IX, X, XI	-	TP	Unzicker et al. 1982
*Mountain		-	MA	
*Piedmont		-	SS	
*Coastal				
LA:Tangipahoa	X-14 to XI-7	-	-	Holzenthal et al. 1982

*= region of state or province, county unknown.

TABLE 16. Distribution, flight period and habitat associations of *Ironoquia lyrata* in eastern North America. A summary of published collection data. Adult (AD) records as month-day. Larval (LA) records indicated by "+". SP= spring SS= small stream MS= mid-size stream PD=pond.

STATE:County	AD	LA	HABITAT	REFERENCE
WI:Sauk	VIII-9	+	SS MS	Steven & Hilsenhoff 1984
*northern	VIII-25	-	-	Longridge & Hilsenhoff
IL:**Oakwood	IX-20	-	-	Ross 1938
IN:Monroe	-	+	SP SS	Waltz & McCafferty 1983
Tippecanoe	IX-24	-	-	
OH:Portage	VIII-13	-	MS	McElravy & Foote 1978
QUE:**southern	-	+	SS	Mackay 1968
QUE:**southern	VII-31 to IX-7	-	-	Roy & Harper 1981a
QUE:**Laurentian Highlands	-	-	-	Roy & Harper 1981b
ME:Hancock	-	-	-	Blickle & Morse 1966
NH:*Hubbard Brook	-	-	-	McConnochie & Likens 1969
CT:New Haven	IX-1 to IX-19	-	MS	Nelson 1987
NY:Albany	VIII-27 to IX-6	-	SP SS PD	McCabe 1980
PA:Bradford	VII-7	-	-	Ross 1938

*= region of state or province, county unknown
 **= town locale, county unknown

TABLE 17. Distribution, flight period and habitat associations of *Ironoquia parvula* in eastern North America. A summary of published collection data. Adult (AD) records as month-day. Larval (LA) records indicated by "+". SP= spring SS= small stream MS= mid-size stream MA= marsh TP= temporary pool.

STATE:County	AD	LA	HABITAT	REFERENCE
NH	-	-	-	Flint 1958
MA:*western	-	-	-	Neves 1979
MA:Hampshire	-	+	SS	Flint 1958
CT:New Haven	X-8 to X-13	-	MS	Nelson 1987
NY:Tompkins	-	+	TP	Flint 1958
NJ	-	-	-	Banks 1900
DL:New Castle Kent	X	+	-	Lake 1984
OH:Carroll	IX-25 to X-13	-	MA MS	Usis & MacLean 1986
OH:Columbiana	X-4	-	MA SP	MacLean & MacLean 1984
OH:Portage	X	-	-	McElravy & Foote 1978

*= region of state or province, county unknown.

TABLE 18. Distribution, flight period and habitat associations of Ironoquia punctatissima in eastern North America. Adult (AD) records as month-day. Larval (LA) records indicated by "+". SP= spring SS= small stream MS= mid-size stream RI= river MA= marsh TS= temporary stream TP= temporary pool.

STATE:County	AD	LA	HABITAT	REFERENCE
AK:*Popof Island	doubtful record			Banks 1900
KS:Allen-Chataqua	-	+	TP	Hamilton & Schuster 1980
Cherokee-Crawford				
Douglas-Franklin				
Jefferson-Lyon				
Wabaunsee				
MN:Lake	-	-	SS MS	Lager et al. 1979
MI:Crawford-Lake	VIII-23 to	-	-	Leonard & Leonard 1949
Macomb	IX-3			
WI:*south central	VIII to X-19	-	MA SP	Longridge & Hilsen-
*Pine Popple				hoff 1973
IL:Champaign	X-6	-	-	Ross 1944
IN:Brown-LaGrange	VIII-27	+	SS SP	Waltz & McCafferty 1983
Munroe-Scott				
Tippecanoe				
IN:Brown	VIII-25	+	TS	Clifford 1966
OH:Portage	late VIII to	+	SS MS	McElravy & Foote 1978
	late IX			
OH:Cuyahoga	IX-7	-	MS	Peterson & Foote 1980
OH:Carroll	VIII-28 to	-	MA MS	Usis & MacLean 1986
	X-13			
OH:Columbiana	IX-1 to X-4	-	-	MacLean & MacLean 1984
OH:Ashtabula	early VIII	-	-	Masteller & Flint 1979
ONT:Waterloo	-	+	TS	Williams & Williams 1975
QUE:*southern	VIII-29 to	-	-	Roy & Harper 1979
	IX-4			
NBR	-	-	-	Fischer 1967
NSC	-	-	-	Ross 1944
ME:*Mt. Desert	-	-	-	Blickle & Morse 1966
NH:Grafton	-	+	SS	Glime & Clemons 1972
MA:*western	-	-	-	Neves 1979
CT:New Haven	IX-1 to 21	-	MS	Nelson 1987
NY	-	-	-	Fischer 1967
				Betten 1934
				Hyland 1948
PA:Huntington	IX-3	-	-	Ross 1944
PA:Bradford	VII-7	-	-	Masteller & Flint 1979
PA:Erie	early IX	-	-	Lake 1984
DL:New Castle	IX, X	+	-	
Kent-Sussex				
MD	-	-	-	Ross 1944
WV:Grant-Harrison	VII-30	-	-	Hill & Tarter 1978;
Monroe-Putnam				Tarter & Hill 1979, 1980
Raleigh-Tucker				
Wayne-Webster				
VA	-	-	-	Parker & Voshell 1982
KY:Carroll-Spencer	X-4 to X-11	-	-	Resh 1975
Jefferson				
KY:Rowan	-	-	MS	Picazo & DeMoss 1980
TN:Cumberland-Knox	IX-7 to X-11	-	-	Etnier & Schuster 1979
Madison				
NC:Swain	IX	-	MS	Armitage & Tennesan 1984
NC and SC:				
*mountain	-	-	SS MA TP	Unzicker et al. 1982
*piedmont				
*coastal				
SC and GA:				
*Savannah R.	IX-22 to X-9	+	MA MS	Sherberger 1970
FL:Leon	-	-	-	Gordon 1984
AL:*Cahaba River	IX, X	-	SS MS RI	Harris et al. 1984
MS:*NCen. Plateau	IX-9 to XI-8	-	-	Holzenthal et al. 1982
*Coastal Plain				
LA:West Feliciana	-	-	-	Holzenthal et al. 1982

** region of state or province, county unknown.

Habitats

Larvae of all species have been reported from temporary pool or stream habitats (Clifford 1966; Flint 1958; Hamilton and Schuster 1980; Wiggins 1973, 1977; Williams and Williams 1975), along with larval behavior (migration and terrestrial aestivation), pupation habitat (terrestrial), and oviposition behavior (terrestrially in absence of surface water) that would indicate adaptations to temporary conditions. These characteristics are atypical for western North American dicosmoecines (Wiggins 1977).

Table 19 summarizes the habitat associations of Ironoquia species. Even though adult-habitat associations are suspect due to adult vagility, there is strong evidence that Ironoquia spp. are not obligate inhabitants of temporary waters. In fact, the majority of purely larval records are associated with perennial conditions, which include lentic and lotic waters. More confirmed associations are required to characterize the spectrum of habitat types that larvae of this genus inhabit.

Feeding Habits

Decaying leaves were found to be the primary food of I. punctatissima larvae in a temporary stream in Ontario (Williams and Williams 1975). Wiggins (1977) found that filamentous algae and vascular plant fragments were the dominant items in guts of Ironoquia spp. larvae. The above reports of detrital and algal material in the guts may

TABLE 19. The number of collections of Ironoquia spp. associated with particular habitat types.

HABITAT	<u>KASKASKIA</u>	<u>LYRATA</u>	<u>PARVULA</u>	<u>PUNCTATISSIMA</u>
Temp. pool	1	-	1	2
Temp. stream	-	-	-	2
Marsh	1	-	2	4
Pond	-	1	-	-
Spring	-	2	1	2
Small stream	1	4	1	6
Mid-size strm.	-	3	2	8
River	1	-	-	1

indicate an omnivorous proclivity, a condition common in western North American dicosmoecines (Wiggins and Richardson 1982, 1987; this report).

Adult Flight Period

All Ironoquia spp. appear to be late-season fliers, with the greatest concentration of records in September and October (Table 20). This type of adult seasonality is typical for many of the western dicosmoecine genera possessing similar large-bodied larvae (Wiggins and Richardson, 1982, 1987; this report).

Temporary water inhabitants within the Limnephilinae typically exhibit a prolonged flight period, with adults emerging when pools or streams dry out (usually in the late spring or early summer in the temperate northern latitudes). This is often followed with a summer adult diapause, and with oviposition occurring just prior to fall rains and the return of surface water (Wiggins 1973). From the limited reports available (Clifford 1966; Flint 1958; Williams and Williams 1975) it appears that some Ironoquia spp. survive the dry period with larval and/or pupal quiescence instead of by an extension of the adult stage.

Phylogeny

The phylogenetic position of Ironoquia in relation to the western North American genera is currently being examined (Flint and Wiggins in prep.). The morphology of

TABLE 20. The number of monthly records of adult flight activity of Ironoquia spp. in eastern North America.

MONTH	<u>KASKASKIA</u>	<u>LYRATA</u>	<u>PARVULA</u>	<u>PUNCTATISSIMA</u>
July	-	2	-	2
August	-	5	-	7
September	4	6	1	17
October	4	-	6	10
November	2	-	-	1

the adult, larvae and case plus certain life history features suggest a relation between Ironoquia and the western genus Amphicosmoecus. The limited habitat and life history information available to date indicates that this sole representative of the dicosmoecine genera restricted to eastern North America possesses a mixture of shared and unique characteristics with the western genera.

DISCUSSION

This thesis is a field study within a taxonomic framework and provides a literature review of the distribution and biology of the genera of dicosmoecine caddisflies. Although there are some similarities in the genera in habitat requirements, the differences or variability is such that we cannot generalize a "typical" dicosmoecine life-history strategy. A common thread for the subfamily is the association with cool, montane streams. However, within this stream category, habitat associations range from semi-aquatic (Cryptochia), through first-order specialists (Ecclisocosmoecus), to river inhabitants (Dicosmoecus gilvipes). In feeding habits most species are omnivorous, but they range from being primarily detritivorous (Ecclisocosmoecus), to scraping algae (Allocosmoecus), to predaceous (Dicosmoecus atripes). The seasonal occurrence of the different life stages and voltinism patterns are also variable.

IN summarizing the life-history parameters within the subfamily, the focus of this discussion is to compare and contrast the life stages of the several species to indicate how these interact with the physical environment to produce unique life-history patterns (Figure 17).

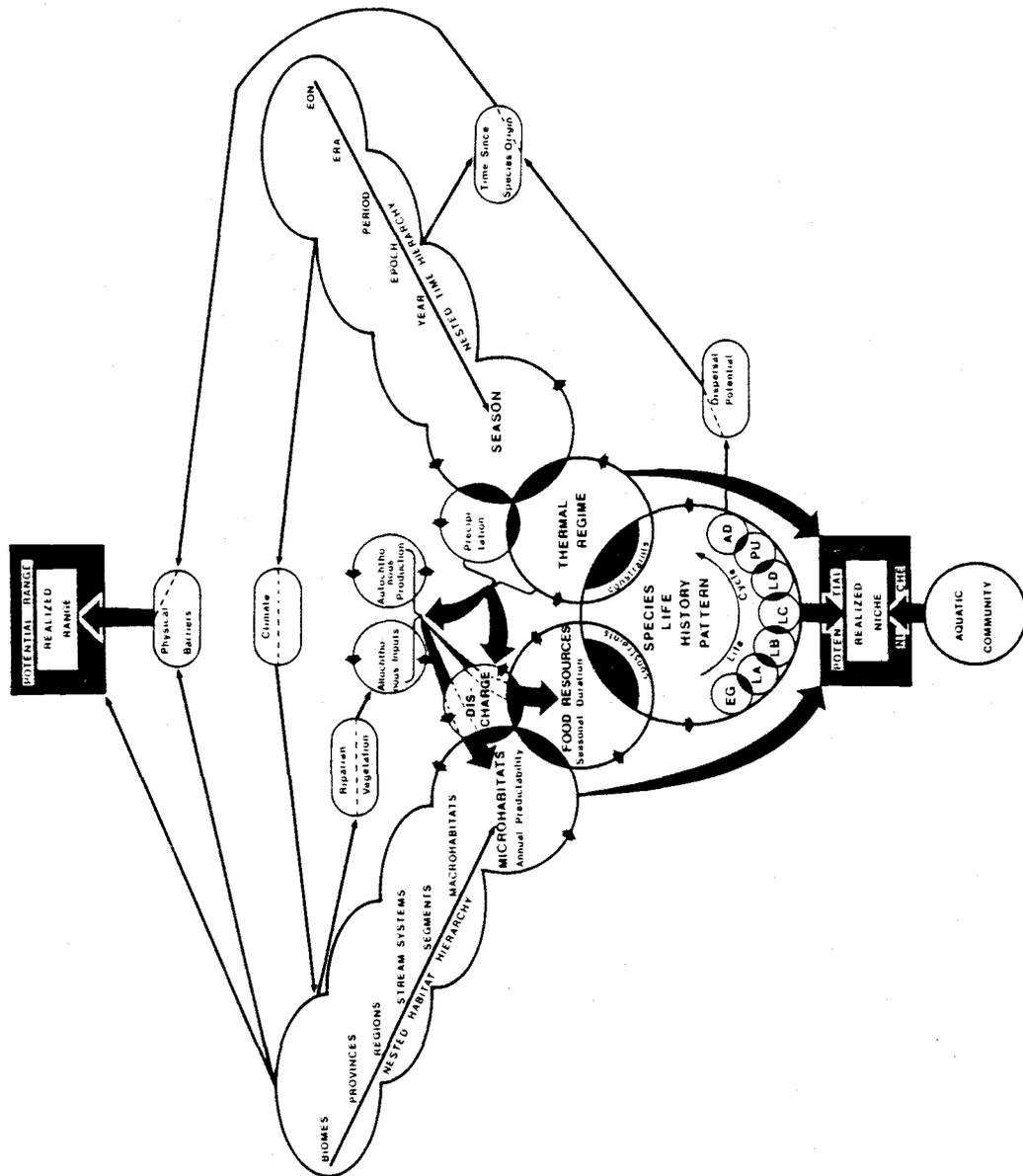


Figure 17. The interaction of Dicosmoecinae life history patterns with space and time.

Eggs

Egg masses of Ecclisocosmoecus scylla, Onocosmoecus unicolor, and Cryptochia pilosa have been observed in the field. Masses of Dicosmoecus spp. have been described by Gotceitas and Clifford (1983), Wiggins (1973), and J. Li (pers. comm., Oregon State University). These were all obtained from captive females.

Masses, and the eggs they contain, appear to be unspecialized within the Limnephilidae (Wiggins 1973). The gelatinous matrix is amorphous, clear, and possesses no surface skin that could assist in resisting desiccation. Eggs are straw colored and arranged in rough rows within the matrix. Development is direct and presumably the rate is temperature dependent. Delayed hatching has not been observed.

Though oviposition in the water cannot be ruled out for genera such as Dicosmoecus and Allocosmoecus, the tendency to oviposit out of water is suggested for this subfamily based on the known egg-laying habits of three genera.

Larval Intervals

Larval intervals A-D (Table 21) are used here, instead of instars. Instars provide useful information on the morphology and allometry of developing larvae (important for systematics and other purposes), but provide little insight into functional differences between larval development stages.

TABLE 21. Life history stages of the Dicosmoecinae.

STAGE	ATTRIBUTES
Egg	Oviposited in gelatinous masses, above the waterline in some genera. No specialized adaptations to resist dessication. Embryonic diapause or quiescence unknown.
Larval Interval A	First-instar larvae. Quiescence within the gelatinous matrix unknown. Accomplishes eclosion from the mass matrix, migration to microhabitat, case and feeding initiation.
Larval Interval B	Instars II to IV. High SGR but low biomass gain. Little contribution to nutrient reserves for reproduction. "Molting up" of sclerotized parts of head and thorax to final form, or "launching platform" for accumulation of biomass and nutrients. Often displays a more passive (drifting) foraging strategy, utilizing buoyant cases.
Larval Interval C	Instar VF (feeding). Exponential biomass accumulation. Reservoir of nutrients for reproduction acquired. Often displays a more active (crawling) foraging strategy, utilizing smooth cases.
Larval Interval D	Instar VR (resting). Has achieved maximum biomass and nutrient reserves. Migration to pupation microhabitats. May display quiescence to delay adult emergence or span unfavorable seasonal periods.
Pupa	Transition phase to adult. Quiescence or diapause unknown.
Adult	Reproduction and dispersal. May exhibit some delay in oviposition (i.e. preoviposition period), but no extended quiescence nor diapause known.

Larval interval C, the feeding phase in the final instar, is a pivotal stage in development. In the Dicosmoecinae examined, it accounts for about 90% of the total biomass accumulated during the entire larval period (Table 22, Figure 18). It is the interval when lipids and proteins are stored which ultimately determines successful pupation, adult eclosion and dispersal, and fecundity (Cargill 1984, Hanson et al. 1983).

Though the first four instars contribute little to the overall biomass, they can be viewed as a process where external, sclerotized body parts (the machinery for foraging and feeding activities) are "molted up" to the "launching platform" for biomass and nutrient accumulation during larval interval C.

Growth, as biomass accumulation over time, in the Dicosmoecinae appears to fit a logistic model (Kaufman 1981). The period of rapid biomass accumulation (larval interval C) lasts about 2-2.5 months in univoltine populations in the Oregon Coast Range and about 4-5 months for biennial populations. This is consistent with findings on other Limnephiloidea species from western Oregon (Wisseman, unpublished data).

Dicosmoecus spp. and Ecclisocosmoecus scylla display facultative voltinism, and can default to a biennial life cycle under suboptimal thermal-discharge regimes.

Cryptochia spp. appear to have an obligate biennial life

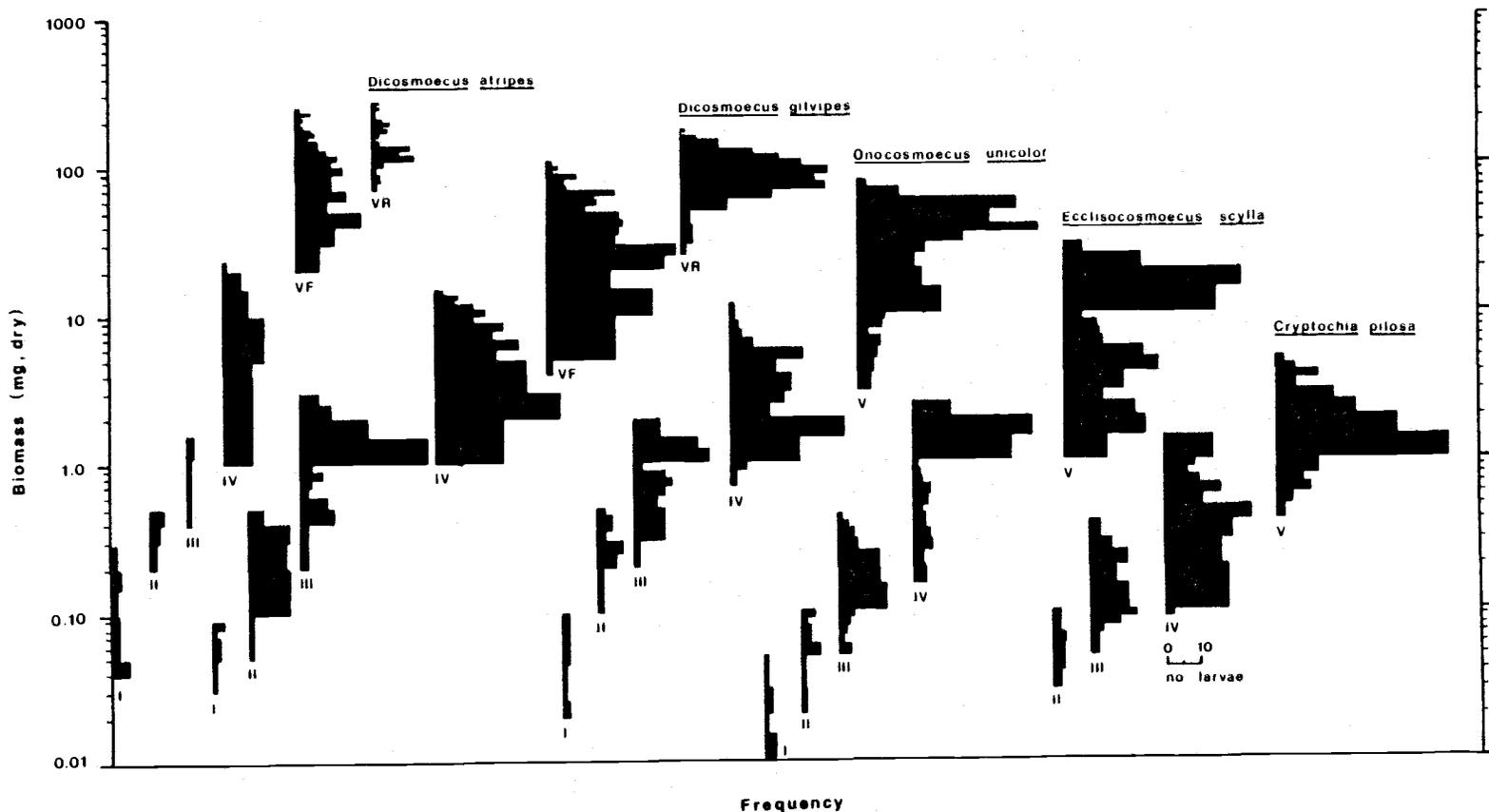


Figure 18. Biomass range and frequencies by larval instar of five Dicosmoecinae species in western North America. Assembled from field collected larvae.

TABLE 22. Comparison of instar biomass and growth for five species of Dicosmoecinae. Number of larvae weighed, absolute range of biomass, adjusted range of biomass and percentage contribution to the total larval biomass of each instar is provided. MEM= mean eclosion mass MIM= mean initial mass MMM= mean molting mass MTM= mean total mass (see methods for explanation).

INSTAR	n	ABSOLUTE RANGE (mg)	ADJUSTED RANGE (mg)	PERCENTAGE
<u>Dicosmoecus atripes</u>				
I	9	0.04- 0.30	0.04 (MEM) - 0.25 (MMM-I)	0.13
II	9	0.20- 0.50	0.25- (MIM) - 0.45 (MMM-II)	0.12
III	2	0.40- 1.60	0.45- (MIM) - 1.30 (MMM-III)	0.5
IV	32	1.00- 24.0	1.30 (MIM) - 22.5 (MMM-IV)	13
VF	148	20.0 - 245		
VR	59	75.0 - 260		
VTotals	207	20.0 - 260	22.5 (MIM) - 167.5 (MTM)	87
I-V	259	0.04- 260	0.04 (MEM) - 167.5 (MTM)	100
<u>Dicosmoecus gilvipes</u>				
I	9	0.03- 0.09	0.03- 0.07	0.04
II	37	0.05- 0.50	0.07- 0.35	0.3
III	98	0.20- 3.00	0.35- 2.00	1.6
IV	216	1.00- 15.0	2.00- 9.50	7.3
VF	283	4.00- 110		
VR	255	25.0 - 180		
VTotals	538	4.00- 180	9.50- 102.5	91
I-V	898	0.03- 180	0.03- 102.5	100
<u>Onocosmoecus unicolor</u>				
I	10	0.02*- 0.10	0.02*- 0.10	0.2*
II	26	0.10- 0.45	0.10- 0.325	0.5
III	95	0.20- 1.80	0.325- 1.25	1.9
IV	140	0.70- 11.0	1.25- 7.0	12
V	307	3.0 - 72.0	7.0 - 48.5	85
I-V	578	0.02- 72.0	0.02- 48.5	100
<u>Ecclisocosmoecus scylla</u>				
I	13	0.01- 0.40	0.01- 0.03	0.1
II	100	0.02- 0.10	0.03- 0.075	0.2
III	115	0.05- 0.45	0.075- 0.29	1.1
IV	115	0.15- 2.40	0.29- 1.7	7
V	244	1.00- 29.0	1.7 - 19.7	91
I-V	587	0.01- 29.0	0.01- 19.7	100
<u>Cryptochia pilosa</u>				
I	-	-	-	0.7*
II	17	0.03- 0.09	0.03- 0.07	1.2
III	63	0.05- 0.30	0.07- 0.195	3.6
IV	136	0.09- 1.45	0.195- 0.925	21
V	181	0.40- 4.70	0.925- 3.50	74
I-V	397	0.01*- 4.70	0.01*- 3.50	100

*= no larvae available, estimated mass used

cycle. Voltinism patterns within the remaining genera are generally consistent with a univoltine life cycle interpretation. Whether this is an obligate condition is not known.

Interval D includes the resting instar-V larvae and the prepupal stage. Several species have an aestivation period during the summer. A photoperiod cue may be the stimulus that initiates transition to the prepupal or pupal stage in species such as D. gilvipes. The resting interval may be important in enhancing synchrony of adult emergence and reproduction.

Quiescence is also used to span periods of suboptimal conditions for foraging or growth and is not limited to interval-D larvae. It occurs in situations where larvae are confronted by very low or very high temperatures, high stream discharge conditions, or drought.

Pupae and adults

Quiescence or diapause is unknown from either of these life stages in the western Dicosmoecinae. A specialized condition is found in the terrestrial pupation behavior of Ironoquia parvula (Flint 1958). This trait is seen in Cryptochia pilosa (Wisseman and Anderson 1987), but probably arose independently.

Adults range in size from small in Cryptochia, to being amongst the largest of all Trichoptera (e.g. Dicosmoecus spp.). Larger-bodied adults are late summer and fall

fliers, while the smaller and moderate sized species have spring and summer flight periods.

At Flynn Creek, in the Oregon Coast Range, adults exhibited strong upstream flight behavior in two species, Onocosmoecus unicolor (this report) and Cryptochia pilosa (Wisseman and Anderson 1987). This was evidenced by the near total concentration of egg masses in the upper watershed. Ecclisocosmoecus scylla eggs were concentrated at the ridge-foot of first-order streams, but all life stages have a restricted distribution, so this pattern does not involve a significant distance of upstream flight.

From UV light trap studies, large dicosmoecine adults are known to be strong fliers, and presumably to have a high dispersal potential (Anderson and Wisseman 1987). Barriers to adult dispersal are not anticipated to be a major factor in determining species ranges in western North America, although large intervening lowland areas may inhibit genetic exchange as suggested for Ecclisocosmoecus scylla.

Larval Case Architecture

Wiggins (1984) stated that:

"Our understanding of the ecological basis of diversification within the Hydropsychoidea and Rhyacophiloidea is fairly well advanced....families in these groups exploit similar food resources in elegantly different ways. By contrast, the Limnephiloidea of running waters give the impression of greater homogeneity in feeding....it is possible, and perhaps more likely, that we have not penetrated beyond the superficial sameness of portable cases in understanding how different types of cases do in fact contribute to utilization of different resources."

Evidence is presented in previous chapters, that for some western Dicosmoecinae, case architecture may be manipulated to increase foraging efficacy in seasonally changing and patchily distributed microhabitats. Larval intervals B and C in some species are ecologically segregated, showing clear differences in feeding habits, foraging strategy and microhabitat distribution. These species also have two clearly distinguished case types.

Buoyant-drifting type cases of interval B O. unicolor larvae may appear to be crude organic cases with no special design features, but they serve as efficient mechanisms for the exploitation of seasonally available food resources. This involves regulation of the specific gravity and drifting characteristics of the case to match those of particles in various detrital microhabitats, and allows larvae to passively "drift forage" in these patchily distributed microhabitats.

A major transition in case architecture to **smooth-crawling** type cases in O. unicolor signals a change in feeding habits and foraging strategies. The crude organic case forms of interval B larvae are transformed to a smooth, woody tube in interval C (or instar V) larvae. More active (crawling) foraging occurs, and there is a shift in food resources consumed.

In Allocosmoecus and Dicosmoecus, a transition to a smooth, mineral case from an organic one occurs between larval intervals B and C. D. atripes becomes an active predator-omnivore, while D. gilvipes and A. partitus migrate to swifter mid-stream microhabitats to scrape periphyton.

Ecclisomyia larvae have predominantly mineral tube cases in all larval intervals. However, they attach conifer needle vanes to this coarse sand tube in earlier instars. The functional significance of this is not understood at present.

Ecclisocosmoecus scylla larvae are restricted to small stream systems over a short longitudinal distance. They construct tubular, coarse-sand cases in all larval intervals. They appear to have lost the organic or partially organic buoyant-drifting case of interval-B larvae. This may be related to a number of factors. First, the longitudinal range of the habitat is small, and mineral cases would minimize transport. Second, these detritivores forage in shallow water where leaf packs are easily accessible by crawling short distances across the stream bottom. Finally, mortality factors, such as predation by other stream invertebrates and crushing by substrate movement during spates may select for a stronger mineral case (Wisseman and Anderson 1984).

The unusual case form of the semi-aquatic Cryptochia spp., allows larvae to drift on the water surface, which

enhances the probability of encountering debris jams, a preferred microhabitat. This case type does not appear to be related to that of any other discosmoecine caddisfly.

Diverse case forms reflect a diversity in life-history patterns in the Dicosmoecinae. If the western Dicosmoecinae are representative, then the diversity in case architecture exhibited in the Limnephiloidea may reflect different mechanisms employed for finer partitioning of food resources. Sharp distinctions in case types within species, may also signal alterations in feeding habits, foraging strategies, and microhabitat distribution.

Space and Time

The action of space and time on a species' life-history pattern are interdependent (Figure 17). A theme that has emerged in this study is the influence of seasonal stream-discharge patterns on life cycles. Discharge is viewed as a dominant factor in determining microhabitat and food resource availability. Species respond directly to these patterns with alterations in voltinism, microhabitat distribution, feeding habits, case architecture, growth rate, quiescence, and foraging strategy.

Thermal barriers to growth and development of these holometabolous insects may only be present at temperature extremes, either high or low, and may not have a direct influence on most populations (e.g. Dicosmoecus and Ecclisocosmoecus). Thermal barriers are obviously important

at the edge of a species' range. Low annual temperature regimes in northern latitudes or at high elevations may directly influence the degree of a species' extension into these zones. Similarly, high summer maximum temperatures, will preclude successful penetration of this cool adapted subfamily into arid, lowland regions.

Distributional Patterns

Factors important in determining a species' range are outlined in Figure 17. The distribution of the western Nearctic genera of Dicosmoecinae is summarized in Table 23. Adaptation of the subfamily to cool environments seems evident. Genera are virtually absent from basin and lowland provinces of the western United States (Figure 1). These are generally xeric regions with few small, cool-stream habitats (Table 2).

As stated in the introduction, within the provinces and regions of western North America, the Dicosmoecinae are generally confined to areas where humid coniferous forests occur. The distribution of coniferous forests generally indicates where cool, small-stream habitats will be present in the more arid regions of the western United States.

Wiggins and Mackay (1978) have related the distributional patterns of the Nearctic caddisfly genera to habitat and food, and comment that unspecialized predators tend to be more widely distributed than are genera dependent on more locally occurring food resources. Dicosmoecus

TABLE 23. Presence of Nearctic and Holarctic genera of the Dicosmoecinae in physiographic provinces and regions of the world. "I" indicates existence in isolated locales only.

W. North America PROVINCE Region	<u>Dicosmoecus</u>	<u>Onocosmoecus</u>	<u>Allocosmoecus</u>	<u>Amphicosmoecus</u>	<u>Ecclisocosmoecus</u>	<u>Ecclisomyia</u>	<u>Cryptochia</u>	<u>Ironoquia</u>	Total
Ia	+	+	+		+	+	+		6
Ib	+	+	+		+	+	+		6
Ic	+	+	+		+	+	+		6
Id									0
Ie	+	+	+			+	+		5
If	+	+							2
Ig									0
IIa	+	+	+		+	+	+		6
IIb	+	+	+		+	+	+		6
IIc	+	+	+		+	+	+		6
IIId	+	+	+		+	+	+		6
IIe	+	+	+			+	+		5
III	+	+	+	+		+	+		6
IV	+	+	+	+	+	+	+		7
V									0
VI	+	+		+		+	+		5
VIIa	+I	+I		+I		+I			4
VIIb	+I	+I		+I					
VIIIa	+	+	+	+		+	+		6
VIIIb	+	+	+			+	+		5
VIIIc	+	+	+			+			4
IX									0
X		+I							1
XI		+I		+I		+I		+	4
E. North America		+						+	2
Northeast Asia	+				+	+			3

atripes, Ecclisomyia conspersa, and Onocosmoecus unicolor are the most widely distributed western North American species. Though they have divergent life history patterns and habitat associations, all three are broadly omnivorous in instar V (interval C).

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