

AN ABSTRACT OF THE THESIS OF

Christopher D. Beatty for the degree of Master of Science in Environmental Sciences presented on August 19, 2002.

Title: Habitat Associations and Life Histories of Odonata in Riverine Wetlands of the Willamette Valley, Oregon

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Abstract approved _____

Paul C. Jepson

This thesis explored the distributions and life histories of dragonflies and damselflies (Insecta: Odonata) of the riverine wetlands of the Willamette Valley in western Oregon, USA. Odonate species distributions were characterized over two seasons—in the autumn of 2000 and the spring of 2001—at twenty-seven wetlands located throughout the valley. Distributions of nymphs and adults were compared with wetland habitat conditions that may affect odonate diversity.

Odonate nymph and adult distributions were analyzed through Hierarchical Agglomerative cluster analysis (HA). HA identified discrete clusters of sites based on the distributions of species in the genera *Aeshna*, *Erythemis*, *Lestes*, *Libellula*, *Pachydiplax*, *Sympetrum* and *Tramea*. To identify habitat associations with odonate species, nymph and adult data were analyzed by Non-metric Multidimensional Scaling (NMS). NMS revealed that odonate distributions are associated with site hydrology, water depth and temperature, the presence of large emergent plants (e.g. *Typha latifolia*), the presence of fish, and surrounding landcover. These data will provide guidance for wetland managers in the use of odonates as indicators of wetland health.

To further examine the relationship between odonate species and their wetland habitats, quantitative life history data for the 27 odonate species were analyzed to determine functional associations between species attributes and the

environments in which they are found. Oviposition location, presence of a resting egg, over-wintering life stage, nymphal foraging strategy and adult flight season were subjected to NMS, to determine biological similarities between species occupying particular locations. Life history patterns correlated strongly with hydrology. Analysis of sites by odonate species richness found a relationship between richness and site hydrology, but failed to explain the distribution of several species associated with wetlands that dry during part of the year. We conclude from our results that species-level life history data are essential for explaining odonate distributions.

We determined that the presence of odonate species in a wetland is indicative of habitat condition, that analysis of odonate distributions at the species level is necessary to understand habitat associations, and that analysis of life-history attributes provides a functional understanding of odonate distributions that measurements of species richness or the distributions of genera or families alone cannot explain.

Habitat Associations and Life Histories of Odonata in Riverine Wetlands of the
Willamette Valley, Oregon

by
Christopher D. Beatty

A THESIS
submitted to
Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented August 19, 2002

Commencement June 2003

Masters of Science thesis of Christopher D. Beatty presented on August 19, 2002

APPROVED:

Redacted for privacy

Major Professor, Representing Environmental Sciences

Redacted for privacy

Chair of Graduate Program in Environmental Sciences

Redacted for privacy

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Christopher D. Beatty, Author

ACKNOWLEDGEMENTS

I would like to thank my advisors, Dr. Paul C. Jepson and Dr. Judith L. Li, for their guidance, patience and inspiration. I have become a better scientist and a better person through knowing them. Thanks go also to Dr. Mary Kentula and Dr. Daniel Sudakin for their service on my committee; the work herein is much improved for their involvement. This research was funded by a grant from the US Environmental Protection Agency/National Science Foundation Watersheds program, and would not have been possible without this support.

I would very much like to thank Dr. Paul Adamus, for providing a great deal of background data on the sites in this study, and on the condition of wetlands throughout the Willamette Valley. Dr. Phil Heneghan was immensely helpful in the development of the database for this project. Kathleen Harding, Belinda Schantz and Itzel Spihar provided excellent help during sample events. Finally, many thanks go to Steve Valley, whose expertise in the identification of odonate nymphs and adults, and general fascination with all things “dragonfly” were invaluable to this project.

CONTRIBUTION OF AUTHORS

Dr. Judith L. Li was involved in all aspects of this project, in experimental design and implementation, and in the development and production of this thesis. While serving as minor professor on my committee, Judy has functioned as a co-advisor, and is listed as co-author on all manuscripts.

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DEDICATION

This thesis is dedicated to the memory of Ed Hoffmann. When it comes to your dreams, always swing for the fence.

Habitat Associations and Life Histories of Odonata in Riverine Wetlands of the Willamette Valley, Oregon

CHAPTER 1

GENERAL INTRODUCTION

The order Odonata contains the dragonflies (suborder Anisoptera) and damselflies (suborder Zygoptera). The odonates are a broadly distributed group, found on all continents excluding Antarctica. It is estimated that 3000 extant odonate species currently exist globally (Dunkle 2001). Approximately 350 species are found in North America (Needham, Westfall and May 2000, Westfall and May 1996).

Odonates have an aquatic nymph stage, which can last from several weeks to several years (Needham, Westfall and May 2000). After emergence, odonates spend several weeks as aerial adults, during which time they utilize terrestrial habitats to forage, returning to aquatic habitats to mate and oviposit (Corbet, 1999). These distinct life stages are characterized by discrete morphologies and habitat requirements, and the successful completion of the life cycle is a function of both aquatic and terrestrial habitat quality. Odonates are predatory as both nymphs and adults. Nymphs feed on a range of aquatic insects and crustaceans as well as tadpoles and juvenile fish, while adults feed on a variety of flying insects.

Odonate species are found in a broad range of environments. Species in the family Pseudostigmatidae utilize water-filled tree stumps as nymph habitat (Finke 1992). Nymphs of other dragonflies, such as those in family Petaluridae, inhabit high-altitude bogs and wet meadows; digging burrows that fill with water in the saturated soil (Corbet 1999, Selys 1879). The majority of odonate species

are found in more open aquatic environments. Several species are associated with streams and rivers, including members of the families Macromiidae and Gomphidae. Species in temperate regions (Corbett 1999) are found to use wetlands and ponds as nymph habitat.

Wetland-dwelling dragonflies are distributed between several families. Members of family Aeshnidae (Anisoptera) are commonly known as “darners” (Figure 1.1 A), because of their long, slender abdomens (Dunkle 2000). They are large dragonflies, ranging from 5 to 7 cm in length, and are commonly found in sluggish streams, wetlands and ponds. Common aeshnid genera in North America include *Anax* and *Aeshna*. *Aeshna* contains approximately 500 species worldwide, with 39 occurring in North America.

The family Coenagrionidae (Zygoptera) (Westfall and May 1996) represents a broadly distributed group that prefers bogs and wet meadows. These damselflies are relatively small (2 to 3 cm in length). *Enallagma* (“bluets”) (Figure 1.1 B) and *Ishnura* (“forktails”) are two coenagrionid genera common to North America; Coenagrionidae contains a total of 115 North American species.

The Lestidae (Zygoptera) are known as “spreadwings” and are common to bogs, wet meadows and prairie wetlands in North America (Figure 1.1 C). These damselflies range in size from 4 to 6 cm, and hold their wings spread at rest, the source of their common name. Lestidae is not as speciose as other odonate families in North America, with 19 species.

Members of family Libellulidae are by far the most common dragonflies in still waters (Dunkle 2000). These species, known commonly as “skimmers”, often demonstrate conspicuous wing patterns, such as black and white banding or red coloration. The males of several species demonstrate pruinescence—a waxy blue or white powder covering the body—when sexually mature. Over a thousand species of libellulids are found worldwide, with 103 occurring in North

America. Common genera of this group are *Libellula* (Figure 1.1 D), *Sympetrum* (Figure 1.1 E) and *Tramea* (Figure 1.1 F).

These odonate groups, while common in wetlands, exploit a range of habitat conditions (Corbet 1999). These odonates also demonstrate a range life history attributes (Walker 1956). These variations between species found in wetland habitats, combined with the broad geographic distribution of these species, make odonates an excellent candidate for use as indicators of wetland health.

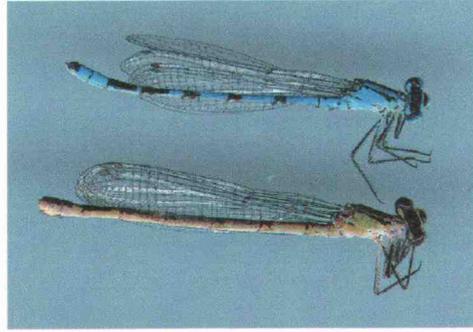
Approximately fifty odonate species are common to the Willamette Valley (Oregon Dragonfly and Damselfly Survey 2002). Species that use wetlands make up half that number. Wetlands are a major component of the Willamette Valley landscape, providing a range of odonate habitats. These wetlands have been considerably altered by human activity. Historically, as much as 57% of the pre-settlement wetlands in the valley have been destroyed (Christy et. al., 1998, Morlan, 2000). As wetland managers work to protect and restore wetlands, information on the habitat responses of a group such as odonates would be would provide an indication of ecosystem response to restoration activities.

In this research, we explore quantitatively the relationship between odonate distributions and habitat conditions. Through the use of multivariate analytical techniques, we determine how their unique odonate assemblages characterize wetland sites, and identify the habitat attributes that are associated with particular odonate species. While a number of bioindicators employ lower taxonomic scales or functional metrics (Merritt and Cummins 1996, Plafkin et. al. 1989) we consider the merits of analysis of habitat associations at the species level.

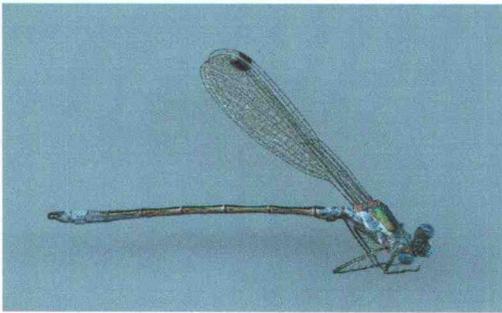
To further examine the relationship between odonate species and their wetland habitats, we also analyze life history characteristics of the odonate



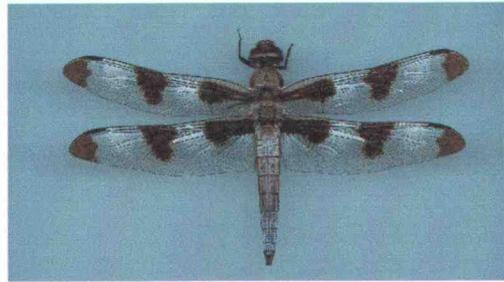
(A)



(B)



(C)



(D)



(E)



(F)

Figure 1.1: Examples of odonates common to North American riverine wetlands: (A) *Aeshna multicolor*, male (Anisoptera: Aeshnidae) (B) *Enallagma cyathigerum*, male and female (Zygoptera: Coenagrionidae) (C) *Lestes dryas*, male (Zygoptera, Lestidae) (D) *Libellula pulchella*, male (Anisoptera: Libellulidae) (E) *Sympetrum ilotum*, male (Anisoptera: Libellulidae) (F) *Tramea lacerata*, male (Anisoptera: Libellulidae). Images courtesy of D. Paulson.

species identified in our study. Similarity between species is determined through multivariate analysis of life history attributes. Patterns in life history are then compared to species distributions within sites, to identify correlations between distribution, life history, and habitat condition. The incorporation of fine-scaled autecological information, rather than more generalized information, allows species distributions to be considered from a perspective of biological function. If we consider these life history attributes as adaptations (Gould and Lewontin 1979) we can associate species with habitats that they are adapted to exploit, allowing for more effective management for odonate diversity, and a better understanding of the response of these species to wetland restoration efforts.

CHAPTER 2

CHARACTERIZATION OF ODONATE HABITAT IN RIVERINE
WETLANDS OF THE WILLAMETTE VALLEY, OREGONABSTRACT

This study investigated the spatial and temporal distribution of dragonfly and damselfly (Insecta: Odonata) species in riverine wetlands of the Willamette Valley in western Oregon, USA. In 2000 and 2001 odonate nymphs were surveyed in twenty-seven wetlands and odonate adults were surveyed at twenty-five wetlands. Species distributions were correlated with habitat conditions at these sites, to identify wetland habitat attributes that are associated with odonates.

A total of 27 species were found at the sites. Twenty of the twenty-seven sites contained odonate nymphs. Analyzed separately, twenty-three sites contained odonate adults. Nymph and adult distributions, in Non-metric Multidimensional Scaling (NMS), determined site similarity based on odonate assemblage. When NMS results were compared to a matrix of 35 habitat variables, odonate species distributions were associated with hydrologic pattern (temporary or permanent), presence of submerged wood and presence of large emergent vegetation and presence of fish. The presence of wooded and grassland buffers surrounding wetlands were also associated with species distributions, as was the presence of cropland. Species in *Libellula*, *Aeshna*, *Lestes* and *Sympetrum* demonstrated specific associations to these habitat variables. With

their relationship to habitat condition, broad distribution and ease of identification, odonates are effective indicators of wetland habitat quality.

INTRODUCTION

The significance of wetlands as a component of an ecologically functioning landscape has begun to receive recognition (Mitsch and Gosselink 1993). This is particularly true with regard to the roles wetlands play in nutrient processing, water quality maintenance, as refugia for organisms from adjoining aquatic and terrestrial environments, and in supporting diverse native communities. Interest in wetland protection and restoration is increasing, and public concern for wetland habitat loss in the Willamette Basin in Oregon has prompted efforts in wetland preservation and restoration (Oregon Progress Board 2000).

The Willamette Valley in western Oregon, USA contained historically a complex of prairie, gallery forests and floodplain wetlands that extended north to the confluence of the Willamette and Columbia Rivers (Willamette Valley Livability Forum 2002). The valley is now home to 2.3 million residents and is cultivated extensively for a variety of crops, with 526,500 hectares in production. This increase in residential and agricultural development has resulted in alteration of the valley landscape, including filling and removal of many wetlands. Historically, as much as 57% of the pre-settlement wetlands in the Valley have been destroyed (Christy et. al., 1998, Morlan, 2000), with approximately 6,877 acres of wetlands being lost between 1982 and 1994 to agriculture (64%), rural development (23%), forestry (2%) and other causes (11%) (Bernert et. al. 1989, Oregon Progress Board, 2000).

Riverine wetlands, the focus for our study, are those associated with the

floodplains, oxbows and former channels of streams and rivers (Brinson 1993). These wetlands may receive water from rainfall and groundwater recharge, but to be considered riverine wetlands they must receive water from an adjoining stream or river, through direct connection to the river or through capture of floodwaters (Brinson 1993). These wetlands represent a broad range of habitat conditions. Overall sizes and depths vary considerably from extensive floodplain wetlands to small, isolated former channels. Hydroperiod varies between wetlands, from those that contain standing water year-round to those that are wet only for a few months in the year. A diversity of vegetation types is observed in wetlands. In the Willamette Valley wooded margins of willow (*Salix spp.*), Oregon Ash (*Fraxinus latifolia*) and open prairie surround these riverine habitats. Obligate wetland vegetation of several types is present, including submerged pondweed (*Potamogeton spp.*), floating water lily, emergent rushes (*Scirpus spp.*) and cattail (*Typha spp.*). Wetland substrates range from the cobbled bottoms of previous river channels to the thick layers of silts and organic detritus associated with backwaters.

To explore the structure of wetland communities and to measure the effect and extent of anthropogenic impact, a number of assessment techniques have been developed (Adamus 1996). Wetland assessment techniques utilize a range of metrics, including soil type, vegetation and distributions of wetland fauna. The distribution of a select group of organisms that is representative of the diverse biota of a region has proven an effective metric of both ecological variation and habitat quality (Kremen et. al., 1993).

In Target Taxon Analysis (Kremen 1994), a methodology for biological indicator development, a taxon is selected whose member species demonstrate a range of ecological responses to an environmental gradient of interest. To be an effective choice for this methodology, a taxon should be speciose, possess a range of ecological responses to habitat conditions, be present in abundance in

the habitat under study and demonstrate a high level of endemism. Local radiation of species into a number of microhabitats generates species adapted to local environmental conditions; these species can then serve as indicators of habitat change.

To select taxa that are indicative of wetland condition, the unique nature of wetland habitats must be considered. As an ecotone, wetlands grade both spatially and temporally from an aquatic to a terrestrial habitat (Mitsch and Gosselink 1993). Organisms that utilize both of these habitat types would prove especially appropriate for the analysis of wetland community integrity. Odonates represent such a group. Odonates possess an aquatic nymph stage that can last from several weeks to several years (Needham, Westfall and May 2000). After emergence, odonates spend several weeks as aerial adults, when they use wetlands and adjoining terrestrial habitats to forage, returning to aquatic habitats to mate and oviposit (Corbet, 1999). These distinct life stages are characterized by discrete morphologies and habitat requirements. Odonates are predators in both nymph and adult stages: nymphs feed on a range of aquatic insects and crustaceans as well as tadpoles and juvenile fish, while adults feed on a variety of flying insects. As predators, odonates can be considered “integrators”, reflecting the status of the wetland communities that they exploit (Corbett 1999).

Odonates also demonstrate scales of dispersal and movement appropriate for their use as site-specific habitat indicators. The nymph stage has a low dispersal capacity and is unlikely to move from its wetland habitat. Adults can move considerable distances, and are therefore able to disperse to wetland habitats across the landscape. Odonates thus have the capacity to access multiple sites within a landscape, but are still tied biologically to the habitat quality of individual sites.

Odonates are diverse and widespread in the Pacific Northwest. There are approximately 88 odonate species in Oregon; approximately 50 are found within

the Willamette Valley (Oregon Dragonfly and Damselfly Survey, 2002). Many of these species inhabit wetlands and ponds. The objective of this study was to characterize odonate adult and nymph distributions in riverine wetlands of the Willamette Valley. In exploring odonate diversity we sought to answer several questions. How are odonates distributed in riverine wetland habitats? How do odonate distributions correlate with habitat conditions? How do nymphs and adults differ in their responses to habitat conditions? What level of taxonomic resolution is necessary to understand these responses? How do odonate habitat associations compare to site species richness as a measure of habitat quality? Though bio-indicators are often developed to study pollution or land use effects, we chose to study odonate distributions at sites that are minimally impacted by human activity (Adamus 1998). Through the identification of odonate responses to natural variation in wetland habitats, we hope to understand their distributions in functioning systems, and to determine what information odonate surveys can provide for wetland management and restoration.

METHODS

Site selection: Sites were selected from a pool of 66 sites assembled for the hydro-geomorphic (HGM) assessment program for the Willamette Valley in western Oregon (Adamus, 1998). These HGM survey sites represent a range of size, surrounding land use, hydro-period (permanent or seasonal), connectivity to lotic habitat, and other habitat parameters (vegetation, substrate). The sites are “functional” wetlands; although anthropogenic uses have affected many of these sites, they are still considered healthy wetland habitats. The sites are also located primarily on public lands, providing easy access for sampling.

This research focused on the HGM sites of the riverine subclass.

Restriction to a single subclass limited potential variance introduced by habitat differences between subclasses. Sites classified as riverine that did not contain some standing water during the winter of 1999-2000 were excluded from the study. A total of twenty-seven sites were selected for study (Figure 2.1, Table 2.1). These sites are all considered part of the *reference domain* of riverine wetlands for the Willamette Valley: as a group they are representative of the range of condition of riverine wetlands in this region. Two sites in this study, Jackson-Frasier (JF) and Willow Creek (WC) were determined to be *reference standards* for riverine wetlands in the region. Reference standard sites represent a high level of ecological function, and are considered to be examples of the optimum habitat found within the reference domain (Brinson and Rheinhardt 1996).

Odonate nymphs: From June 28th to August 10th 2000 and May 4th to June 1st 2001, odonate nymphs were collected at all 27 sites with D-frame nets (500 μ m mesh). Sample locations within each wetland were chosen based on the microhabitats favored by odonate nymphs (Corbett 1999). Microhabitats included submerged vegetation, floating vegetation, submerged wood and substrate (Table 2.2). Benthic sampling effort was equalized at each wetland by sampling for 20 minutes, not including travel between microhabitats. One sample was collected from each microhabitat present at each site, and preserved in plastic bags (Whirl-Pak®) in 80% ethanol. Odonates were identified and counted in the laboratory using Westfall and May, (1996), and Needham, Westfall and May (2000), with specimens identified primarily to species. When specimens were small or

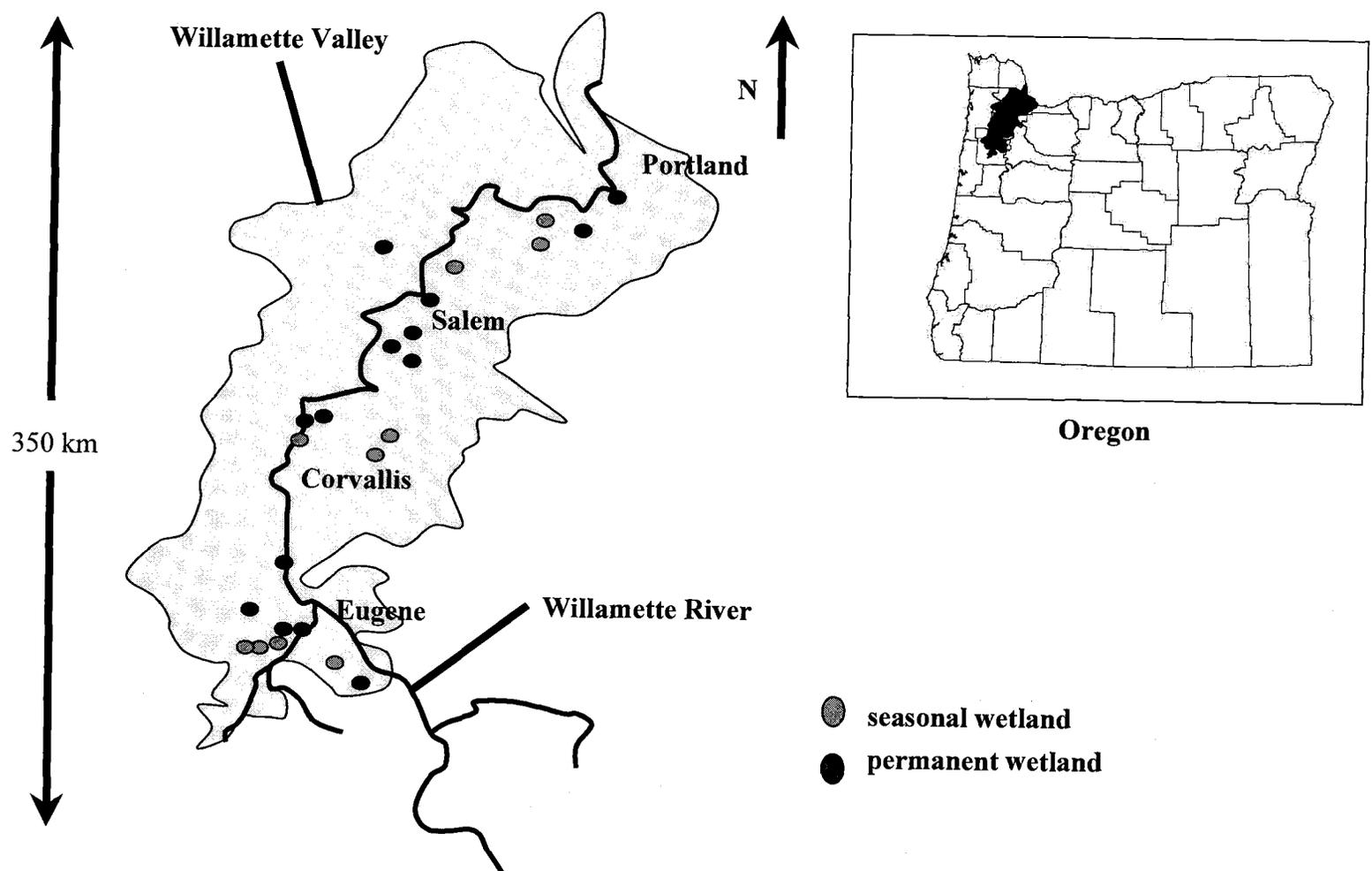


Figure 2.1: Wetland sample locations in the Willamette Valley

Table 2.1: Riverine wetland sites

SiteName	SiteCode	County	Nymphs	Adults
Alton Baker West	ABW	Lane	Y	Y
Brown's Ferry Pond	BL	Washington	Y	Y
Buford West slough	BW	Lane	Y	Y
Coffin Butte Pond	CB	Benton	Y	Y
Coyote Creek 1	CC1	Lane	Y	Y
Coyote Creek 2	CC2	Lane	Y	Y
Coyote Creek 3	CC3	Lane	Y	Y
Coyote Creek 4	CC4	Lane	Y	Y
Cascades Gateway Slough	CG	Yamhill	Y	Y
Cook Park Slough	CP	Washington	Y	Y
Champoeg State Park	CR	Marion	Y	Y
Christensen slough	CS	Lane	Y	Y
Delta Ponds	DP	Lane	Y	Y
Wilson Wildlife Area Pond	EE	Benton	Y	Y
Fanno Creek Duck Donut	FC	Washington	Y	Y
Grand Island Slough	GI	Yamill	Y	N
Hedges Creek Duck Ponds	HC	Washington	Y	Y
Jackson-Frasier Floodplain	JF	Benton	Y	Y
Jasper Park Slough	JP	Lane	Y	Y
Kirk Ponds abandoned channel	KP	Lane	Y	Y
Minto-Brown Slough 1	MB	Marion	Y	Y
Novitzki Restoration	NR	Benton	Y	Y
Oak Bottom Backwater	OB	Multnomah	Y	Y
Spongs Landing	SL	Marion	Y	N
Thackaberry pond	TF	Linn	Y	Y
Willow Creek Riverine	WC	Lane	Y	Y
Willamette Mission Slough	WM	Marion	Y	Y

Table 2.2: Microhabitats sampled for odonate nymphs by wetland site

SiteName	SiteCode	Sediment	Sub. Vegetation	Sub. Wood
Alton Baker West	ABW	Y	Y	N
Brown's Ferry Pond	BL	Y	Y	Y
Buford West slough	BW	Y	Y	Y
Coffin Butte Pond	CB	Y	Y	N
Coyote Creek 1	CC1	Y	Y	N
Coyote Creek 2	CC2	Y	Y	N
Coyote Creek 3	CC3	Y	Y	N
Coyote Creek 4	CC4	Y	Y	N
Cascades Gateway Slough	CG	Y	Y	N
Cook Park Slough	CP	Y	Y	N
Champoeg State Park	CR	Y	Y	N
Christensen slough	CS	Y	Y	Y
Delta Ponds	DP	Y	Y	Y
Wilson Wildlife Area Pond	EE	Y	Y	N
Fanno Creek Duck Donut	FC	Y	Y	N
Grand Island Slough	GI	Y	Y	N
Hedges Creek Duck Ponds	HC	Y	Y	Y
Jackson-Frasier Floodplain	JF	Y	Y	Y
Jasper Park Slough	JP	Y	Y	Y
Kirk Ponds abandoned channel	KP	Y	Y	Y
Minto-Brown Slough 1	MB	Y	Y	Y
Novitzki Restoration	NR	Y	Y	N
Oak Bottom Backwater	OB	Y	Y	Y
Spongs Landing	SL	Y	Y	N
Thackaberry pond	TF	Y	Y	N
Willow Creek Riverine	WC	Y	Y	Y
Willamette Mission Slough	WM	Y	Y	N

incomplete identification was possible only to genus, primarily for the nymphs of Coenagrionidae. Specimens from this family were recorded as *Enallagma spp.* or *Ishnura spp.*

Odonate adults: From August 23rd to September 23rd 2000 and July 5th to August 9th 2001, adult odonate abundance was estimated at twenty-five of the twenty-seven wetlands where nymphs were sampled. Adults were sampled at this reduced number of sites for logistical reasons during the 2000 sample season.

Adult odonates were observed using a binocular survey during which individual odonate adults were sighted with binoculars and identified to species (Dunkle 2000). I walked the perimeter of each wetland until it was circumnavigated, or a maximum of one hour was reached. The wetland perimeter was defined as the edge of standing water if present, or if no standing water was found, the presence of emergent wetland vegetation. Latitude and longitude of observations were recorded to 1 one-hundredth of a degree using a Garmin GPS3- Plus Global Positioning System (GPS). A small number of specimens were also collected from each site, returned to the laboratory, and preserved as voucher specimens for field identifications.

Habitat: At the beginning of each survey time, date, location, and habitat conditions were recorded. When odonate adults were sampled, prevailing weather conditions (sunny, partly cloudy, cloudy, rain), air temperature and wind speed were reported. Air temperature was taken with a hand-held thermometer calibrated in the laboratory and recorded to the nearest degree Celsius. Wind speed was measured with a hand-held anemometer held at a height of 1.5 meters. Wind-speed was taken in open ground and recorded as the range of values observed during one minute. Under conditions of high winds or clouds adult flight activity may be diminished (Corbet 1999). These conditions were monitored to insure that climatic conditions were acceptable for odonate

population assessment, and to establish site-to-site sampling consistency.

Odonate surveys were postponed if cloudy, hazy or rainy conditions existed, or if there were sustained wind speeds above 15 miles per hour. If weather conditions became limiting during a survey (for example, clouds passing over the sun for a period of several minutes), sampling was interrupted, or postponed if conditions did not improve.

During odonate nymph sampling, pH, temperature and dissolved oxygen were recorded in 2000 with a Solomat® 520c multimeter if standing water was present. In the laboratory, water samples were stored at 4° C, and allowed to acclimate to room temperature prior to analysis for nitrates using an Orion meter.

Obligate wetland vegetation was surveyed at each site during nymph sampling. Plants within five meters on either side of the water edge were identified to species (Guard, 1995). Vegetation was categorized as either submerged, floating or emergent. Relative abundance of each species was assessed through visual estimates and identified as rare, abundant or very abundant. Substrate within the nymph sampling area was described qualitatively using the Wentworth classification system and the depth of substrate was measured. If fish or bullfrogs were seen or heard they were noted.

Analytical methods: To determine similarity of wetland odonate assemblages, nymph and adult abundance data were subjected to Non-metric Multidimensional Scaling (NMS) using the software PC-ORD version 4 (McCune and Mefford 1999). NMS is an ordination technique based on rank similarity distances (Mather 1976, Kruskal 1964), which tends to relieve the zero-truncation problem often associated with community data (McCune 1994). NMS is a robust method, particularly with non-normal, heterogeneous data (B. McCune, pers. com.). Outlier analysis identified two sites, CS and CC1 with outlier statistics of 2.38 and 2.21, respectively. Because these did not represent problematic outliers, all data were used in the analysis. Adult and nymph data

were analyzed separately. Abundances within each dataset did not vary by more than one order of magnitude so initially untransformed data were used in the analysis. For each life stage, data from both sample years were combined. Sorensen's distance measure was used to determine similarities. The matrices were analyzed with a random starting configuration, using 40 runs with real data, compared to a Monte Carlo test with 50 runs on randomized data. The appropriate number of dimensions for the final ordination was determined by examining stress values. Final stress for a given dimensionality was lower than that for 95% of the randomized runs (i.e. $p \leq 0.05$ for the Monte Carlo test). Stress is a measure of distance in the ordination space and the corresponding dissimilarity between sample units (i.e. wetlands).

NMS was unable to find a satisfactory solution for the nymph matrix, because the data structure was weak: 81% of cells were empty, coefficient of variation (CV) among sites was 124%, CV among species was 193%. To improve the ordination, the nymph abundance data were transformed through Beals smoothing, which is a multivariate smoothing function well suited to heterogeneous data with a high percentage of zeros (McCune 1994). The smoothing function converts matrix cells to presence-absence data, then calculates for each cell the probability of a species being present based on its pattern of co-occurrence with other species present in the sample unit. The adult matrix was more robust (63% of cells were empty, CV among sites was 82%, CV among species was 96%) and did not require Beals smoothing.

To identify correlations between species distributions and habitat characteristics, thirty-five variables (Table 2.3), including data from this project and site-specific data compiled in the HGM survey, were compared to NMS

Table 2.3: Habitat variables for wetland analysis

HABITAT ATTRIBUTE	DESCRIPTION
Hydro-period	number of months annually that wetland contains water
Fish present	presence of fish-potential nymph predators
Bullfrogs present	presence of bullfrogs--tadpoles prey for some nymphs
H2O Temperature (degrees Celcius)	water temperature in nymph sampling area
H2O pH	water pH in nymph sampling area
H2O dissolved oxygen (mg/L)	water dissolved oxygen in nymph sampling area
H2O depth (cm)	water depth in nymph sampling area
Sediment depth (cm)	depth of upper layer of sediments in nymph sampling area
Wetland area (m2)	total area of wetland within walking perimeter (see adult sampling)
Wetland perimeter	perimeter of standing water or obligate wetland vegetation
Shorline complexity (area/perimeter)	ratio of area to perimeter--indicates shoreline complexity
Anadrmous fish access*	access to wetland by anadramous fish populations
Connectivity type*	type of connection to other water bodies 0= none, 1= seasonal constricted, 2= seasonal diffuse, 3= permanent constricted, 4= permanent diffuse
Logs*	presence of sumberged logs in wetlands
Mow*	percentage of site subject to mowing or extreme grazing
Buffer_Crop_G*	Percent of land cover in 200 ft buffer zone that is grassland or cropland
BufCropGabc*	Mean percent of land cover in 200, 1000, & 5280 ft buffer zones that is grassland or cropland
BuffGrass*	Percent of land cover in 200-ft buffer zone that is grassland or wetland/water
BufGrassAB*	Mean percent of land cover in 200 & 1000 ft buffer zones that is grassland or wetland/water

*Habitat attribute collected as part of HGM development project (Adamus and Field 2001)

Table 2.3: Habitat variables for wetland analysis (continued)

BuffNat*	Percent of land cover in 200-ft buffer zone that is “natural” (wooded or grass or wetland/water)
BufNatAB*	Mean percent of land cover in 200 & 1000 ft buffer zones that is “natural” (wooded or grass or wetland/water)
BuffWet*	Percent of land cover in 200 ft buffer zone that is “water” or “wetland”
BufWetABC*	Mean percent of land cover in 200, 1000, & 5280 ft buffer zones that is “water” or “wetland”
BuffWood*	Percent of land cover in 200-ft buffer zone that is woodland (forested or shrubland or parkland)
BufWoodAB*	Mean percent of land cover in 200 & 1000 ft buffer zones that is woodland (forested or shrubland or parkland)
Development	presence of buildings or pavement in wetland area
Agriculture	presence of crop cultivation in wetland area
H_Percent_Perm*	Percent of permanent zone containing herbs
H_Percent_Season*	Herbs as % of seasonal zone
HcvNN*	Relative spatial prevalence of non-native herbs 1= Non-natives predominate, 2= Cannot determine (about equal), 3= Natives predominate
Hsp_Percent_NN*	Percent of common herb species that are non-native
VegMixL*	Number of vegetation forms & their distribution during low water
VegPct*	Percent vegetated (as viewed from above)
<i>Typha latifolia</i> presence	presence of <i>T. latifolia</i> within wetland
<i>Alisma plantago-aquatica</i> presence	presence of <i>A. plantago-aquatica</i> within wetland

*Habitat attribute collected as part of HGM development project (Adamus and Field 2001)

ordinations of nymph and adult data. The habitat matrix included data on water quality, soil substrate, wetland size, wetland vegetation and surrounding land use (Table A.2.3).

Hierarchical-agglomerative (HA) cluster analysis, using Sorensen's distance and a group average linking method, was performed to identify groups of sites based on odonate assemblages. Nymph and adult data were transformed to presence/absence for this analysis. HA relates groups in a step-wise manner. First, the average distance between all groups is calculated. The two groups found to be most similar (with the shortest distance between them) are combined, and distances are recalculated for the new groups. For a given number of sites (n) this process is repeated n-1 times, until all groups are combined. The HA results dendrogram indicates the relationship between groups based on the amount of assemblage information used to generate the relationship. HA cluster analysis was performed on nymph and adult data separately.

HA was also utilized to identify groups of sites based on habitat similarity. In this analysis the 35 habitat variables were analyzed for each site to define groups of sites sharing similar habitat conditions. NMS was also performed on the habitat attributes to determine which habitat variables were responsible for site clustering.

To compare the distributions of nymph and adult life stages of each species, the Presence/Absence matrices for nymphs and adults were combined to develop a table showing distributions of each life stage at each site. The state of each species at each site was assigned a distributional code as follows: 1=adults and nymphs of a species both absent; 2=adults present but nymphs absent; 3=adults absent but nymphs present; 4=adults and nymphs both present. After the number and percentage represented by each code at each site was tabulated, sites were ranked based on the total number of species present as both nymph and

adult at the site (distribution code “4”). Of the 27 sites sampled, only 25 were sampled for both nymphs and adults; only data for these sites were used in this analysis. To compare results to a more traditional metric of habitat quality, odonate species richness was calculated for each site in the previous dataset. Sites were then ranked in order of decreasing species richness to compare the species richness gradient to habitat gradients between sites.

RESULTS

The total odonate assemblage in the Willamette Valley wetland sites consisted of 27 species, represented by at least one life-stage (Table 2.4). They included species from five families: Aeshnidae, Gomphidae and Libellulidae (Anisoptera) and Coenagrionidae and Lestidae (Zygoptera). The Gomphidae were represented by *Gomphus kurilis* nymphs, found at only one site (ABW). There were also three other species, *Aeshna umbrosa*, *Archilestes californica* and *Sympetrum danae*, found at only one site. Nymphs of twenty-six species were found at 20 of the 27 sites, with a total of 1245 individuals (Table A.2.1). The combined adult surveys included 22 species at 23 of 25 sites sampled, with a total of 2005 individuals observed (Table A.2.2).

Total adult species richness at individual sites ranged from zero to 20 species. Total nymph species richness was lower, ranging from zero to 8 species per site. Comparing seasons, mean species richness per site was higher in the spring (Figure 2.2) though overall nymph and adult species richness was higher in the fall (Figure 2.3). Total abundance was much greater in the spring (Figure 2.4). Abundance differences between anisopterans (dragonflies) and zygopterans (damselflies) occurred seasonally and between life-stages. Nymph abundance was higher for Zygoptera, most prominently in the spring when zygopteran nymphs

Table 2.4: Odonate species assemblage in riverine wetlands

SUBORDER	FAMILY	GENUS	SPECIES
ANISOPTERA	AESHINIDAE	<i>Aeshna</i>	<i>californica</i>
		<i>Aeshna</i>	<i>multicolor</i>
		<i>Aeshna</i>	<i>palmata</i>
		<i>Aeshna</i>	<i>umbrosa</i>
		<i>Anax</i>	<i>junius</i>
	GOMPHIDAE	<i>Gomphus</i>	<i>kurilis</i>
	LIBELLULIDAE	<i>Erythemis</i>	<i>collocata</i>
		<i>Libellula</i>	<i>forensis</i>
		<i>Libellula</i>	<i>luctuosa</i>
		<i>Libellula</i>	<i>lydia</i>
		<i>Libellula</i>	<i>pulchella</i>
		<i>Pachydiplax</i>	<i>longipennis</i>
		<i>Sympetrum</i>	<i>corruptum</i>
		<i>Sympetrum</i>	<i>danae</i>
		<i>Sympetrum</i>	<i>illotum</i>
		<i>Sympetrum</i>	<i>madidum</i>
		<i>Sympetrum</i>	<i>occidentale</i>
		<i>Sympetrum</i>	<i>pallipes</i>
		<i>Sympetrum</i>	<i>vicinum</i>
		<i>Tramea</i>	<i>lacerata</i>
ZYGOPTERA	COENAGRIONIDAE	<i>Enallagma</i>	<i>civile</i>
		<i>Enallagma</i>	<i>cyathigerum</i>
		<i>Ishnura</i>	<i>cervula</i>
	LESTIDAE	<i>Archilestes</i>	<i>californica</i>
		<i>Lestes</i>	<i>congener</i>
		<i>Lestes</i>	<i>disjunctus</i>
		<i>Lestes</i>	<i>dryas</i>

were more abundant by greater than a factor of ten (Figure 2.4). Among adults, Anisoptera were more abundant in the spring when Anisoptera outnumbered Zygoptera by approximately a factor of two. In the fall there was no difference between Anisoptera (428) and Zygoptera (408) adults. Zygopterans represent 22% of the total number of species (6 of 27) observed.

At any given site, no more than 21% of the species present were found as both adults and nymphs. Many sites were visited by a small number of species. Twenty-five percent of sites were visited only by adult odonates. Sites with the largest percentage of species represented by both the nymph and adult stage were also the sites with the highest species richness.

HA cluster analysis distinguished sites by the nymphal distribution of species in six genera: *Aeshna* (four species, groups 1 and 2), *Gomphus* (one species, group 1) *Lestes* (three species, groups 3, 4, and 5), *Libellula* (four species, groups 1, 3 and 4) and *Sympetrum* (five species, groups 3, 4, and 5). Three other species in family Libellulidae—*Erythemis collocata*, *Pachydiplax longipennis* and *Tramea lacerata*—grouped together (groups 4 and 5) (Figure 2.5). Groups 6 and 7 each contained only one site and only members of the damselfly genera *Enallagma* and *Ishnura*; these genera were found to be present in all HA site clusters.

Cluster Analysis of the adult assemblage data also found sites grouped by the generic distributions. Twelve groups of sites were identified with 80% information remaining (Figure 2.6). Group 1 was divided into two groups, 1A and 1B, because of its size and the distinct distribution of *Aeshna* adults within the group. Groups were clustered by distributions of *Aeshna* (Groups 1A, 2, 3 and 5), *Lestes* (3 and 9) and *Libellula* (1A, 1B, 2, 3 and 4). *Sympetrum* were more broadly distributed in the adult cluster analysis results (1A, 1B, 5 and 9).

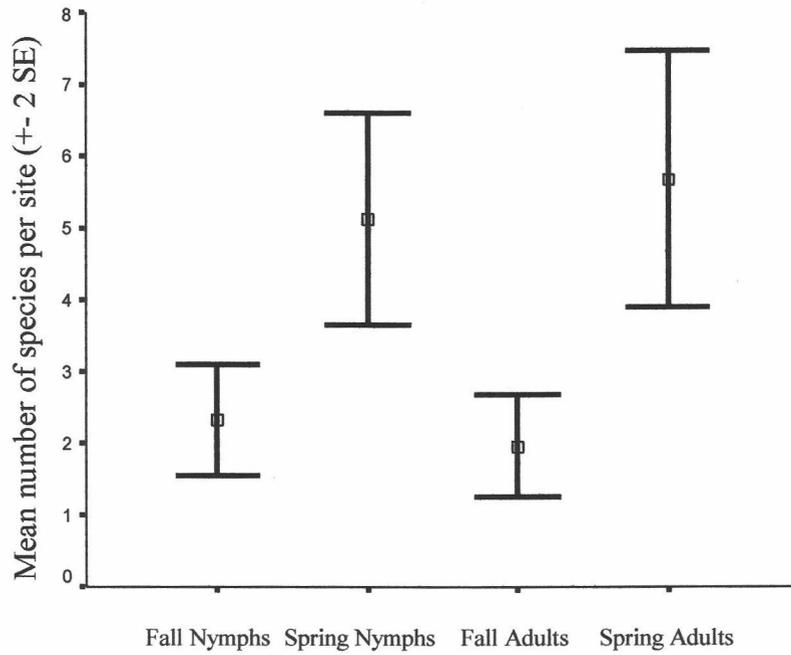


Figure 2.2: Mean odonate species richness per site by season and life stage

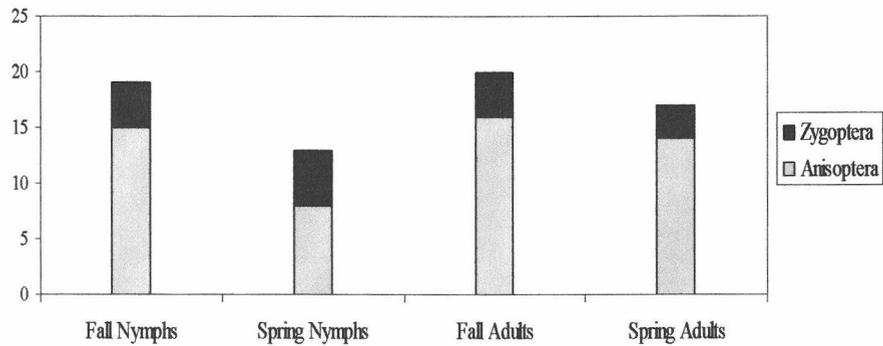


Figure 2.3: Total Odonate species richness at all sites by season and life stage

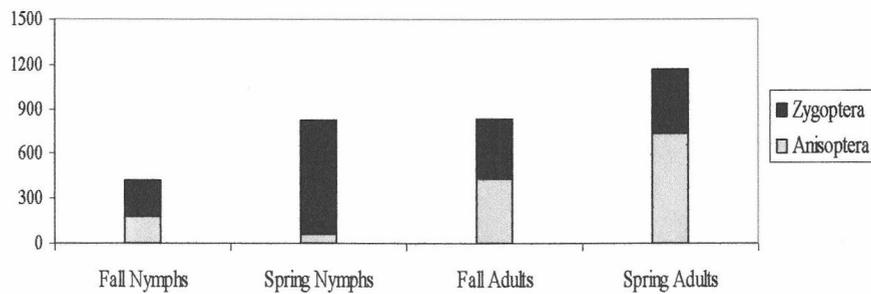


Figure 2.4: Total Odonate abundance at all sites by season and life stage

The three genera *Erythemis*, *Pachydiplax* and *Tramea* clustered together as they did in the nymphal analysis (Groups 1A, 1B and 3).

NMS analysis resulted in a 3-dimensional solution for both nymph and adult data (Table 2.5). Ordination produced similar associations to those found with HA cluster analysis; sites clustering together in HA appear near each other in ordination space (Figures 2.7 and 2.8). Several habitat variables were identified as significant on at least one of the three axes (r -value >0.350) of the nymph and adult ordinations. Of the matrix of 35 total variables (Table 2.3), NMS found

Table 2.5: Summary statistics of NMS ordinations of Odonate nymph and adult data

Analysis	Nymph	Adult
n-Dimensions	3	3
Cumulative r-Squared	0.955	0.78
Final stress	6.21478	12.0614
Final instability	0.00008	0.00001
Iterations	53	73
Monte Carlo p-Value	0.0196	0.0196
Beals Smoothing	Yes	No

8 significant habitat associations for the nymph ordination (Table 2.6) and 6 for adults (Table 2.7). Significant water quality parameters were hydro-period (permanent or temporary), water temperature and depth. Sediment depth, fish presence and presence of submerged wood also showed strong correlations. Significant landscape variables included agricultural activity, percentage of wooded cover and percentage of grassland cover (Figures 2.9-2.11).

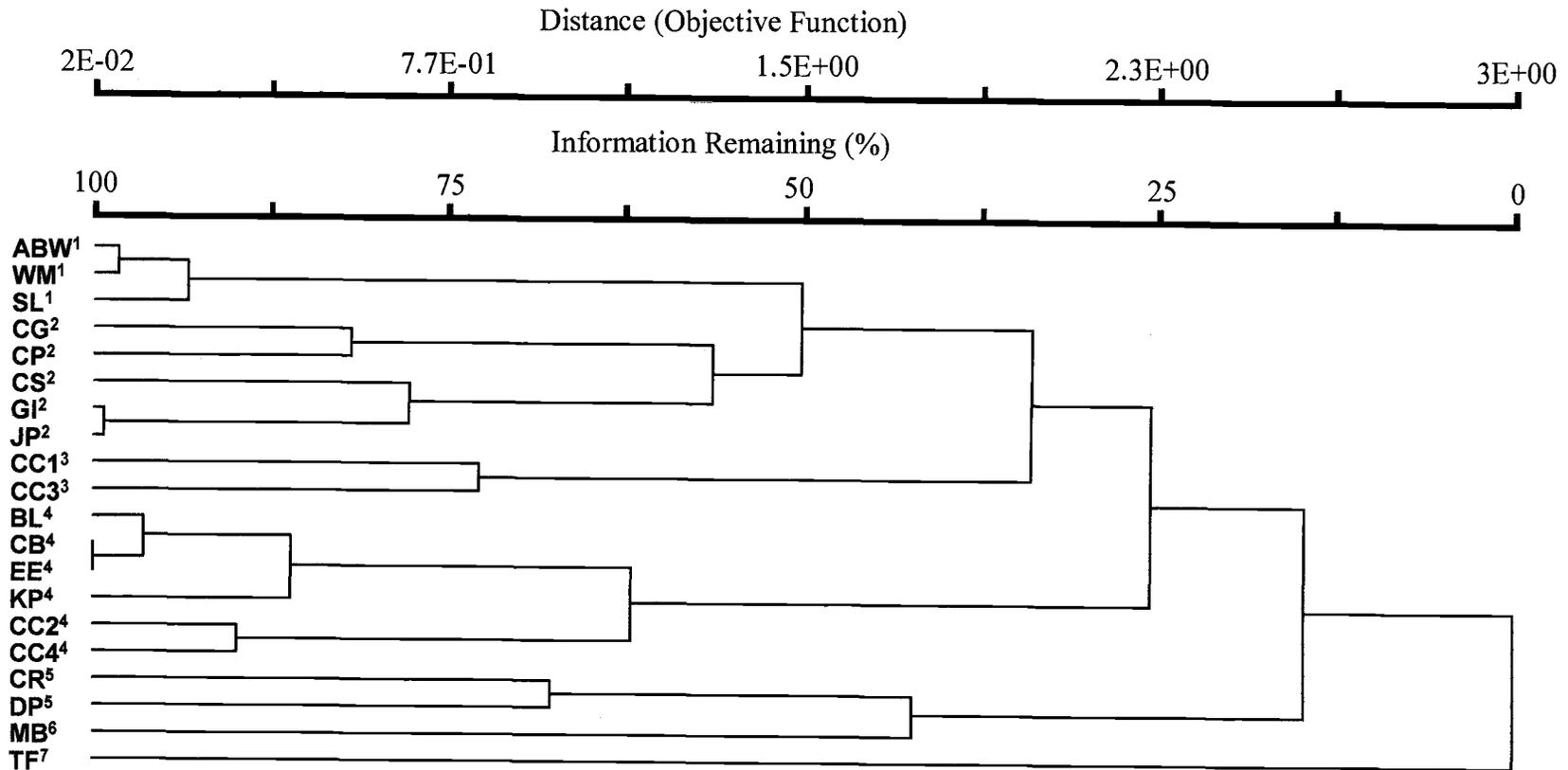
Table 2.6: r-Values for significant (>.350) habitat variables--NMS ordination of nymph species

Axis:	1	2	3
	r	r	r
Hydrology	--	--	0.546
H2O Temperature (degC)	--	--	-0.514
H2O depth (cm)	--	--	0.376
Sediment depth (cm)	-0.389	--	--
Fish Presence	--	--	0.537
Grassland Buffer	--	--	-0.638
Wooded Buffer	0.554	--	0.632
<i>Typha latifolia</i>	--	--	-0.481

Table 2.7: r-Values for significant (>.350) habitat variables--NMS ordination of adult species

Axis:	1	2	3
	r	r	r
Hydrology	0.737	--	--
H2O depth (cm)	0.390	--	0.351
Sediment depth (cm)	--	-0.493	--
Submerged wood	--	-0.397	0.397
Wooded Buffer	--	-0.596	--
Agriculture	--	--	-0.633

Comparison of habitat data to HA cluster analysis of odonate distribution data found correlation between habitat variables and HA groupings of both nymphs (Table 2.8) and adults (Table 2.9). Site grouping was related to hydroperiod and fish presence. Groups 1A and 1B in the adult HA analysis differed in the presence of *Typha latifolia* (Table 2.9).



Cluster 1: *Aeshna*, *Gomphus*, *Libellula*

Cluster 2: *Aeshna*

Cluster 3: *Lestes*, *Libellula*, *Sympetrum*

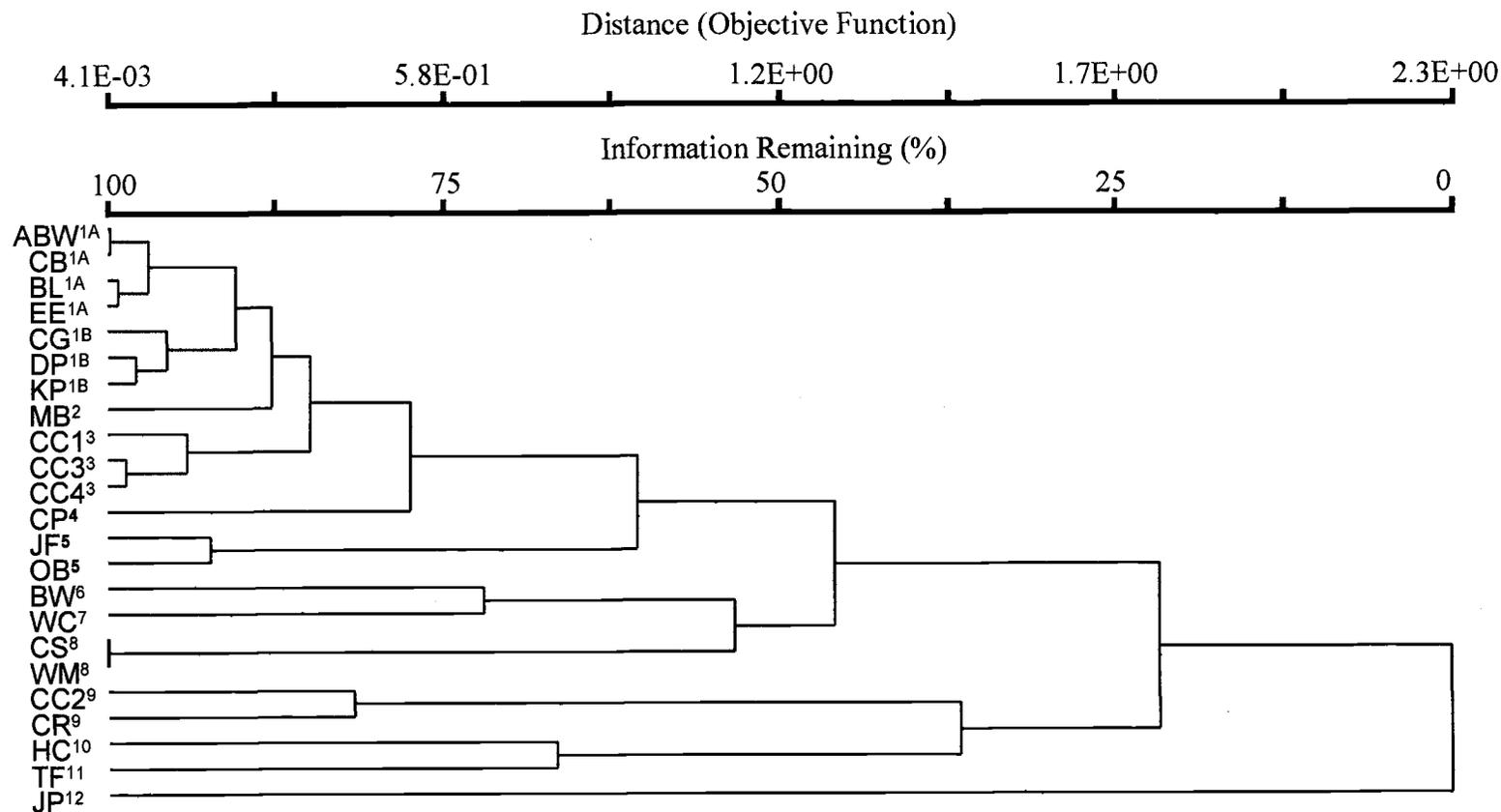
Cluster 4: *Lestes*, *Libellula*, *Sympetrum*, *Erythemis/Pachydiplax/Tamea*

Cluster 5: *Lestes*, *Sympetrum*, *Erythemis/Pachydiplax/Tamea*

Cluster 6:--

Cluster 7:--

Figure 2.5: HA cluster analysis of nymph Odonate assemblage data. Each site is indicated in the dendrogram by its site code (see Table 2.1). The superscript number indicates the cluster to which the site belongs.



- Cluster 1A: *Aeshna*, *Libellula*, *Sympetrum*, *Erythemis/Pachydiplax/Tamea*
- Cluster 1B: *Libellula*, *Sympetrum*, *Erythemis/Pachydiplax/Tamea*
- Cluster 2: *Aeshna*, *Libellula*
- Cluster 3: *Aeshna*, *Lestes*, *Libellula*, *Erythemis/Pachydiplax/Tamea*
- Cluster 4: *Libellula*

- Cluster 5: *Aeshna*, *Sympetrum*
- Cluster 6-8:--
- Cluster 9: *Lestes*, *Sympetrum*
- Cluster 10-12:--

Figure 2.6: HA cluster analysis of adult Odonate assemblage data. Each site is indicated in the dendrogram by its site code (see Table 2.1). The superscript number indicates the cluster to which the site belongs.

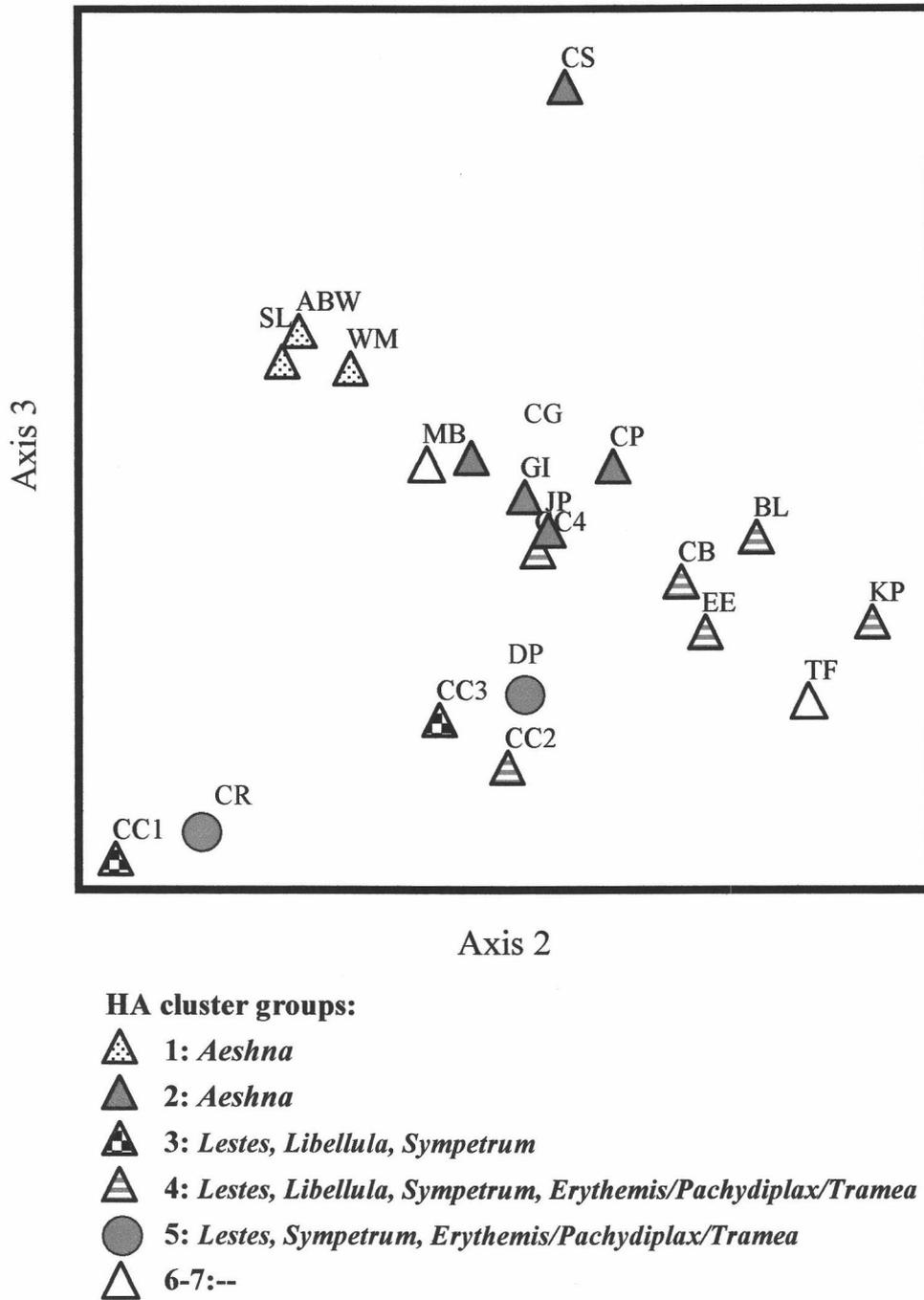


Figure 2.7: NMS ordination of nymph HA cluster groupings. Sites are coded to correspond with HA clusters. Sites clustered by HA ordinate together in NMS. Each site is identified by its site code (see Table 2.1)

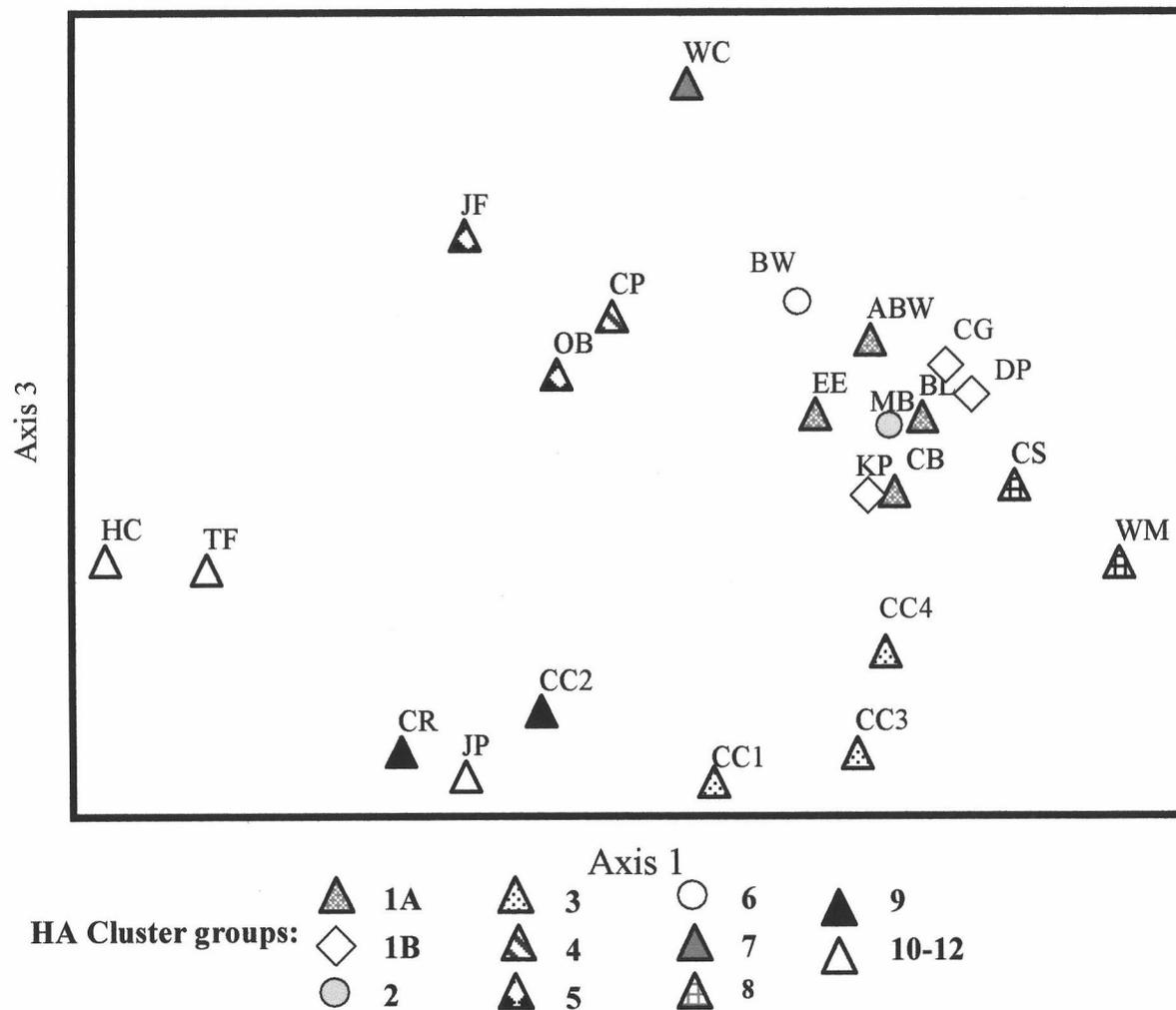


Figure 2.8: NMS ordination of adult HA cluster groupings. Sites are coded to correspond with HA clusters. Sites clustered by HA ordinate together in NMS. Each site is identified by its site code (see Table 2.1)

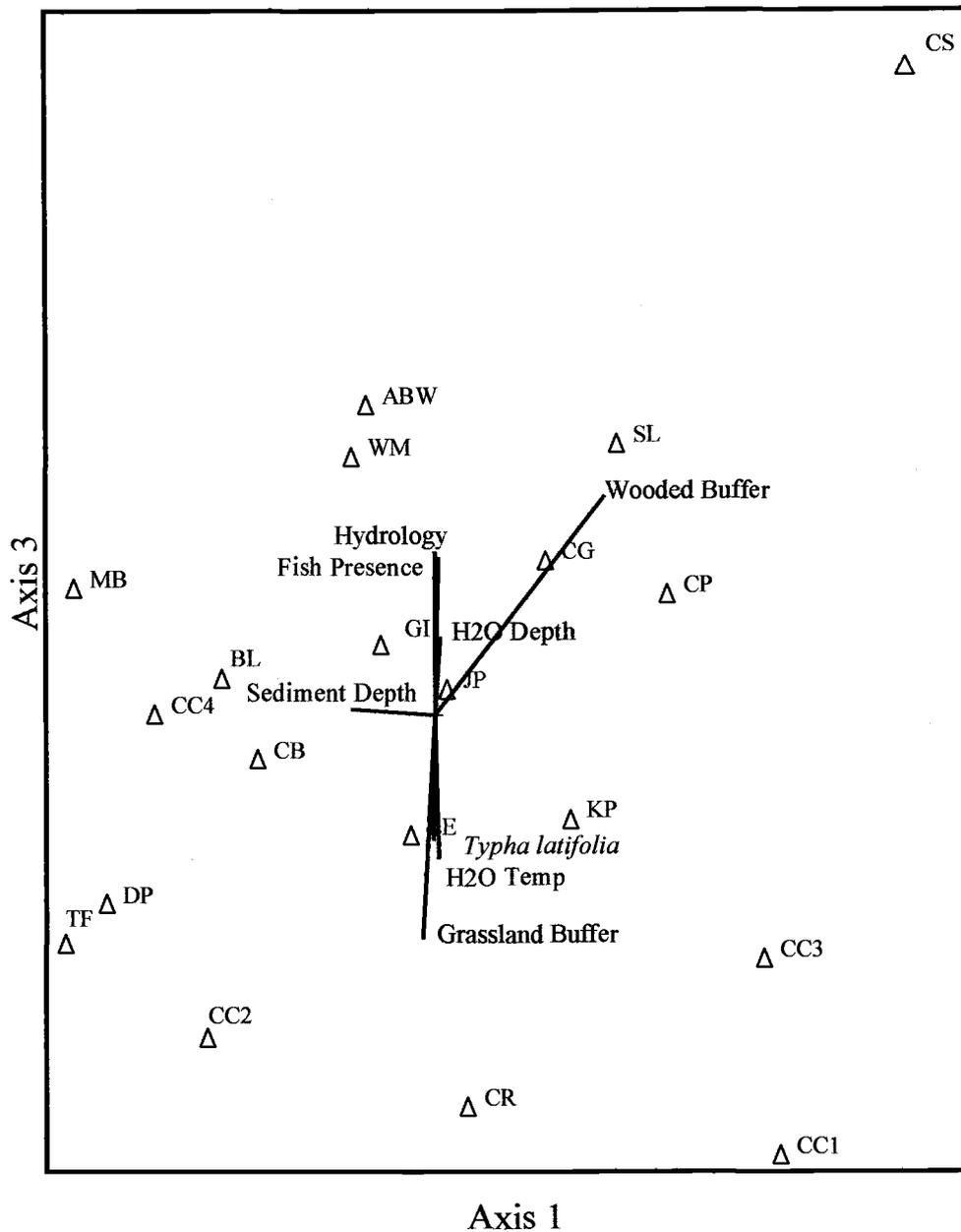


Figure 2.9: Bi-plot of significant habitat variables on NMS ordination of wetland sites by nymph species data: Axes 1 and 3. The length of the vector indicates the relative strength of the correlation. The direction of the vector indicates the axis or axes with which the variable is correlated.

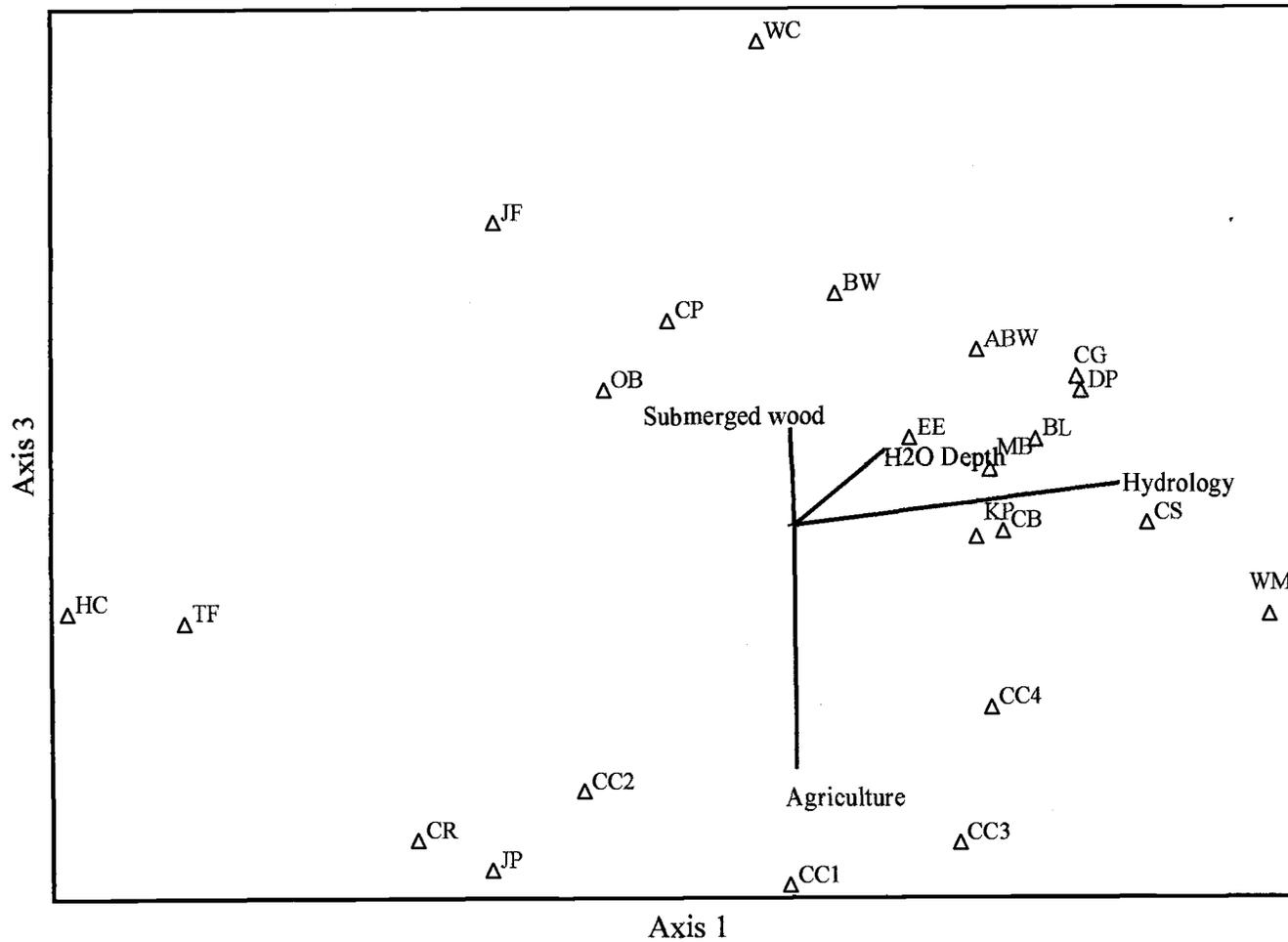


Figure 2.10: Bi-plot of significant habitat variables on NMS ordination of wetland sites by adult species data: Axes 1 and 3. The length of the vector indicates the relative strength of the correlation. The direction of the vector indicates the axis or axes with which the variable is correlated.

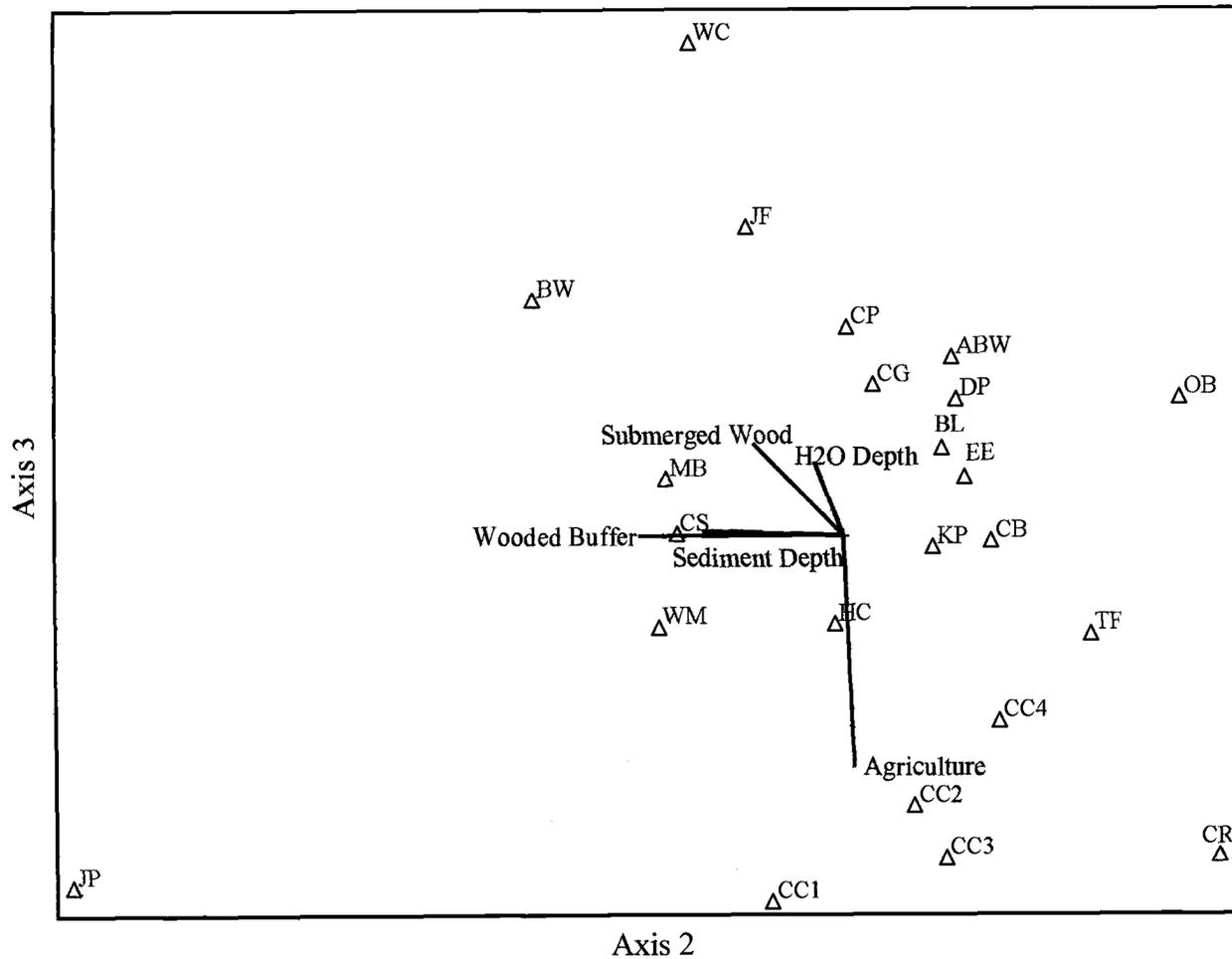


Figure 2.11: Bi-plot of significant habitat variables on NMS ordination of wetland sites by adult species data: Axes 2 and 3. The length of the vector indicates the relative strength of the correlation. The direction of the vector indicates the axis or axes with which the variable is correlated.

Table 2.8: Habitat conditions at sites clustered by HA of nymph data

Site Code	Cluster	Hydroperiod	<i>Typha latifolia</i>	Submerged wood	Fish Presence	Dominant odonate taxa
ABW		P	Y	N	Y	
WM	1	P	N	N	N	<i>Aeshna, Gomphus, Libellula</i>
SL		P	N	N	Y	
CG		P	N	N	Y	
CP		T	Y	N	Y	
CS	2	P	N	Y	Y	<i>Aeshna</i>
GI		P	N	Y	Y	
JP		T	N	Y	Y	
CC1	3	T	Y	N	N	<i>Lestes, Libellula, Sympetrum</i>
CC3		P	N	N	N	
BL		P	Y	Y	Y	
CB		P	Y	N	Y	
EE	4	P	Y	N	Y	<i>Erythemis, Lestes, Libellula,</i>
KP		P	N	Y	Y	<i>Pachydiplax, Sympetrum, Tramea</i>
CC2		T	Y	N	N	
CC4		P	Y	N	N	
CR	5	T	Y	N	N	<i>Erythemis, Lestes, Pachydiplax,</i>
DP		P	N	Y	Y	<i>Sympetrum, Tramea</i>
MB	6	P	Y	Y	Y	no distinct taxa
TF	7	T	N	N	N	no distinct taxa

P=permanent

T=temporary

Table 2.9: Habitat conditions at sites clustered by HA of adult data

Site Code	Cluster	Hydroperiod	<i>Typha latifolia</i>	Submerged wood	Fish Presence	Dominant odonate taxa
ABW	1A	P	Y	N	Y	<i>Aeshna, Erythemis, Libellula, Pachydiplax, Sympetrum, Tramea</i>
CB		P	Y	N	Y	
BL		P	Y	Y	Y	
EE		P	Y	N	Y	
CG	1B	P	N	N	Y	<i>Erythemis, Libellula, Pachydiplax, Sympetrum, Tramea</i>
DP		P	N	Y	Y	
KP		P	N	Y	Y	
MB	2	P	Y	Y	Y	<i>Aeshna, Libellula</i>
CC1	3	T	Y	N	N	<i>Aeshna, Erythemis, Lestes, Libellula, Pachydiplax, Tramea</i>
CC3		P	N	N	N	
CC4		P	Y	N	N	
CP	4	T	Y	N	Y	<i>Libellula</i>
JF	5	T	Y	Y	N	<i>Aeshna, Sympetrum</i>
OB		P	Y	Y	Y	
BW	6	P	Y	Y	Y	no distinct taxa
WC	7	T	Y	Y	N	no distinct taxa
CS	8	P	N	Y	Y	no distinct taxa
WM		P	N	N	N	
CC2	9	T	Y	N	N	<i>Lestes, Sympetrum</i>
CR		T	Y	N	N	
HC	10	T	N	Y	Y	no distinct taxa
TF	11	T	N	N	N	no distinct taxa
JP	12	T	N	Y	Y	no distinct taxa

P=permanent

T=temporary

In HA cluster analysis using site habitat parameters, rather than odonate assemblages, clusters did not match clusters formed by odonate assemblages. NMS resulted in a one-dimensional ranked ordination, which revealed that wetland area (m²) and perimeter were most significant in the ordination of sites by habitat attributes. Wetland area and perimeter did not correspond to ordination of sites by odonate assemblage. Odonate species distributions were found to correlate with individual habitat variables within wetlands, rather than grouping with wetland clusters.

The distribution of members of *Libellula* correlated strongly to wetlands where water was present throughout the year (Figure 2.12). Water permanence also correlated with the distributions of *Erythemis collocata*, *Pachydiplax longipennis* and *Tramea lacerata*. Distributions of the damselfly genera *Enallagma* and *Ishnura* were also associated with permanent wetlands.

Distributions of *Aeshna* and *Lestes* nymphs and adults did not associate strongly with water permanence, and were found at a range of permanent and temporary sites. These species did associate with the distribution of large emergent plants, specifically *Typha latifolia* (Figure 2.13). HA cluster analysis revealed that *Aeshna* and *Lestes* clustered at sites with *T. latifolia* present. *T. latifolia* distributions were related to the separation of HA cluster 1 into 1A and 1B (Figure 2.6). 1A sites containing *T. latifolia* had *Aeshna* and *Lestes* in their assemblages; sites in 1B lacked *T. latifolia*, where *Aeshna* and *Lestes* were not abundant. *Aeshna* adults also associated with wetlands that contained fallen logs (Figure 2.13). *Aeshna umbrosa* in particular was found to correlate with sites that were surrounded by a high percentage (>50%) of wooded land cover.

Lestes adult and nymph distributions correlated negatively with fish, i.e. they were present where fish were absent (Figure 2.14). A comparison of the

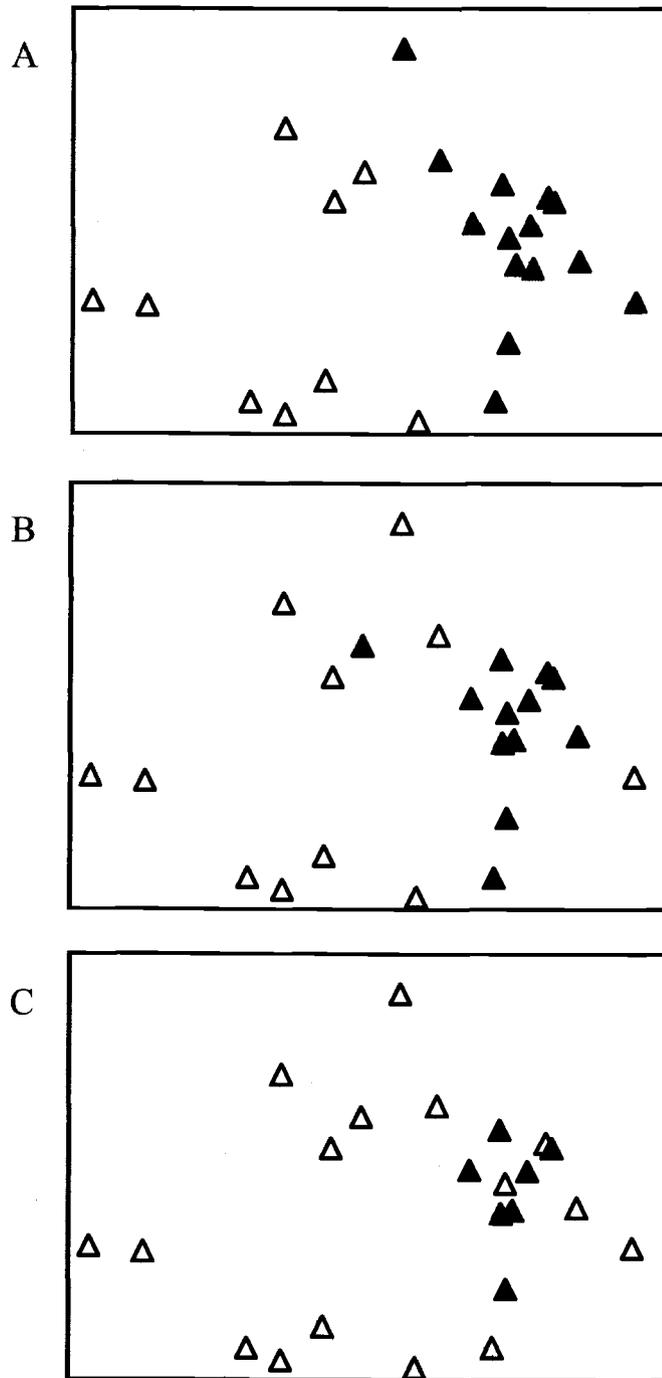


Figure 2.12: Comparison of distribution of *Libellula* and *Erythemis collocata* adults to site hydroperiod. Ordinations are (A) sites where *Libellula* are present (black triangles) (B) sites where *E. collocata* is present (black triangles), and (C) distribution of permanent sites (black triangles). Strong correlation can be seen between these odonates and hydrologic permanence.

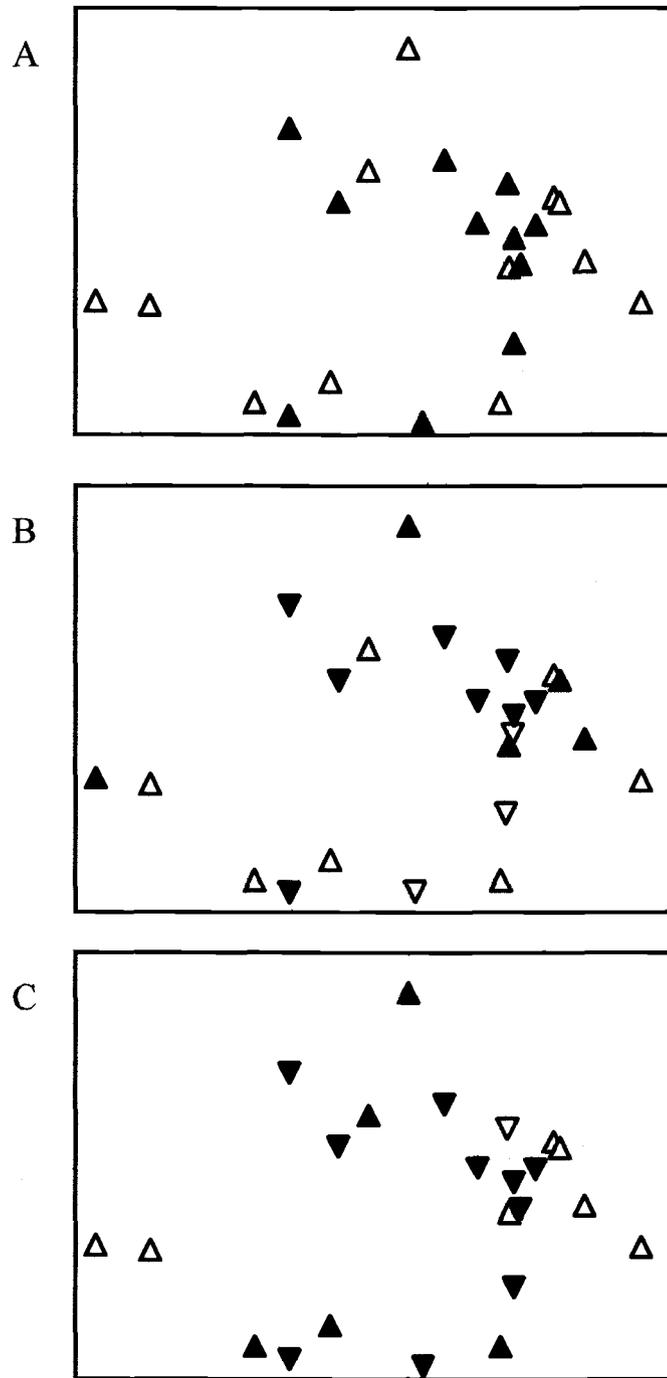


Figure 2.13: Comparison of *Aeshna* adults to distributions of submerged wood and *Typha latifolia*. Ordinations are (A) distribution of *Aeshna* (black triangles), (B) distribution of sites with submerged wood (black triangles) and (C) distribution of sites with *T. latifolia* present (black triangles). In B and C, sites where *Aeshna* are present are rotated 180°. *Aeshna* adults are found at sites where *T. latifolia* or submerged wood are present.

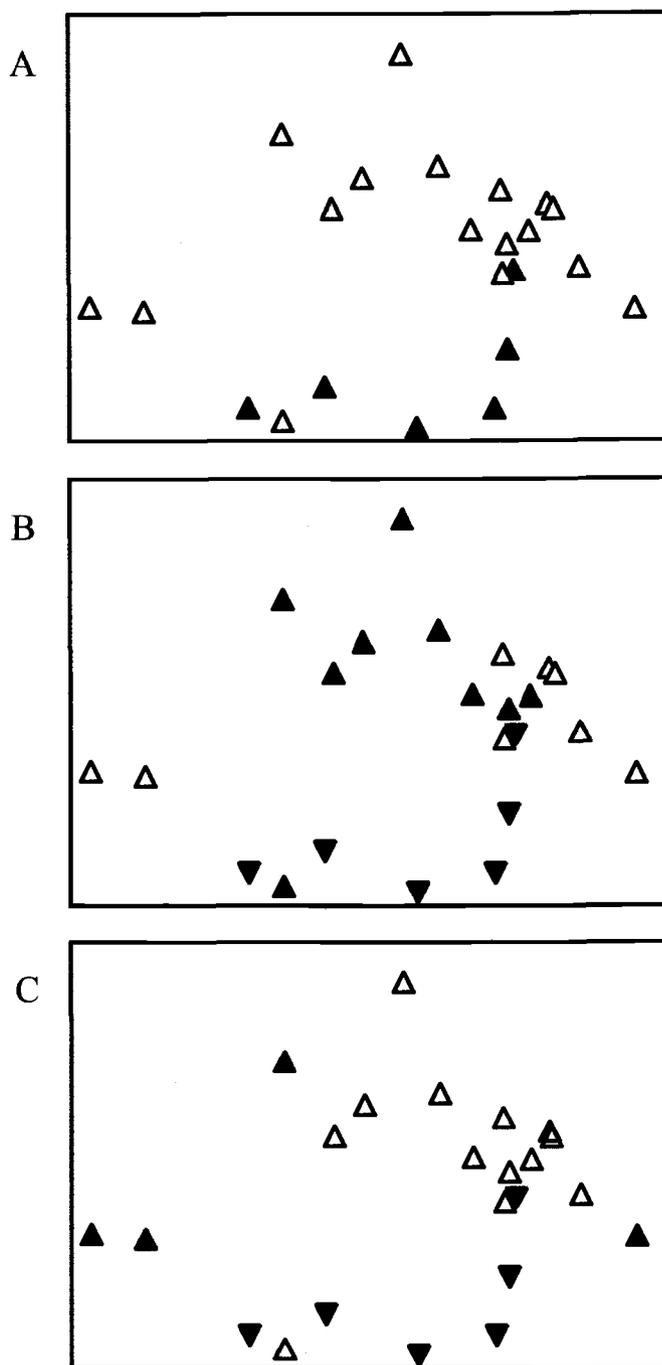


Figure 2.14: Comparison of *Lestes* adults to distributions of *Typha latifolia* and fish presence. Ordinations are (A) distribution of *Lestes* (black triangles) (B) distribution of *T. latifolia* (black triangles) and (C) distribution of sites without fish (black triangles). In B and C, sites where *Lestes* are present are rotated 180°. *Lestes* were found only at sites with *T. latifolia* present and fish absent.

adult and nymph stage distributions of *Aeshna* and *Lestes* reveals a difference in life stage distribution patterns. *Aeshna* adults were found at a greater range of sites than their nymphs, while *Lestes* nymph and adult distributions were quite similar. *Aeshna* nymphs were found predominantly at sites where fish were absent, but those sites also had a longer hydro-period than sites where *Lestes* occurred.

Distributions of *Sympetrum* species were more variable than other dragonflies in this study. Though *Sympetrum* adults were found at a range of permanent and temporary sites, *S. occidentale* and *S. pallipes* were found more commonly at temporary sites than other *Sympetrum* species. *Sympetrum* nymphs were also found at temporary sites. An overall correlation with sites surrounded by grassland and cropland (habitat factors Grassland Buffer and Agriculture) was observed for this genus (Figure 2.15). *Sympetrum* inhabited only two sites—Oaks Bottom (OB) and Delta Ponds (DP)—that did not have large grass buffers. These sites were two of the largest included in the survey (21,000 and 28,000 m², respectively).

Using data from adult distributions, sites were ranked in order of decreasing species richness (Figure 2.16). When ranked in this manner, sites that were permanently wet demonstrated the highest overall richness, and sites with few or no species were dry for a large portion of the summer (May-November). Consideration of species abundance distributions shows a more complex pattern. Most species are found at permanent sites, and species adapted to permanent sites such as *Libellula* are found to be most abundant there (Figure 2.17). Species adapted to temporary sites such as *Lestes* reach peak abundance in temporary environments (Figure 2.18).

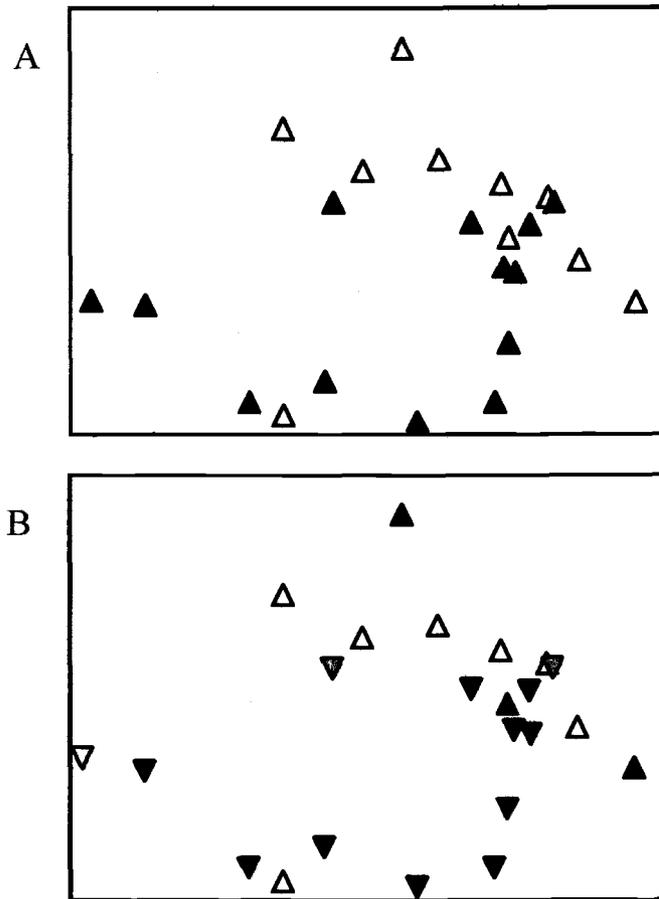


Figure 2.15: Comparison of *Sympetrum* adults to grassland buffer. Ordinations are (A) distribution of *Sympetrum* (black triangles) and (B) distribution of sites with surrounding 200-foot buffer area containing greater than 50-percent grasslands (black triangles). In this view, sites where *Sympetrum* are present are rotated 180°. *Sympetrum* are associated with grassland sites. Two sites, Oaks Bottom (OB) and Delta Ponds (DP) (gray triangles) correlated with *Sympetrum* but had lower than 50-percent grassland buffer.

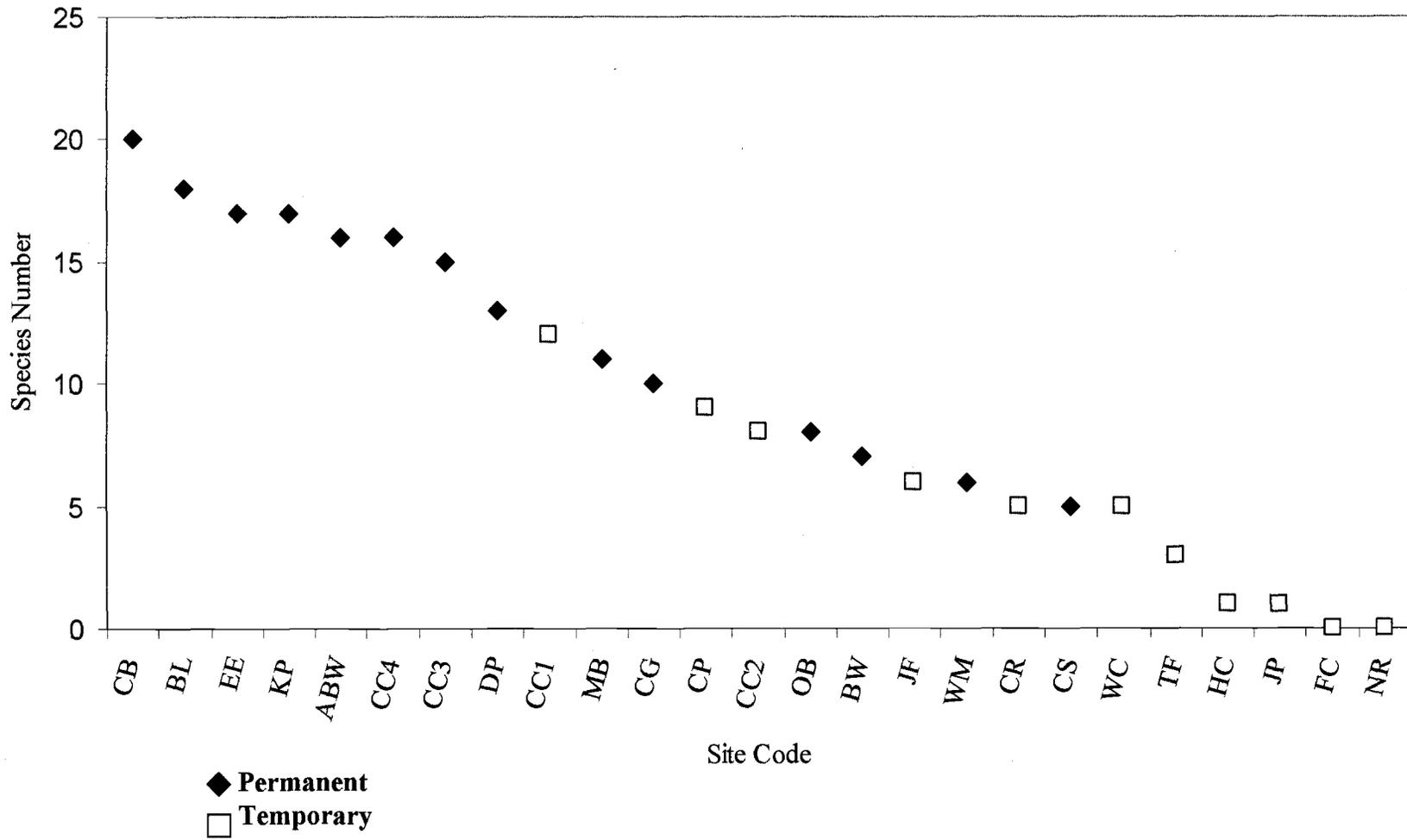


Figure 2.16: Sites ranked by adult Odonate species richness. Symbols are coded to reflect site hydroperiod. An overall correlation is seen between hydrologic permanence and species richness.

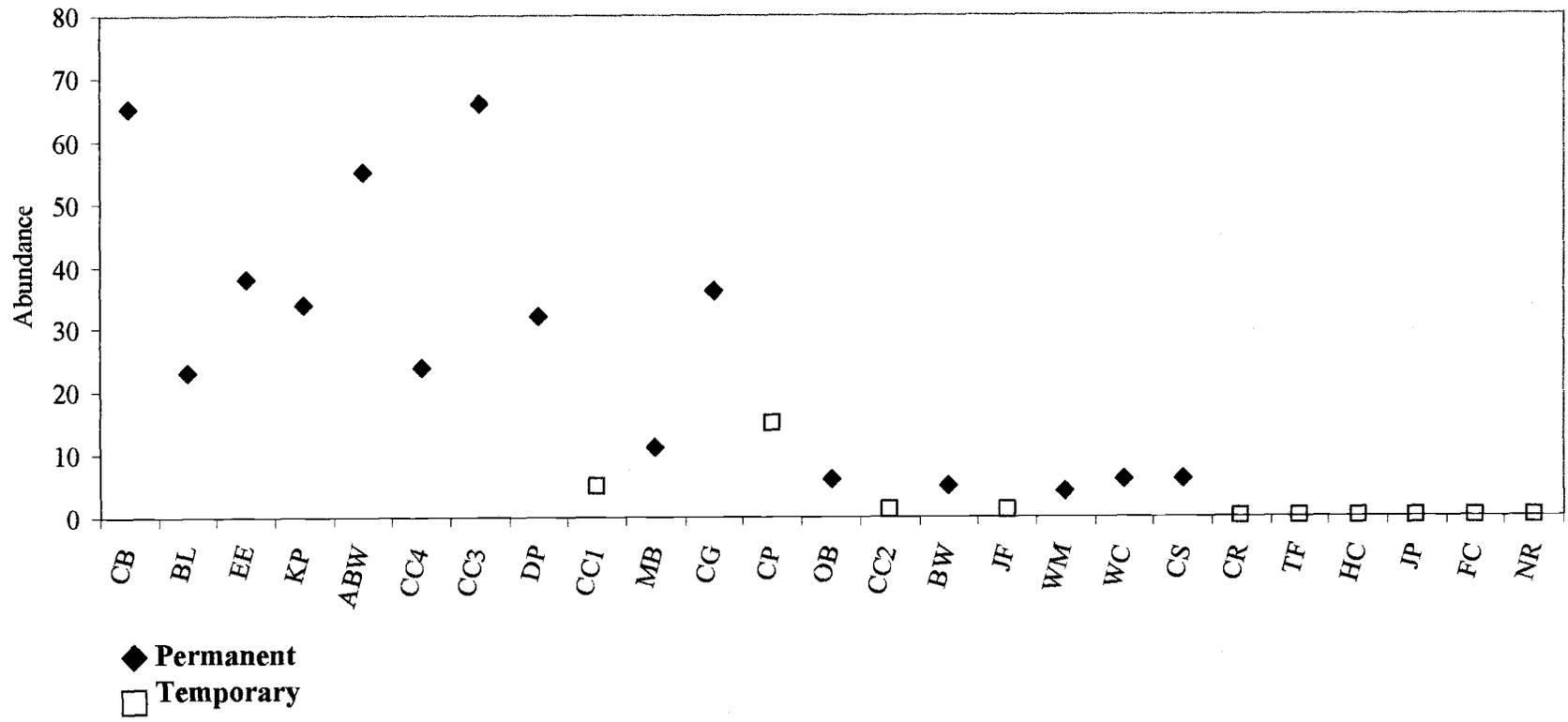


Figure 2.17: *Libellula* abundance vs. sites ranked by species richness. Like species richness (Figure 2.16) abundance of the four species in *Libellula* is highest at sites with hydrologic permanence.

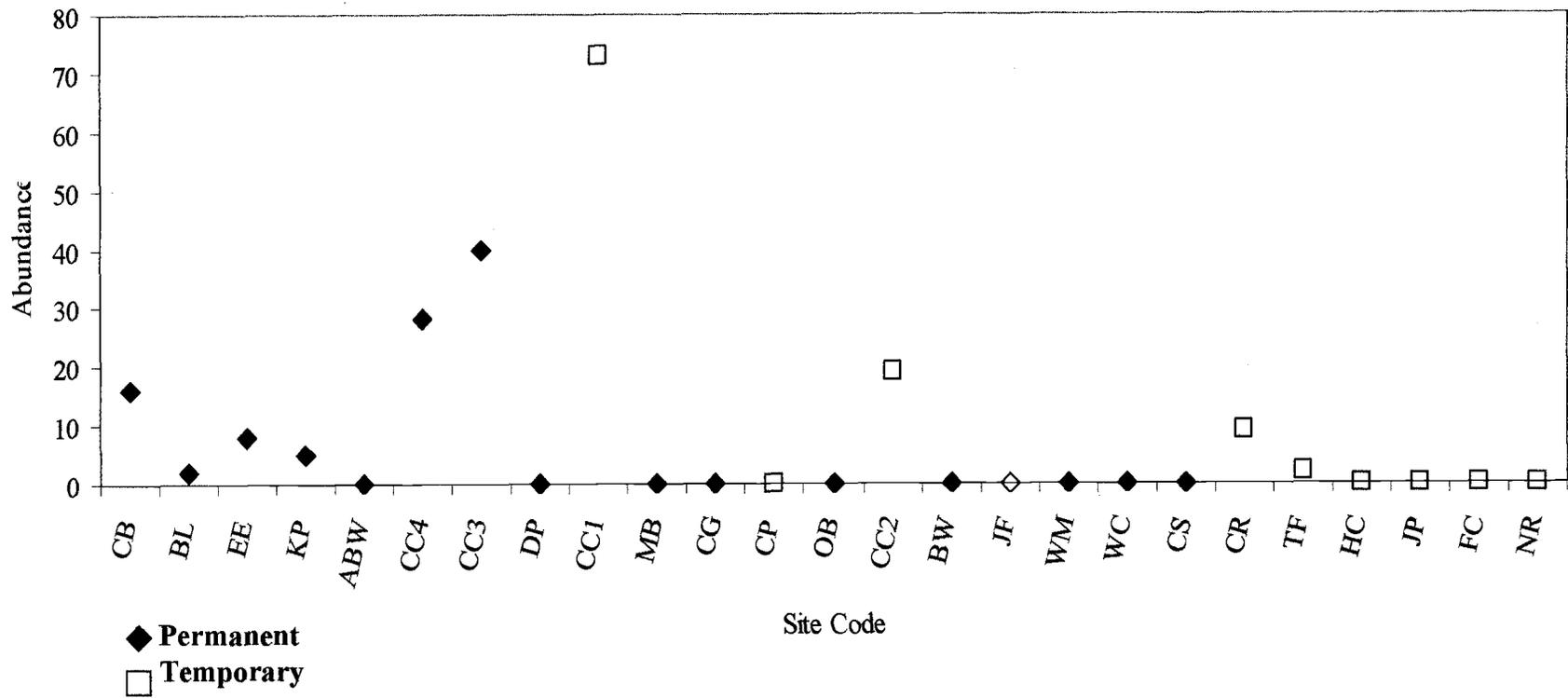


Figure 2.18: *Lestes* abundance vs. sites ranked by species richness. Abundance of the three species in *Lestes* is not highest at sites with hydrologic permanence, as *Lestes* often exploits temporary habitats. Species richness is a less effective measure of habitat quality for these species.

DISCUSSION

How are odonates distributed in riverine wetland habitats? While the odonate species identified in this study have been documented throughout the Willamette Valley, species were not distributed at all sites. Sites were often inhabited by several species within a single genus, but genera were distributed within individual sites based on habitat conditions within a wetland. Most odonate species identified in this study, 23 of the 27 total species, were distributed at multiple sites throughout the valley. Four species, *Aeshna umbrosa*, *Archilestes californica*, *Gomphus kurilis* and *Sympetrum danae*, were each found at a single site. All these uncommon species are active as adults in the middle to late summer except *G. kurilis*, which begins its adult flight season in May (Kennedy 1913, Needham, Westfall and May 2000). According to county distribution records (Oregon Dragonfly and Damselfly Survey 2002) *A. californica* and *S. danae* are not as widely distributed in the Valley as many species in this study, but are found often enough not to be considered "rare". *Aeshna umbrosa* is broadly distributed in Oregon, but prefers heavily wooded habitat in sluggish streams and ditches (Walker 1956). Lack of these habitats in the study, only four, may explain their rarity. *G. kurilis* is found in a broad range of habitats, but is more commonly associated with stream rather than wetland environments.

Seasonal differences in adult and nymph activity were observed in the odonate assemblage. Species such as *Sympetrum pallipes* and *Lestes congener* were active as adults in the late summer, reaching their peak abundance in September, while *Aeshna californica* and *Libellula lydia* are active as adults in

May (Walker 1956). Sampling periods for wetland odonates should account for these differences in phenology; a single sample or repeated samples at the same time each year will not characterize the total odonate assemblage at a site.

How do odonate distributions correlate with habitat conditions? Hydro-period demonstrated the strongest habitat correlation with both nymphs and adults. *Erythemis collocata*, *Libellula forensis*, *L. luctuosa*, *L. lydia*, *L. pulchella*, *Pachydiplax longipennis*, and *Tramea lacerata* were all limited to sites that had permanent standing water throughout the year. These species also correlated with water depth and temperature. These habitat variables correspond with hydro-period; permanent sites often have greater water depth and lower water temperatures than temporary sites (Table A.2.3). Permanent sites had the highest species richness in the study, containing from 15 to 20 species. Other species in this study were found at both permanent and temporary wetlands.

Temporary sites in this study can be further divided into sites that contain standing water from the autumn to early summer (September/October—June) and sites that contain water from winter into early spring (November—April/May). Sites with this shortest period of inundation often had few or no odonates present. These sites may be dry for too long during the winter season to support odonate nymphs (Corbet 1999).

Vegetation structure, particularly *Typha latifolia*, correlated with distributions of *Aeshna palmata*, *A. multicolor*, *Lestes congener*, *L. disjunctus* and *L. dryas*. Species within these genera use the stems of these emergent plants as oviposition sites (Corbet 1999, Walker 1956). *Aeshna californica* and *A. umbrosa* oviposit their eggs within the tissue of submerged logs. Adults of these species were associated with submerged wood distributions.

Lestes distributions correlated negatively with fish presence. *Lestes* were found at sites that contained *T. latifolia* but did not contain fish. Both nymphs

and adults of *Lestes* were associated with fishless sites. While fish are common predators of nymphs (C. Pearl, pers. comm.), they have fewer opportunities to prey on adults, and would not be expected to correlate as strongly with adult distributions. Negative correlation of fish presence with *Lestes* adult presence may be a result of the short dispersal distance of these species. *Lestes* adults are more likely to be found at nymphal sites, which would explain the indirect effect of fish on *Lestes* adult distributions. *Aeshna* nymphs were also commonly found in fishless sites, but *Aeshna* adults were distributed at sites with fish. *Aeshna* are stronger flyers than *Lestes*, and are likely to disperse farther from their emergence site.

Five sites within this study had a speciose adult assemblage, but a depauperate nymph assemblage. While some of these sites were dry for long periods in the summer others were permanently wet. Lack of nymphs at these permanent sites (BW, OB) may be explained by fish predation. Adults cannot detect the presence of fish at a site (Corbett 1999), and may therefore oviposit in sites where their nymphs will be consumed by fish.

Surrounding land cover correlated with nymph and adult distributions. The predominance of wooded and grassland cover was associated with nymphs, while wooded and cropland cover was associated with the distribution of adults. The presence of a wooded buffer was associated with the distribution of *Aeshna umbrosa*. While this association with wooded sites is expected based on the literature for this species (Walker 1956) it should be noted that *A. umbrosa* was found at a single site in this study. *Sympetrum* were associated with sites surrounded by grasslands (Figure 2.16). Temporary sites are often associated with grassland or cropland environments. *Sympetrum* were found in temporary sites; which may explain this habitat correlation.

How do nymphs and adults differ in their responses to habitat

conditions? Comparison of life-stage distributions indicates that adults were more widely distributed than nymphs. Only 21% percent of the total species list was found as both adult and nymph at any site. Considering the habitat requirements of these species, we would not expect to find all species at the same site, but many sites were found to contain only adults. While these results may be affected by differences in sampling efficiency of nymph and adult assemblages, adult odonates are able to move considerable distances, and many species tend to disperse in their subimago stage (Corbett 1999). These adults range widely to forage before ovipositing, and may visit a number of wetlands. These wetlands may offer acceptable foraging habitat for odonate adults, but may be unacceptable habitat in which to complete the life cycle.

While nymphs and adults were associated with similar habitat characteristics, some characteristics distinguished nymphs and adults. Nymph distributions corresponded not only to hydro-period, but also to water temperature. These variables would be expected to correlate; permanent sites tend to be deeper, which would cause water temperatures to be lower. Nymph assemblages also demonstrated a much stronger correlation with the distribution of *T. latifolia* than the adults. This correlation can again be related to the differing dispersal ranges of nymphs and adults. Though several species require these plants for oviposition sites, adults move from their emergence sites while foraging, and are observed at sites without these plants. Nymphs are found near the oviposition site, and are much more likely to correlate to distributions of *T. latifolia*. *Lestes* adults are an exception to this, as described above.

Some observations should be made on the effects of Beals smoothing on interpretation of nymph NMS results. *Libellula* nymphs demonstrated an unexpected lack of correlation with hydro-period when analyzed by NMS. *Libellula* were found only at permanent sites, but do not correspond with

permanence on Axis 3 of the ordination (Figures 2.9 and 2.10). Beals smoothing transforms presence absence data into probability data based on species associations. The co-occurrence of two species at one or more sites increases the calculated probability that these species will be found together at another site. While *Libellula* distribute exclusively at permanent sites, those species that use temporary sites are commonly found at permanent sites as well. The presence of these species in the assemblage at permanent sites may establish associations between these species and *Libellula*, increasing probability estimates of its appearance at temporary sites. The nature and limitations of NMS as an exploratory analytical technique should be kept in mind when interpreting results.

What level of taxonomic resolution is necessary to understand odonate-habitat responses? Many of the habitat associations found in this study can be interpreted at the generic level. While the genera found in this study often contain a number of species, these congeners demonstrate similar responses to habitat conditions. Some intra-generic variation is observed however in *Aeshna*, where *A. californica* and *A. umbrosa* favor oviposition in fallen, submerged logs rather than emergent wetland plants as practiced by *A. multicolor* and *A. palmata*. *Sympetrum* species also appear to vary in their preference for temporary sites; *S. corruptum* and *S. ilotum* are found more commonly at permanent sites than their congeners. An explanation for this pattern was not found. Analysis at the species level provided the most detailed information on habitat correlations.

Do odonates meet the criteria of Target Taxon Analysis? Odonates were found to be abundant in the wetlands in this study. While endemism was not high in the odonate assemblage, species richness and response to varying habitat conditions make odonates potential candidates for Target Taxon Analysis (Kremen 1994). The species identified in this study, particularly those within family Libellulidae, demonstrate a broad range of responses to habitat conditions

in wetlands. In this research, odonate distributions were studied at non-impacted wetlands. Further study of the response of odonate assemblages to pollution and habitat degradation is necessary to determine their response to environmental stressors.

A further benefit in using odonates in habitat assessment is their worldwide distribution. The genera found at these wetland sites are distributed on many continents. Development of comparable surveys for local species assemblages could extend the use of this technique to wetlands in many temperate regions.

How do odonate habitat associations compare to site species richness as a measure of habitat quality? Species distributions reflect the correlation between species richness and permanence (Figure 2.16). Permanent sites tend to have more species overall, with species adapted to both permanent and temporary conditions. Temporary sites have only species adapted to drying conditions. Two sites from this study contained no odonate species. These sites were dry for six to seven months of the year.

Though species richness serves as a general indicator of habitat quality, it is not sensitive to species distributions on a landscape level. Fourteen species in this study demonstrated adaptations to temporary sites, and are often found to be most abundant in those sites. Species richness does not reflect these patterns. While sites that support high odonate species richness are important to odonate diversity, other sites that contain only a few species provide habitat that these species are specialized to use (Figures 2.16 and 2.17). Managing for large-scale habitat diversity would be more effective than attempting to maximize site-to-site diversity.

What information do surveys of odonate diversity provide to wetland managers? Based on our findings, several recommendations can be made in the use of odonate distributions as indicators of habitat condition or quality.

Hydro-period. Wetland habitat is often degraded by the alteration of hydrologic patterns, by filling of the wetland or water control, measures. Wetland restoration often involves the removal of these water control devices. An increase in odonate diversity, or a change in the odonate species assemblage of a site can indicate a positive ecological response to alteration of hydro-period.

Vegetation structure. The planting of wetland plant species or removal of invasive plants is a common restoration activity. Odonates depend on wetland vegetation for nymph habitat and for oviposition sites. The presence of species that depend on these native wetland plants could be used to evaluate the ecological response to plantings.

Fish presence. While degradation of wetland habitat often involves drainage, wetlands are also altered by increasing the amount of water they contain. Wetlands transformed into pond environments are sometimes stocked with non-native fish. Research has shown that these fish have a negative effect on the wetland invertebrate community, and can decimate odonate populations (Pearl and Adams, in prep). Attempts to control or remove introduced fish can be evaluated for effectiveness by the presence of odonates, monitoring odonate nymph populations or sampling with emergence traps.

Surrounding land cover. The development of buffer zones of grassland, wood or shrubs around wetlands can be measured by an increase in species such as *Aeshna umbrosa*, *Sympetrum spp.* or other odonates associated with these land cover conditions.

Synthesizing the findings in this study (Table 2.10) provides information on the expected odonate species in a particular wetland habitat, and allows the

Table 2.10: Wetland habitat information indicated by odonate species

Species	Hydrology	Vegetation Structure	Fish Presence	Surrounding Landcover		
<i>Aeshna californica</i>	Species that utilize both temporary and permanent habitats	Species that associate with large emergent vegetation and submerged wood	Species that demonstrate a negative correlation with fish, appearing more commonly in their absence	No association w/ land cover		
<i>Aeshna umbrosa</i>				Associated w/ wooded buffer sites		
<i>Aeshna multicolor</i>						
<i>Aeshna palmata</i>		Species that associate with large emergent vegetation		No apparent land cover preference		
<i>Lestes congener</i>						
<i>Lestes disjunctus</i>		Species that demonstrate no association with vegetation structure		Species that demonstrate no association with vegetation structure	Species that are associated with wetlands that contain greater than 50% grassland in a 200-foot buffer	
<i>Lestes dryas</i>						
<i>Sympetrum corruptum</i>						
<i>Sympetrum danae</i>						
<i>Sympetrum ilotum</i>						
<i>Sympetrum madidum</i>						
<i>Sympetrum occidentale</i>						
<i>Sympetrum pallipes</i>						
<i>Sympetrum vicinum</i>						
<i>Libellula forensis</i>	Species that utilize permanent habitats exclusively		Species that demonstrate no association with vegetation structure			Species that appear in both fish inhabited and fishless wetlands
<i>Libellula luctuosa</i>						
<i>Libellula lydia</i>						
<i>Libellula pulchella</i>						
<i>Erythemis collocata</i>						
<i>Pachydiplax longipennis</i>						
<i>Tramea lacerata</i>						

odonate assemblage to serve as a wetland habitat indicator. Assessing the odonate habitat characteristics of a wetland site. The lack of expected odonate species can indicate compromised habitat quality, and can be suggestive of potential restoration options.

Suggestions for future research would include investigation into the response of odonate species to restoration efforts. Study of odonate responses to environmental stressors is also suggested. Investigation of the ecology of key groups within the odonate assemblages, such as the members of *Sympetrum*, would better define the habitat associations of these species, and improve their effectiveness as wetland indicators.

The use of odonates as habitat indicators is made more effective by the relative ease with which wetland odonate species can be identified. The genera within this study are all morphologically distinct, and many species are easy to identify on the wing. Excellent field guides (Dunkle 2000) are now available for odonates. Competency in species identification can be gained with a minimum of time and effort. The genera observed in this study are also broadly distributed, with many found throughout the world. The global distribution of odonates makes the development of local indicators possible in many parts of the world.

While our results indicate several key habitat variables that are associated with odonate species distributions, habitat management decisions made with these findings should be performed from an ecosystem perspective. The maximization of a single habitat attribute, without consideration of other factors, is not likely to improve overall habitat quality or improve odonate diversity. As an example, while odonate species richness was observed to be highest in wetlands that have permanent standing water, the introduction of permanent water alone would not be an effective restoration approach, especially in areas where permanent wetlands are not a natural feature. Management of wetland habitat on a

landscape level, to insure a diversity of native habitat types, would be the most effective approach for maximizing odonate diversity and improving wetland habitat quality.

CHAPTER 3

ODONATE LIFE HISTORY AND SPECIES DISTRIBUTIONS

ABSTRACT

Hydro-period, vegetation structure, presence of fish and surrounding land cover are associated with the distributions of dragonflies and damselflies (Insecta: Odonata) in the riverine wetlands of the Willamette Valley in western Oregon, USA. Life history and natural history attributes for 27 odonate species were analyzed to identify associations with species distributions. Life history data for each species present in the wetlands were subjected to Non-metric Multidimensional Scaling (NMS) to evaluate biological similarities between species. Life history patterns correlated strongly with hydro-period, as did species richness. Life history and natural history variables such as oviposition location, presence of a resting egg, over wintering life stage and nymph foraging strategy were all associated with hydro-period, and were related to species distributions at a given site. Sites with permanent standing water contained species adapted to both permanent and temporary habitats, while temporary sites contained only species adapted to this environment. Permanent sites therefore had higher species richness overall, though only species adapted to permanent habitats were found at their highest abundance at these locations. Understanding the life history and natural history attributes of species and their correlations with habitat conditions reveals patterns not detected by richness measures.

INTRODUCTION

While identifying organism-habitat interactions is integral to developing biological indices of habitat quality, often the correlation of faunal distributions to habitat gradients is made without studying the biology or life history of the organism in question (Kremen et. al. 1993). This absence of life history information is considered acceptable for two reasons. When correlations between a species (or assemblage) response and a particular habitat attribute (pollution level, land-use practice) can be made, the underlying biology of this response may not be necessary for the index to be effective. The life history of indicator organisms is also often unknown, and would be extremely difficult to study.

In our research, we explore the degree to which individual odonate species attributes can be used to explain patterns of species distribution in riverine wetlands. In this approach we consider attributes of **life history**—the significant features of the life cycle through which an organism passes, with particular reference to strategies influencing survival and reproduction. We also consider **natural history**, which includes qualitative phenomena such as behavior. As organisms have adapted to local habitats, their distributional gradients likely reflect significant selective forces behind speciation (Townsend and Hildrew 1994). Individual species may have developed a number of adaptations that predispose them to exist under certain conditions. It is the interaction of these adaptations and natural history traits that affect their distribution in present habitats; specifying life history would therefore be useful in assessing biological conditions.

In a previous paper (Beatty, Jepson and Li, in prep) we analyzed the distribution of 27 odonate species at riverine wetland sites in the Willamette Valley in western Oregon and identified wetland habitat attributes that are associated with odonates. Hydro-period, vegetation type, presence of fish and

surrounding land cover were associated with the distribution of several species. In this paper we associate biological differences between species with differences in habitat relationships by answering the following questions: How are odonate life history attributes related to wetland habitat attributes? How are odonate life history attributes related to species distributions? Are life history attributes interrelated?

METHODS

Through literature review and consultation with odonate biologists, a list of life history attributes was developed for analysis. Attributes describing all life stages were included. Attributes were selected based on their presumed biological significance, anticipated variation within odonate assemblages, and their habitat specificity. Life history data were collected from peer-reviewed journal articles and monographs on odonate ecology and life history (Corbet 1999, Kennedy 1913.) A subset of the initial attribute list found for all species in the study wetlands was selected for analysis. The attributes chosen were: drying resistant egg (presence/absence), over wintering life stage (egg/nymph), nymph foraging strategy (ambush/pursuit), adult flight season (assigned a code of 1 through 5 based on month flight season begins from April through August), and oviposition location (assigned code of 1 through 6, see Table 3.1 legend for definitions). Flight-season data were predominantly taken from Walker (1956) for data collected in British Columbia. These temporal data were corrected for the Willamette Valley.

To examine biological similarities between species, data were subjected to Non-metric Multidimensional Scaling (NMS) (Mather 1976, Kruskal 1964) using the software PC-ORD version 4 (McCune and Mefford 1999). NMS is a

multivariate method that ordines objects based on their relative similarities. The objects are placed in a non-metric ordination space that can range from one to several dimensions depending on the nature of the data being analyzed. Objects that are placed near each other in ordination space are similar, while those that are distant are dissimilar. For this analysis, each object was a species, and similarity was based on shared biological traits. NMS is a robust method, particularly with non-normal, heterogeneous data such as community data (B. McCune, pers. com.). The matrix was analyzed with a random starting configuration, using 40 runs with real data. The results of this analysis were compared to a Monte Carlo test with 50 runs on randomized data to determine the likelihood that ordination results would be generated by chance.

The results of this ordination were compared to species distributions at sites from our previous study (Beatty et. al., in prep) to identify correlations between species distributions and species similarity in the life history ordination. Relating the ordination to the species assemblages at these wetlands allowed for comparison of habitat conditions to species distributions at sites, and ultimately to the biological traits of individual species.

RESULTS

Data from the literature review revealed that seven (26%) of the species present at the wetland study sites possessed an egg that was resistant to desiccation (Walker 1956, Corbet 1999) (Table 3.1). These species were in the genera *Lestes* and *Sympetrum*. These genera also overwintered in the egg stage, as did members of *Aeshna*, *Archilestes*, *Enallagma* and *Ishnura*. A total of fifteen species (56%) overwintered as eggs rather than as nymphs. The list of

Table 3.1: Biological and life-history attributes for 27 Odonate species

SPECIES	drying- resistant egg	overwintering stage	foraging strategy	adult flight season	oviposition location
<i>Aeshna californica</i>	0	1	1	Ap	2
<i>Aeshna multicolor</i>	0	1	1	M	5
<i>Aeshna palmata</i>	0	1	1	Ju	5
<i>Aeshna umbrosa</i>	0	1	1	Ju	3
<i>Anax junius</i>	0	0	1	M	4
<i>Archilestes californica</i>	0	1	1	Ag	6
<i>Enallagma civile</i>	0	0	1	Ju	2
<i>Enallagma cyathigerum</i>	0	0	1	M	2
<i>Erythemis collocata</i>	0	0	0	Jn	4
<i>Gomphus kurilis</i>	0	0	0	M	1
<i>Ishnura cervula</i>	0	0	0	M	2
<i>Lestes congener</i>	1	1	1	Ag	6
<i>Lestes disjunctus</i>	1	1	1	Ju	5
<i>Lestes dryas</i>	1	1	1	Jn	6
<i>Libellula forensis</i>	0	0	0	Jn	1
<i>Libellula luctuosa</i>	0	0	0	Jn	1
<i>Libellula lydia</i>	0	0	0	M	1
<i>Libellula pulchella</i>	0	0	0	Ju	1
<i>Pachydiplax longipennis</i>	0	0	0	Jn	1
<i>Sympetrum corruptum</i>	0	1	1	Jn	1
<i>Sympetrum danae</i>	0	1	1	Jn	1
<i>Sympetrum ilotum</i>	0	1	1	M	1
<i>Sympetrum madidum</i>	1	1	1	Jn	1
<i>Sympetrum occidentale</i>	1	1	1	Jn	1
<i>Sympetrum pallipes</i>	1	1	1	Ju	1
<i>Sympetrum vicinum</i>	1	1	1	Ju	1
<i>Tramea lacerata</i>	0	0	0	Jn	4

LEGEND

Drying resistant egg

1=resistant

0=non-resistant

Over wintering stage

1=egg

0=nymph

Nymph foraging strategy

0=ambush

1=stalking

Adult Flight Season

Ap=April

M=May

Jn=June

Ju=July

Ag=August

Oviposition Location

1=water or sediments

2=submerged veg

3=submerged wood

4=floating veg

5=emergent veg near water

6=emergent veg away from water

species that possessed a nymph that foraged actively consisted of *Aeshna*, *Archilestes*, *Lestes*, *Sympetrum*, *Anax* and *Enallagma*, with a total of 18 species (67% of total).

Oviposition strategy (Figure 3.1) included five categories: oviposition in open water or sediments, submerged vegetation, submerged wood, floating vegetation, emergent vegetation near the water surface, and emergent vegetation away from the water surface. These categories can be grouped into endophytic (inserting eggs into the tissue of plants) and exophytic (placing eggs into open water or moist sediments) oviposition techniques. Exophytic oviposition was practiced by 13 species (48%), which included 12 species in family Libellulidae (found in the genera *Erythemis*, *Libellula*, *Pachydiplax*, *Sympetrum*, and *Tramea*) and 1 species in Gomphidae (*Gomphus kurilis*). The remaining species practice endophytic oviposition, inserting their eggs into the tissues of a range of submerged, floating and emergent plants (Figure 3.1).

Flight season (categorized by the month in which the season began) occurred from April through August, with the highest number of species emerging as adults in June (10), and with seven species beginning to emerge in May and also in July (Figure 3.2). One species (*Aeshna californica*) begins to emerge in April, and two species (*Archilestes californica* and *Lestes congener*) begin their emergence in August. Variation in emergence time is observed at the generic level, with species in *Aeshna*, *Enallagma*, *Lestes* and *Sympetrum* differing from congeners in their emergence times, often by as much as two months (Walker 1956).

NMS ordination of biological attributes resulted in a 3-dimensional solution (Figure 3.3, Table 3.2). Species grouped taxonomically within the ordination, with congeners appearing close to one another in ordination space (Figure 3.4). Species that practice endophytic oviposition in emergent vegetation

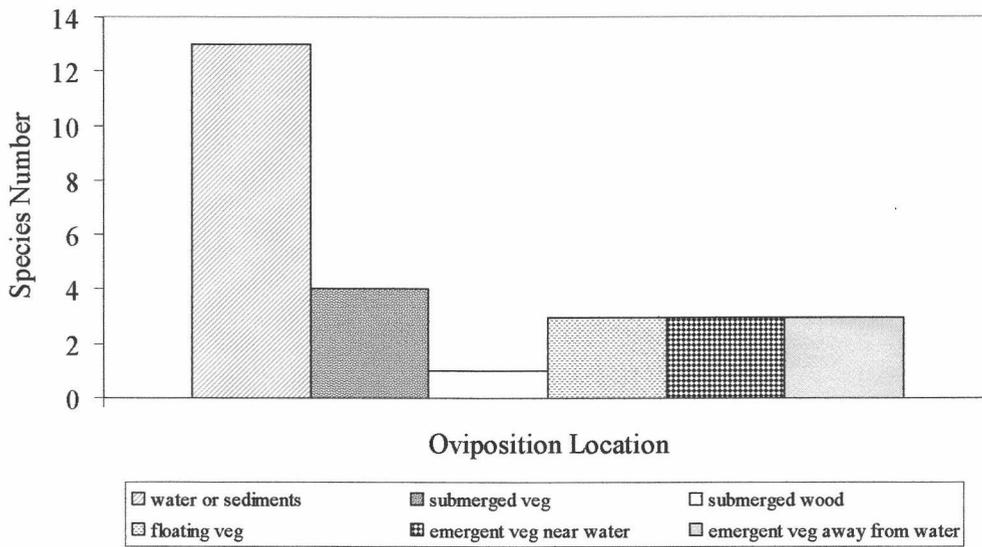


Figure 3.1: Comparison of oviposition strategy of riverine wetland Odonates (total=27)

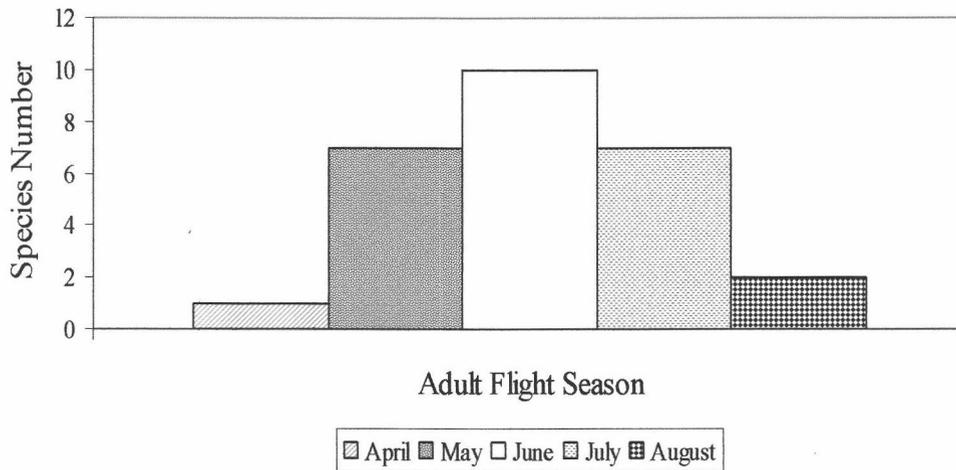


Figure 3.2: Seasonal pattern of Odonate species initiating adult flight (total=27)

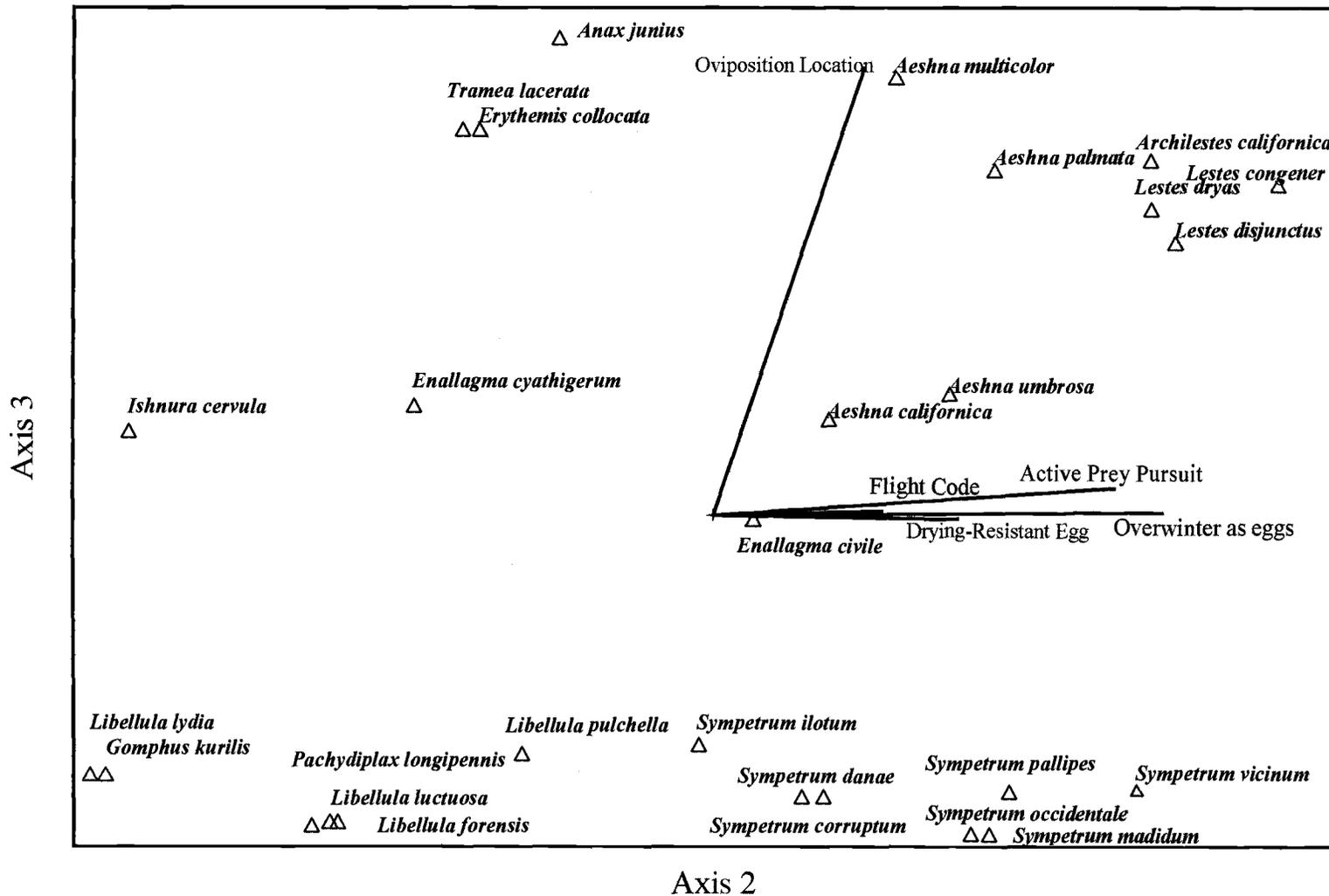


Figure 3.3: Bi-plot of life history attributes on NMS ordination of odonate species: Axes 2 and 3. Vectors represent the direction and relative strength of correlation (r-value) of a natural history attribute. Each triangle represents a species, showing its relative similarity to others species by its position.

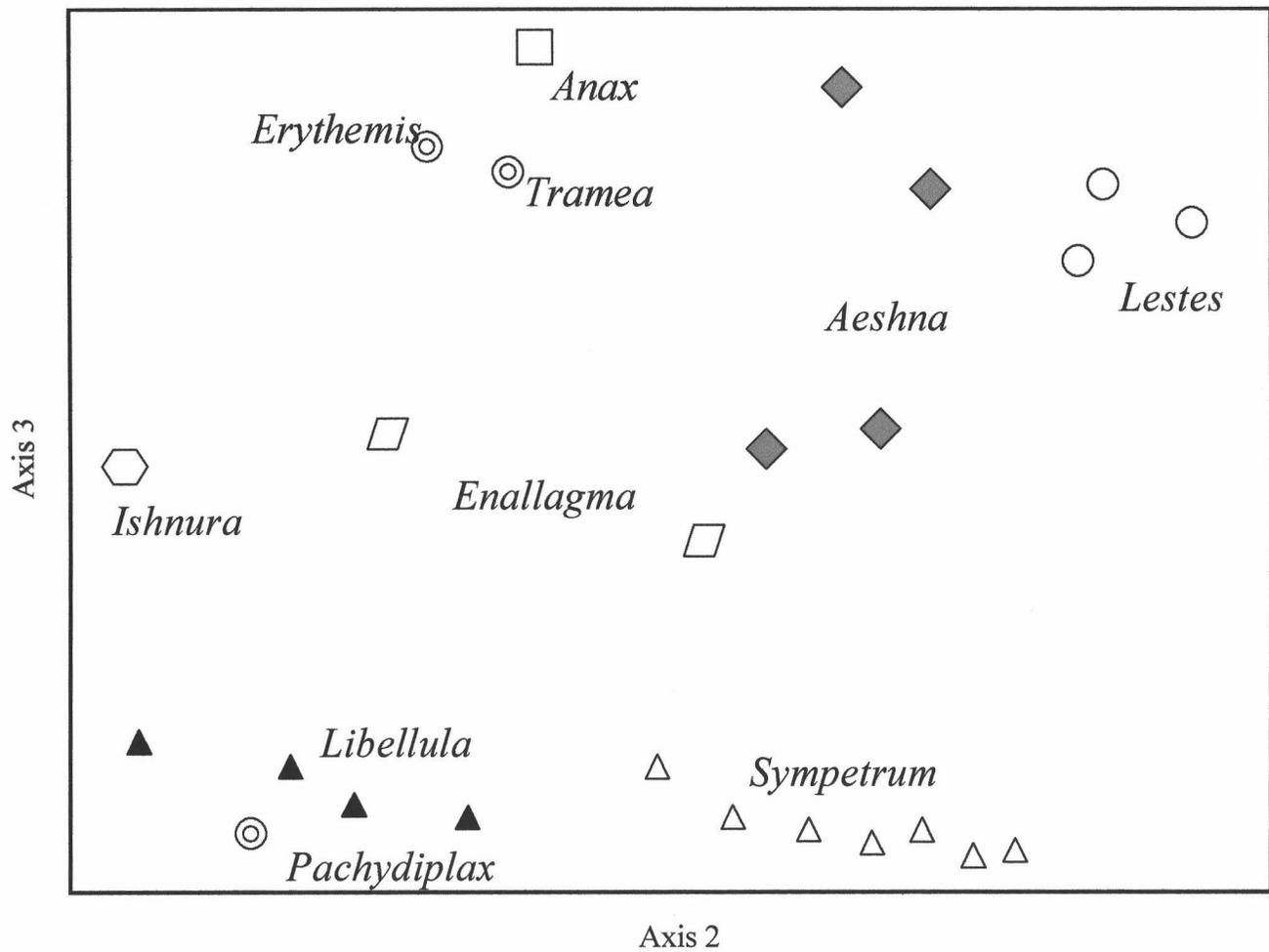


Figure 3.4: NMS ordination of species by life-history attributes showing congener groupings. Each symbol represents the position of a species within the ordination. Species within the same genus are represented by the same symbol, and are labeled with the genus name.

(members of *Aeshna* and *Lestes*) grouped strongly on Axes 2 and 3 (Figure 3.3). Those species that oviposit in open water or in sediments (*Erythemis collocata*, *Libellula spp.*, *Pachydiplax longipennis* and *Tramea lacerata*) were negatively correlated on Axis 3 (Figure 3.3, Figure 3.4). Axis 2 was correlated with oviposition location, and revealed correlations between species that possess a drying resistant egg (*Sympetrum*), species that over winter in the egg stage (*Aeshna*, *Lestes* and *Sympetrum*) versus those that over winter as a nymph, and species whose nymphs actively pursue prey—moving in the water column and among submerged vegetation—versus species whose nymphs ambush prey, hiding in the fine sediments on the bottom (*Erythemis*, *Gomphus*,

Table 3.2: Summary Statistics of NMS ordination of life history data

n-Dimensions	3	
Final stress	6.799	
Final instability	0.00007	
Iterations	100	
Monte Carlo p-Value	0.0196	
Cumulative r-Squared		
Axis:	<u>Increment</u>	<u>Cumulative</u>
	1	0.071
	2	0.572
	3	0.94

Libellula, *Pachydiplax* and *Tramea*). Axis 1 was strongly positively correlated with the beginning of the flight season for a species (Figure 3.5). The cumulative r-squared correlation for the 3 axes was .940. The ordination was rotated to maximize the correlation of the attribute “oviposition location” with Axis 3.

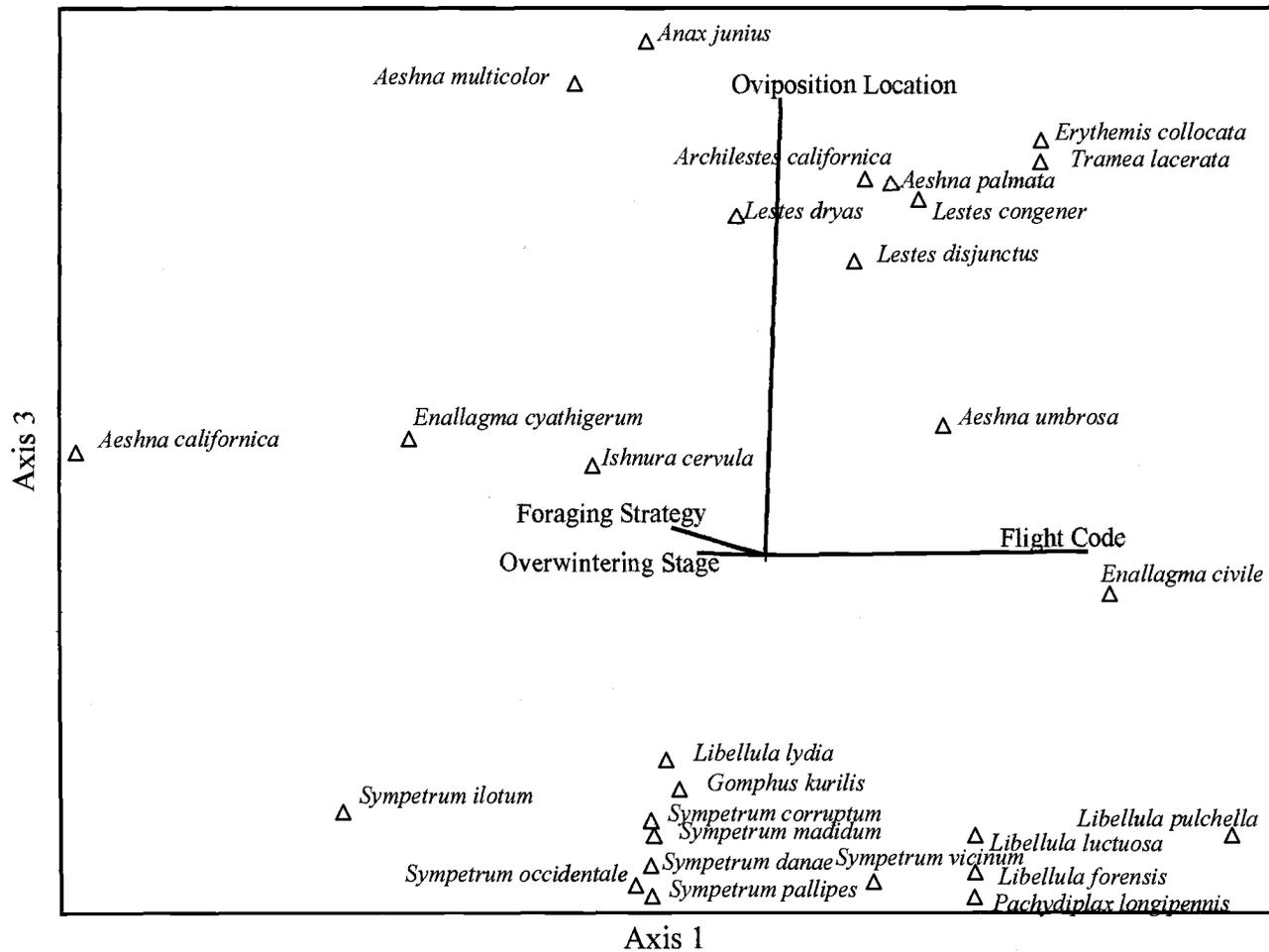


Figure 3.5: Bi-plot of life history attributes on NMS ordination of Odonate species: Axes 1 and 3. Vectors represent the direction and relative strength of correlation (r-value) of a natural history attribute. Each triangle represents a species, showing its relative similarity to other species by its position. Beginning month of flight season (Flight Code) is highly correlated with Axis 1.

Table 3.3: r-Values for life-history attributes in NMS ordination of Odonate species

Axis:	1	2	3
	r	r	r
Drying-resistant egg	0	0.644	-0.089
Overwintering life stage	-0.346	0.871	0.064
Foraging strategy	-0.405	0.824	0.222
Adult flight season	0.749	0.536	0.088
Oviposition location	0.153	0.502	0.913

When sites characterized by species presence/absence (Table 3.4) were overlaid on the ordination, sites with permanent standing water were negatively correlated with axis 2 (Figure 3.6). Temporary sites (those which are dry for some part of the summer) did not correlate with the ordination. Water permanence correlates most strongly in this analysis with members of the family Libellulidae (*Erythemis*, *Libellula*, *Pachydiplax* and *Tramea*).

DISCUSSION

How are odonate life history attributes related to wetland habitat attributes? Through ordination of species by life history and natural history attributes, and comparison to species distributions at a number of sites, we determined that many odonate biological attributes represent adaptations to life in a variably wet environment. Adaptations such as endophytic oviposition,

Table 3.4: Species presence/absence by site in Willamette Valley wetlands

Species	Sites																								
	ABW	BL	BW	CB	CC1	CC2	CC3	CC4	CG	CP	CR	CS	DP	EE	FC	HC	JF	JP	KP	MB	NR	OB	TF	WC	WM
<i>Aeshna californica</i>	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aeshna multicolor</i>	1	1	1	1	0	0	0	1	0	0	0	0	1	1	0	0	1	0	1	1	0	1	0	1	0
<i>Aeshna palmata</i>	1	1	1	1	1	0	1	1	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0
<i>Aeshna umbrosa</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Anax junius</i>	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0
<i>Archilestes californica</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Enallagma civile</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Enallagma cyathigerum</i>	1	1	0	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	1
<i>Erythemis collocata</i>	1	1	0	1	1	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0
<i>Gomphus kurilis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ishnura cervula</i>	0	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1
<i>Lestes congener</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lestes disjunctus</i>	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0
<i>Lestes dryas</i>	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Libellula forensis</i>	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	0	1	0	0	1
<i>Libellula luctuosa</i>	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0
<i>Libellula lydia</i>	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	1	1
<i>Libellula pulchella</i>	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
<i>Pachydiplax longipennis</i>	1	1	1	1	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0
<i>Sympetrum corruptum</i>	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
<i>Sympetrum danae</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sympetrum ilotum</i>	0	1	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0
<i>Sympetrum madidum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Sympetrum occidentale</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sympetrum pallipes</i>	1	0	0	1	1	1	1	0	0	1	1	0	0	1	0	1	1	0	1	0	0	1	1	0	0
<i>Sympetrum vicinum</i>	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
<i>Tramea lacerata</i>	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	0

Absence=0
Presence=1

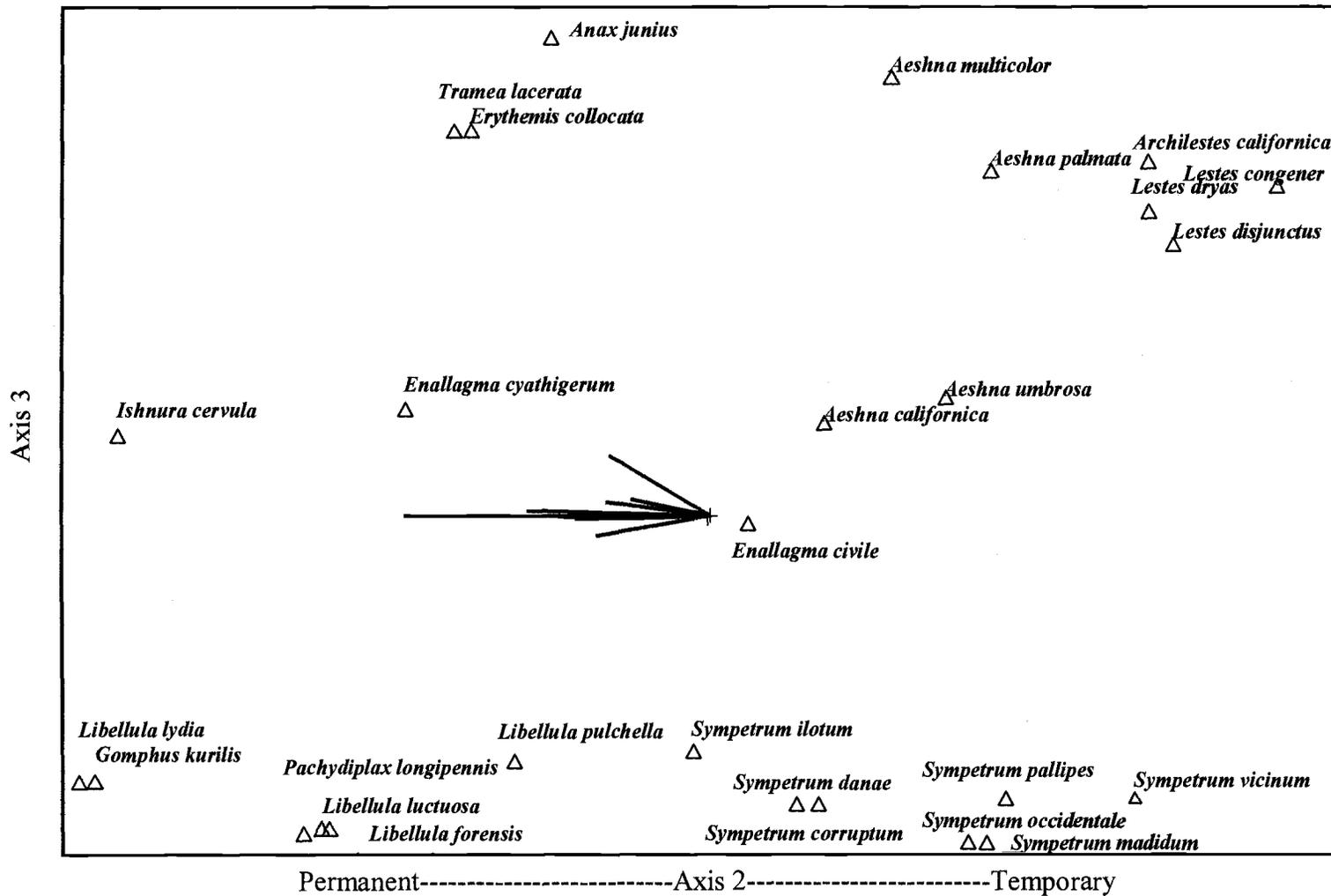


Figure 3.6: Bi-plot of wetland sites by species assemblage on NMS ordination of Odonate species. Each vector represents the direction and relative strength of correlation (r-value) of a site, based on the species assemblage at that site. Permanent sites were found to correlate with the ordination.

a drying-resistant egg and over wintering in the egg stage are responses to hydrologic gradients. Species with these adaptations colonize temporary wetlands while other species are only found at sites where hydrologic patterns are more constant. In Beatty et. al. (in prep), analysis revealed that wetland odonate species distributions correlate with hydro-period, vegetation type, presence of fish and surrounding land cover. Life history analysis provides a functional explanation for these habitat correlations.

Correlations between species distributions and emergent vegetation are associated with oviposition strategy. Ancestrally, odonates were endophytic in their egg laying (Corbett 1999). Females of many odonate species possess some type of rigid ovipositor that allows for the insertion of eggs into living or dead plant material (Walker 1956). Members of genus *Aeshna* insert their eggs into the stems of large emergent plants, such as *Typha latifolia*, or into fallen, often partially submerged logs (Walker 1956, Corbett 1999). *Lestes* insert their eggs into a variety of emergent plants. *Archilestes californica*, a species found at only one of our study sites, inserts its eggs into the limbs of willow trees (*Salix spp.*) that overhang a pond or wetland. It is assumed that this is a strategy to prevent egg desiccation during dry periods, allowing the eggs to hatch in the winter or spring when standing water has returned to the wetland. These strategies allow for the distribution of these species at temporary sites, and also explain correlations between *Aeshna* and *Lestes* with emergent vegetation and submerged logs at these sites.

Some species that have lost the endophytic oviposition strategy, place their eggs into open water or moist sediments (Corbett 1999). These species require habitats that remain somewhat wet throughout the season. Most members of family Libellulidae (including *Erythemis*, *Libellula*, *Pachydiplax* and *Tramea*) demonstrate this strategy, and tend to be found at permanent sites

(Wissinger 1993). The exceptions to this trend in Libellulidae are species in genus *Sympetrum*. *Sympetrum* are commonly found at both permanent and temporary sites, and can be seen ovipositing in wetlands that are completely dry. While the life histories of several of these species are not adequately documented, it is believed that many *Sympetrum* possess an egg that is resistant to desiccation, and can be deposited openly in sites that are dry (Corbett 1999). In Beatty et. al. (in prep) analysis of species distributions revealed that *Sympetrum madidum*, *S. occidentale* and *S. pallipes* were observed at temporary sites more commonly than *S. corruptum* and *S. ilotum*. *Sympetrum* sometimes deposit their eggs into moist sediments on the wetted perimeter of wetlands, the female inserting the end of her abdomen into the sediments to oviposit. This strategy may also offer protection from desiccation.

Phenology represents another response to life at temporary sites. While many species over-winter as a nymph, members of the genus *Lestes* over-winter predominantly in the egg state, hatching and developing rapidly to emergence in the early spring when temporary sites are likely to hold standing water (Walker 1956). *Enallagma* and *Ishnura*, two other common damselfly genera at these sites, overwinter as nymphs and emerge early in summer. These genera oviposit in floating vegetation rather than in emergent vegetation (Walker 1956).

Fish presence was found to be associated with species distributions. While fish presence is likely to co-vary with permanence in many cases, in temporary wetlands with high connectivity to other wetlands or streams, fish may migrate into the wetland seasonally, resulting in fish distribution in many of these sites. Some odonate nymphs are more susceptible to fish predation because of their overall size and their foraging strategy and general behavior. Distributions of *Lestes* are negatively influenced by the presence of fish and they are found in sites where fish are not common. *Lestes* are active predators as nymphs, moving in

open water and among submerged vegetation. This more active prey-acquisition strategy—and the relative large size of these nymphs—make them more susceptible to fish predation (McPeck 1996). *Libellula*, *Erythemis*, *Pachydiplax*, and *Tramea* are predominantly bottom dwellers. These nymphs remain concealed in fine sediments and organic detritus, and ambush their prey (Needham, Westfall and May 2000). The distributions of these odonates are not limited to fishless sites.

How are odonate life history attributes related to species distributions?

When site and species distributions were analyzed, only sites where water is present throughout the year were found to correlate to the life history ordination. Species adapted to dry conditions (*Aeshna*, *Lestes*, *Sympetrum*) are found at temporary sites, but do not use temporary sites exclusively. These species are distributed generally across the landscape, and are present at permanent and temporary sites. Species that require permanent water such as *Erythemis collocata*, *Libellula* spp., *Pachydiplax longipennis* and *Tramea lacerata* are only found at wet sites and are more limited in their overall distribution. From an assemblage perspective, permanent sites are the sites that “stand out”, as they possess both species found at all sites and those specifically adapted to permanent sites. Species at all sites range in their adult flight period during the summer season, with genera common to both permanently and temporarily wet sites containing species that emerge early in the summer and in later months. This explains the lack of correlation of sites with axis 1, which was predominantly driven by adult flight season.

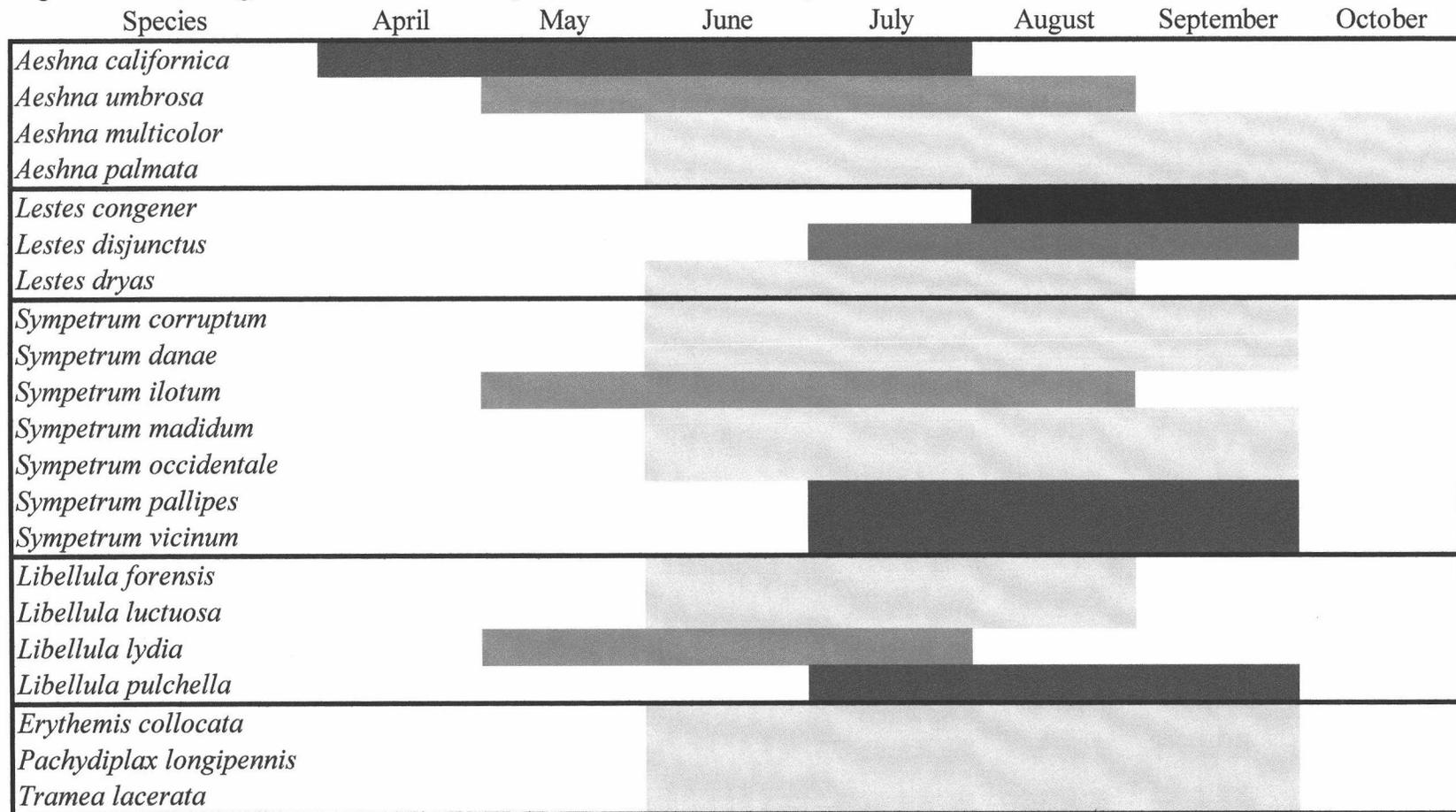
Are life history attributes interrelated? While the overall habitat variable driving species distributions is hydro-period, much of the life history variation observed among Willamette Valley odonates is driven by the loss of a rigid ovipositor in family Libellulidae. This loss initially seems an odd evolutionary

development; it limits libellulids to colonizing permanent sites, which represent only a fraction of wetland habitats. This change would appear to limit the amount of available habitat for this group. However, these species are released from a tie to vegetation structure, and no longer require large emergent plants for oviposition sites. Potential habitat therefore increases because permanently wetted sites lacking emergent vegetation are available for colonization. Libellulid nymphs use a habitat and foraging strategy distinct from the nymphs of endophytic species. Nymphs of these permanently wetted sites tend to hide themselves in sediments on the bottom and ambush prey, rather than pursue their prey among submerged vegetation as nymphs adapted to temporary wetlands do. While the requirement for established vegetation is removed, these species are also at an advantage because they are less conspicuous to fish predators, who are more common in permanent wetlands. Libellulidae are found in wetland and pond environments throughout the world (Silsby 2001); they are often the dominant odonate family in these habitats.

One genus in Libellulidae, *Sympetrum*, does not require water permanence. *Sympetrum* have an egg that can survive desiccation (Corbet 1999). Released from requirements of both emergent vegetation and water permanence, species of this genus often reach maximum abundance in temporary wetlands. *Sympetrum* is the most widely distributed genus in Willamette Valley wetlands.

Odonate species in this study varied in their emergence time and peak adult activity during the summer season (Figures 3.2). A review of species within each of the genera in this study reveals variation between congeners in emergence time, often by as much as two months (Figure 3.7). This variation explains the lack of correlation between flight period (Flight Code) and habitat distributions: considerable temporal variation is seen within both the “permanent” and “temporary” site assemblages. In the Willamette Valley odonate assemblage,

Figure 3.7: Adult flight season for odonate species in Willamette Valley wetlands



congeners often have a large number of natural history attributes in common. Temporal separation between these species provides a potential release from competition for food and oviposition sites, and from interspecies predation as nymphs (Wissinger 1993, Corbet 1999).

Is life history analysis useful in habitat assessment? Analysis of life history attributes of a group of species has great value as a method of understanding organism responses to their habitat. Considerable variation was observed between species in the odonate assemblage of riverine wetlands. Life history and natural history information, when considered with species distributions, provided information on habitat conditions that would not have been detected with less taxonomically resolved analysis.

Our results generate hypotheses about specific adaptive responses to habitat conditions. Further exploration of these hypotheses, and incorporation of more life-history information into this analytical approach, will provide information for management and restoration of habitats such as wetlands. While the analysis of habitat conditions and species distributions in Beatty et. al. (in prep) revealed species correlations with habitat attributes such as hydro-period, emergent vegetation and fish presence, analysis of the biological and ecological interactions of these correlations provided a greater overall understanding of how these organisms “fit” to their environment, and how wetland site management can directly affect odonate diversity.

CHAPTER 4

GENERAL CONCLUSION

My undergraduate years were spent at the University of Illinois, in what was then the department of Ecology, Ethology and Evolution. The building regarded by most as the home of “triple-E” (our nickname for the department) was an early twentieth-century structure known as the Shelford Vivarium. Victor Shelford, for whom the building was named, had been a member of the faculty at Illinois from 1914 until 1947 and had been a prominent figure in the study of animal ecology. Shelford had been instrumental in the establishment of an ecology program at Illinois, and so as a student there I tended to regard him as something of a forebear.

In the spring of 2002 I stumbled upon a biography of Shelford (Pioneer Ecologist—The Life and Work of Victor Ernest Shelford 1877-1968 by Robert A. Croker) and decided to learn more about this academic ancestor. Shelford had completed his doctoral dissertation in 1907 at the University of Chicago, studying tiger beetles (Coleoptera: Cicindellidae) in the sand dune and forest communities along the southern shore of Lake Michigan. Shelford studied much about the behavior and physiology of these beetles, and the relationship of these organisms to their position in the dune habitats.

Shelford begins the introduction of his dissertation with these words:

During the past quarter century, the consideration of life-histories and habitats as a basis for experimental work and for the study of distribution, variation and other evolutionary topics has been far too much neglected. In the study of variation, investigators have too often collected large numbers of specimens, arranged them in classes, calculated indices, constructed curves, and drawn conclusions

regarding the direction of evolution without knowing the life-history of the form...

These words seemed especially poignant as I prepared this thesis, in which I synthesize the habitat preferences and life history attributes of odonates in the process of understanding their distribution. In doing so, I have found that much useful information can be gained about habitat relationships when the life history and natural history of an organism is considered.

In this study, odonates were found to respond to a number of habitat variables within wetlands. Hydro-period, vegetation, presence of fish predators and surrounding land cover were all associated with the distribution of these species. This variation was observed not in sites located along a land-use or pollution gradient, but in the natural variation found in Willamette Valley wetlands, indicating a fine-scale response of these organisms to their environment. Life history analysis offered a functional explanation to the distribution patterns, which would not have been possible with habitat analysis alone.

How would this study have been different without species level analysis? Analysis at the generic level would have revealed some of the habitat associations found in this study, but information would have been lost. Species within *Aeshna* differed in their preference for oviposition location. *A. multicolor* and *A. palmata* favor emergent wetland vegetation, while *A. umbrosa* preferred submerged wood as a site for oviposition. Generic analysis would not have detected this difference. *Sympetrum* tend to prefer temporary sites, but *S. ilotum* and *S. corruptum* were found more often at permanent sites; generic analysis of this group would be difficult to interpret. At the family level, almost all resolution would have been lost. Some correlations to vegetation would have been identified for Aeshnidae and Lestidae, but the divergent habitat preferences between *Libellula* and *Sympetrum* for permanent and temporary wetlands would have made analysis of

Libellulidae un-interpretable. From an assemblage standpoint, family-level resolution would cause many of these sites to become virtually identical.

How would this study have been different without life history analysis? Without analysis of the biological variance in these species, the significance of hydro-period as a factor in the interaction with other habitat associations would not have been understood. Species associations with emergent vegetation, fish presence and other factors would have been identified, but the functional relevance of these associations would not have been examined. Separation of congeners in timing of emergence was a result of life history analysis. Although temporal variability was not associated with habitat preferences, seasonal differences in activity offer an explanation as to why biologically similar species are able to share habitats.

In the century since Victor Shelford studied his cicindellids in northern Indiana, much of animal ecology has moved away from the study of organism life history and natural history. Life history information proved difficult to incorporate into experimental and analytical methods; the data was often too complicated and too arduous to collect, and unwieldy for statistical analysis. Shelford and his colleague Charles Adams often referred to ecology as the “new natural history”, a definition that now seems anachronistic.

With the advent of the personal computer and the development of multivariate techniques, practical methods for the analysis of organism life history are available to most ecologists. At a time when such unprecedented computational power is available, Shelford’s call for consideration of life history analysis in ecological research is a much more attainable goal. As we move into the 21st century, this finer biological detail could vastly expand our understanding of ecosystem dynamics and improve our methods of community analysis and management.

LITERATURE CITED

- Adamus, P.R. 1998 Guidebook for hydrogeomorphic (HGM) assessment of wetland and riparian sites in Oregon. Parts I and II. Oregon Division of State Lands, Salem, OR.
- Adamus, P.R., 1996. Bioindicators for Assessing Ecological Integrity of Prairie Wetlands. US Environmental Protection Agency, Office of Research and Development, Washington DC. EPA/600/R-96/082. 209pp
- Batzer, D.P., and S.A. Wissinger. 1996. Ecology of Insect Communities in Nontidal Wetlands. *Annual Review of Entomology* 41:75-100
- Bernert, J.A., Eilers, J.M., Eilers, B.J., Blok, E., Daggett, S.G., Bierly, K.F. (1999) Recent wetland trends (1981/82-94) in the Willamette Valley, Oregon, USA. *Wetlands*, 19, 545-559
- Brinson, M. M. 1993. A hydrogeomorphic classification for wetlands. Wetlands Research Program Technical Report WRP-DE-4. U.S. Army Corps of Engineers Waterways Experiment Station. Vicksburg, Mississippi, USA.
- Brinson, M. M. and R. Rheinhardt. 1996. The role of reference wetlands in functional assessment and mitigation. *Ecological Applications*, 6(1) 69-76.
- Christy, J.A., Alverston, E., Dougherty, M., Kolar, S., Ashkenas, L., Minear, P. 1998. Presettlement vegetation for the Willamette Valley, Oregon. Compiled from records of the general land office surveyors (c. 1850). Oregon Natural Heritage Program. Portland OR.
- Corbet, Philip S. 1999. Dragonflies: Behaviour and Ecology of the Odonata. Cornell University Press. 829pp.
- Daggett, S. G., M. E. Boule, J. A. Bernert, J. M. Eilers, E. Blok, D. Peters, and J. Morlan, 1998. Wetland and Land Use Change in the Willamette Valley, Oregon: 1982 to 1994. Shapiro and Associates, Inc. Report to the Oregon Division of State Lands

Dunkle, S. W. 2000. *Dragonflies through Binoculars*. Oxford University Press, Oxford, U. K. 266 pp.

Finke, O. M. 1992. Consequences of larval ecology for territoriality and reproductive success of a neotropical damselfly. *Ecology*, 73(2) 449-462.

Gould, S. J. and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London B* 205, 581-598.

Guard, B. J. 1995. *Wetland Plants of Oregon and Washington*. Lone Pine Publishing, Redmond, Washington. 239pp.

Kennedy, C. H. 1913. Notes on the life history and ecology of the dragonflies (Odonata) of Washington and Oregon. *Proceedings of the US National Museum* 49: 259-345.

Kennedy, C. H. 1917. Notes on the life history and ecology of the dragonflies (Odonata) of central California and Nevada. *Proceedings of the US National Museum* 52: 483-635.

Kremen, C., Colwell, R., Erwin, T. L., Murphy, D. D., Noss, R. F. and S. Muttulingam. 1993. Terrestrial arthropod assemblages: their use as indicators for biological inventory and monitoring programs. *Conservation Biology*, 7, 796-808.

Kremen, C. 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar. *Ecological Applications*, 4: 407-422.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115-129.

Lincoln, R., G. Boxshall and P. Clark. 1998. *A Dictionary of Ecology, Evolution and Systematics*. Cambridge University Press, Cambridge, U. K. 361 pp.

Mather, P. M. 1976. *Computational Methods of Multivariate Analysis in Physical Geography*. John Wiley and Sons, New York. 532 pp.

McCune, B., and M. J. Mefford. 1999. *PC-ORD. Multivariate Analysis of Ecological Data, Version 4*. MjM Software Design, Glendenen Beach, Oregon, USA.

- McCune, B. 1994. Improving community analysis with the Beals smoothing function. *Ecoscience*, 1: 82-86.
- McPeck, M. A., A. K. Schrot, and J. M. Brown. 1996. Adaptation to predators in a new community: Swimming performance and predator avoidance in damselflies. *Ecology* 77:617-629
- Mitsch, W. J. and J. G. Gosselink. 1993. Wetlands, 2nd edition. John Wiley and Sons, Inc. New York. 722pp.
- Merritt, R. W. and K. W. Cummins. 1996. An Introduction to the Aquatic Insects of North America. Kendal Hunt, Dubuque, Iowa. 862pp.
- Morlan, J. 2000. *Summary of current status and health of Oregon's freshwater wetlands*. In: The Oregon State of Environment Report 2000, Oregon Progress Board, <http://www.econ.state.or.us/opb/soer2000/index.htm> 214pp.
- Needham, J. G., M. J. Westfall Jr. and M. L. May, 2000. The Dragonflies of North America. Scientific Publishers, Gainesville, Florida USA. 939pp.
- Oregon Dragonfly and Damselfly Survey. August 15, 2002. website: www.ent.orst.edu/ore_dfly/
- Oregon Progress Board 2000. *Oregon State of the Environment Report, 2000 Statewide Summary*. Oregon Progress Board, 775 Summer Street N.E., Suite 330, Salem, Oregon, 97301-1283. 80pp.
- Plafkin, J. L., M. T. Barbour, K. D. Porter, S. K. Gross and R. M. Hughes. 1989. Rapid bioassessment protocols for use in streams and rivers: Benthic macroinvertebrates and fish. U.S. EPA/444/4-89/001.
- Selys-Longchamps, E. 1879. Revision des Ophiogomphus et description des quatres nouvelles gomphines americaines. *Comptes Rendus de la Societe de Enotmologie de Belgique* 22: 62-70.
- Townsend, C. R. and A. G. Hildrew. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, 31: 265-275.
- Walker, E. M. 1956. The Dragonflies of Canada and Alaska. University of Toronto Press, Toronto Canada.

Well born, G. A., D. K. Skelley and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27: 337-363.

Westfall, M. J. Jr. and M. L. May, 1996. The Damselflies of North America. Scientific Publishers, Gainesville, Florida USA. 649pp.

Willamette Valley Livability Forum. 2002. website: www.wvlf.org.

Wilson, E. O. 1987. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* 1: 344-346.

Wissinger, S. A. and J. McGrady. 1993. Intraguild predation and interference competition between dragonflies: direct and indirect effects on shared prey. *Ecology* 74: 207-218.

APPENDICES

Table A.2.1: Odonate nymph species abundance by site

Anisoptera	ABW	BL	BW	CB	CC1	CC2	CC3	CC4	CG	CP	CR	CS	DP	EE	FC	GI	HC	JF	JP	KP	MB	NR	OB	SL	TF	WM	Total
<i>Aeshna californica</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Aeshna multicolor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
<i>Aeshna palmata</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	11	0	0	0	0	0	0	0	13
<i>Aeshna umbrosa</i>	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5
<i>Anax junius</i>	0	3	0	15	0	20	23	20	0	5	5	0	0	7	0	5	0	0	7	2	0	0	0	0	0	0	112
<i>Erythemis collocata</i>	0	1	0	2	0	0	0	8	0	0	0	0	2	9	0	3	0	0	0	0	0	0	0	0	0	0	25
<i>Gomphus kurilis</i>	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
<i>Libellula forensis</i>	5	0	0	1	0	0	2	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	11
<i>Libellula pulchella</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Libellula spp.</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	3
<i>Pachydiplax longipennis</i>	0	0	0	1	0	0	0	26	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	28
<i>Sympetrum corruptum</i>	0	0	0	0	0	2	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5
<i>Sympetrum ilotum</i>	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Sympetrum madidum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
<i>Sympetrum pallipes</i>	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
<i>Sympetrum spp.</i>	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
<i>Sympetrum vicinum</i>	0	0	0	3	0	1	0	0	0	0	0	0	0	3	0	0	0	0	1	1	0	0	0	0	0	0	9
<i>Tramea lacerata</i>	0	2	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	5
Total	18	6	0	23	5	26	27	59	0	5	11	2	4	24	0	9	0	0	19	6	1	0	0	2	0	1	248
Zygoptera	ABW	BL	BW	CB	CC1	CC2	CC3	CC4	CG	CP	CR	CS	DP	EE	FC	GI	HC	JF	JP	KP	MB	NR	OB	SL	TF	WM	Total
<i>Enallagma civile</i>	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16
<i>Enallagma cyathigerum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Enallagma spp.</i>	18	19	0	24	5	0	16	58	2	5	0	10	0	8	0	11	0	0	9	40	0	0	0	1	0	7	233
<i>Ishnura spp.</i>	1	0	0	0	0	24	2	146	0	0	2	0	2	0	0	122	0	0	41	0	17	0	0	1	0	17	375
<i>Lestes congener</i>	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
<i>Lestes disjunctus</i>	0	0	0	0	10	0	75	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	98
<i>Lestes dryas</i>	0	0	0	0	27	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29
<i>Lestes spp.</i>	0	1	0	14	0	189	0	16	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	1	0	231
	19	36	0	38	42	213	95	220	2	19	15	10	2	8	0	133	0	0	50	51	17	0	0	2	1	24	997

Table A.2.2: Odonate adult species abundance by site

Anisoptera	ABW	BL	BW	CB	CC1	CC2	CC3	CC4	CG	CP	CR	CS	DP	EE	FC	HC	JF	JP	KP	MB	NR	OB	TF	WC	WM	Total
<i>Aeshna californica</i>	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Aeshna multicolor</i>	3	2	2	15	0	0	0	13	0	0	0	0	3	3	0	0	3	0	1	1	0	18	0	4	0	68
<i>Aeshna palmata</i>	2	5	7	2	4	0	1	1	0	0	0	0	0	13	0	0	6	0	0	0	0	28	0	0	0	69
<i>Aeshna</i> spp.	5	0	0	2	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	1	0	1	2	0	0	14
<i>Aeshna umbrosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Anax junius</i>	10	6	0	5	1	5	6	32	5	2	0	0	8	3	0	0	2	0	11	4	0	1	0	0	0	101
<i>Erythemis collocata</i>	5	43	0	26	4	0	0	24	0	1	0	0	14	21	0	0	0	0	24	0	0	0	0	1	0	163
<i>Libellula forensis</i>	32	16	4	37	2	0	2	8	10	7	0	6	13	18	0	0	1	0	19	5	0	6	0	0	3	189
<i>Libellula luctuosa</i>	8	4	0	5	0	0	0	0	6	2	0	0	16	6	0	0	0	0	5	1	0	0	0	0	1	54
<i>Libellula lydia</i>	14	3	1	16	2	0	25	6	20	6	0	3	3	14	0	0	0	0	3	3	0	0	0	6	1	126
<i>Libellula pulchella</i>	1	0	0	7	1	1	39	10	0	0	0	0	0	0	0	0	0	0	7	2	0	0	0	0	0	68
<i>Pachydiplax longipennis</i>	7	4	6	19	1	0	1	35	0	0	0	0	4	1	0	0	0	0	0	3	0	0	0	0	0	81
<i>Sympetrum corruptum</i>	0	0	0	0	0	0	1	6	1	0	0	0	8	0	0	0	0	0	3	0	0	0	0	0	0	19
<i>Sympetrum danae</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Sympetrum ilotum</i>	0	10	3	0	1	0	0	0	0	0	0	0	7	3	0	0	0	0	1	0	0	0	0	0	0	25
<i>Sympetrum occidentale</i>	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Sympetrum pallipes</i>	1	0	0	5	1	3	2	0	0	2	28	0	0	4	0	2	1	0	2	0	0	32	6	0	0	89
<i>Sympetrum</i> spp.	1	2	0	6	5	3	5	5	1	0	2	0	2	2	0	0	0	0	1	0	0	0	0	1	0	36
<i>Tramea lacerata</i>	15	5	0	5	0	1	0	0	7	2	0	0	6	5	0	0	2	0	6	1	0	0	0	0	0	55
Total	106	101	23	151	22	13	82	140	50	23	33	9	84	95	0	2	15	1	83	21	0	86	8	12	5	1165
Zygoptera	ABW	BL	BW	CB	CC1	CC2	CC3	CC4	CG	CP	CR	CS	DP	EE	FC	HC	JF	JP	KP	MB	NR	OB	TF	WC	WM	Total
<i>Archilestes californica</i>	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
<i>Enallagma cyathigerum</i>	1	28	0	23	0	0	8	6	21	0	0	12	31	21	0	0	0	0	14	15	0	0	0	0	15	195
<i>Enallagma</i> spp.	22	12	0	29	0	0	9	2	5	1	0	37	2	11	0	0	0	0	14	0	0	3	0	0	98	245
<i>Ishnura cervula</i>	0	2	6	19	7	4	78	25	0	0	0	9	0	0	0	0	0	0	4	9	0	0	0	1	5	169
<i>Ishnura</i> spp.	0	2	0	3	0	0	2	4	1	0	0	0	0	1	0	0	0	0	4	0	0	4	0	0	0	21
<i>Lestes disjunctus</i>	0	2	0	14	0	3	6	0	0	0	1	0	0	8	0	0	0	0	0	0	0	0	2	0	0	36
<i>Lestes dryas</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Lestes</i> spp.	0	0	0	2	73	16	34	27	0	0	8	0	0	0	0	0	0	0	5	0	0	0	0	0	0	165
	23	54	6	90	80	23	137	65	27	1	9	58	33	41	0	0	0	0	41	24	0	7	2	1	118	840

Table A.2.3: Habitat parameters analyzed with NMS of wetland site assemblages*

SiteCode	Species Richness	Perm	FishPres	BfrgsPres	H2OTemp_degC	H2O pH	H2O DO mg L	H2O Depth (cm)
ABW	16	1	1	1	2.25	24.1000004	8.119999886	91.44
BL	18	1	1	1	22.10000038	9.88000011	13.35000038	60.96
BW	7	1	1	1	17.70000076	7.19999981	7.639999866	91.44
CB	20	1	1	1	25.10000038	7.94000006	7.539999962	66.04
CC1	12	0	0	1	34	6.28000021	7.539999962	48.26
CC2	8	0	0	0	28.10000038	6.69000006	9.840000153	40.64
CC3	15	1	0	1	30.5	7.86999989	7.539999962	60.96
CC4	16	1	0	1	27.20000076	6.4000001	6.150000095	53.34
CG	10	1	1	0	28	8.36999989	7.539999962	30.48
CP	9	0	1	0	20.79999924	94.1999969	14	76.2
CR	5	0	0	1	27.29999924	6.42999983	8.449999809	60.96
CS	5	1	1	1	22.29999924	6.6500001	11.57999992	73.66
DP	13	1	1	1	28.10000038	9.25	7.539999962	96.52
EE	17	1	1	1	30.20000076	7.9000001	7.539999962	55.88
FC	0	0	0	0			0	0
GI	5	1	23.3999996	7.55999994	8.329999924	60	8	2.54
HC	1	0	1	1	20.29999924	6.19999981	9.539999962	45.72
JF	6	0	0	0	-999	6.9	7.539999962	33.02
JP	1	1	1	1	17.10000038	7.03000021	7.539999962	60.96
KP	17	1	1	1	28.10000038	7.92000008	7.539999962	50.8
MB	11	1	1	1	26.79999924	6.28000021	7.539999962	45.72
NR	0	0	0	0			0	0
OB	8	1	1	1	24.89999962	6.80999994	3.450000048	45.72
SL	3	1	25.2000008	6.61000013	8.220000267	48	3	2.54
TF	3	0	0	0	23.79999924	6.9000001	7.539999962	43.18
WC	5	1	0	0	27.29999924	6.4000001	6.159999847	106.68
WM	6	1	0	1	26.79999924	9.39999962	7.539999962	96.52

* see table 2.3 for explanation of HGM sample headings

Table A.2.3

SiteCode	Sediment Depth (cm)	Area (m2)	Area (Hectares)	Perimeter	ShorComp	AnadAcc	ConnType	Logs	Mow	Buffer	Crop	G
ABW	7.62	1591.261	1.591261	321.489	0.2	1	1	0	1			15
BL	10.16	5773.483	5.773483	309.079	0.05	1	1	1	1			15
BW	30.48	1802.002	1.802002	332.531	0.18	1	1	1	0			0
CB	10.16	6182.381	6.182381	506.611	0.08	1	0	0	1			2
CC1	5.08	3778.064	3.778064	527.574	0.13	0	0	0	0			22
CC2	15.24	1267.754	1.267754	183.877	0.14	0	0	0	0			70
CC3	10.16	10471.56	10.471563	576.153	0.05	1	1	0	3			82
CC4	7.62	8249.973	8.249973	1027.224	0.12	0	0	0	0			22
CG	5.08	16474.74	16.474739	570.636	0.04	1	2	0	0			10
CP	10.16	1978.706	1.978706	336.202	0.17	1	2	0	0			26
CR	5.08	1415.521	1.415521	814.086	0.58	0	0	0	2			85
CS	12.7	1208.448	1.208448	366.181	0.3	1	1	1	0			0
DP	30.48	28717.26	28.717259	970.627	0.03	1	1	1	0			0
EE	5.08	33460.41	33.46041	1366.025	0.04	1	4	0	0			86
FC	5.08	1679.825	1.679825	168.07	0.10							
GI	0	15000	700	0.05	1	2	0	0	10		41.66666667	
HC	15.24	200.04	0.20004	62.603	0.31	1	2	1	0			0
JF	15.24	22154.08	22.154082	702.304	0.031	1	2	1	0			20
JP	30.48	460.391	0.460391	145.65	0.31	1	1	1	0			0
KP	10.16	2809.503	2.809503	309.981	0.11	0	1	1	0			80
MB	60.96	8643.024	8.643024	558.613	0.06	1	2	1	0			46
NR	5.08	15566.88	15.566883	736.717	0.05	0	0	0	0			
OB	7.62	20773.89	20.77389	884.681	0.04	1	1	1	0			0
SL	0	1100	340	0.31	1	1	0	0	0		34.66666667	
TF	7.62	584.196	0.584196	121.752	0.21	1	1	0	0			99
WC	10.16	294.164	0.294164	125.23	0.43	1	1	1	1			77
WM	7.62	1192.928	1.192928	175.027	0.15	1	1	0	0			40

* see table 2

Table A.2.3

SiteCode	BufCropGabc	BufGrass	BufGrassAB	BufNat	BufNatAB	BufWet	BufWetABC	BufWood	BufWoodAB	Development
ABW	18	17	25.5	69	61.5	2	7	52	35.5	1
BL	11.66666667	37	26	43	53	22	11.33333333	4	27.5	0
BW	30	0	7.5	99	96	0	4	99	86	0
CB	67	10	73.5	11	90	8	3.666666667	1	16.5	0
CC1	43	28	23.5	78	78.5	6	9.333333333	50	55	0
CC2	37.5	70	50	100	92.5	0	8.333333333	25	35	0
CC3	62.66666667	82	69	97	95.5	0	0	15	26	0
CC4	43	28	23.5	78	78.5	6	9.333333333	50	55	0
CG	12.66666667	26	19	85	72	16	7.333333333	69	52.5	1
CP	19	26	22	66	84.5	0	12.66666667	40	62.5	1
CR	76.33333333	85	17	100	26	0	3	2	8.5	0
CS	76	0	25.5	90	34	0	11.33333333	90	7.5	0
DP	4	0	8.5	20	36	5	7.666666667	1	27	1
EE	79.33333333	86	71	93	88	0	0.666666667	7	17.5	0
FC										
GI	10	18	72	76.5	0	11.66666667	40	58.5	0	1
HC	5.333333333	8	8.5	82	53.5	8	5.333333333	74	45.5	1
JF	53.33333333	20	53	90	99.5	0	1	51	47.5	1
JP	45	5	51.5	85	89.5	5	12	80	35.5	0
KP	60	70	50	70	40	30	70	30	50	0
MB	26	56	37.5	72	50.5	10	23.33333333	16	12	1
NR										
OB	1	1	29.5	62	53	27	19.33	35	23.5	1
SL	0	3	91	75	0	4.333333333	91	70	0	0
TF	89.33333333	99	92	100	99	0	0	1	5.5	0
WC	43.66666667	77	56	99	81	0	0	15	24	0
WM	41.33333333	50	60	93	79.5	10	34	43	19	0

* see table 2

Table A.2.3

SiteCode	Agriculture	H Percent Perm	H Percent Season	HcvNN	Hsp Percent NN	VegMixL	VegPct	Typ	lat	Alis	plan
ABW	0	0	50	3	33.33333333	7	10	1		0	
BL	0	10	100	3	66.66666667	1	30	1		0	
BW	0	80	40	1	85.71428571	7	30	1		0	
CB	0	5	100	2	100	2	2	1		1	
CC1	1	0	100	3	63.63636364	5	100	1		0	
CC2	1	0	30	1	50	7	100	1		1	
CC3	1	0	100	3	50	1	100	0		0	
CC4	1	0	100	3	63.63636364	5	100	1		0	
CG	0	0	40	3	50	8	35	0		1	
CP	0	0	35	2	50	8	100	1		0	
CR	1	0	95	3	87.5	4	100	1		1	
CS	1	0	80	1	66.66666667	7	95	0		0	
DP	0	10	90	2	50	2	10	0		0	
EE	0	80	85	2	58.33333333	10	95	1		0	
FC											
GI	0	60	3	50	3	95	0	0			
HC	0	0	60	3	50	1	45	0		0	
JF	0	0	80	1	77.77777778	3	99	1		0	
JP	0	20	60	2	71.42857143	7	40	0		0	
KP	0	0	50	2			0	0		1	
MB	1	10	100	3	50	11	80	1		0	
NR											
OB	0	1	40	3	66.66666667	3	20	1		0	
SL	0	10	2	50	2	95	0	0			
TF	1	0	90	2	66.66666667	2	100	0		0	
WC	0	0	70	2	85.71428571	2	90	1		0	
WM	1	1	20	3	0	7	60	0		1	

* see table 2

Table A.2.4: r-Values for NMS ordination of nymph species

Axis:	1	2	3
	r	r	r
<i>Aeshna californica</i>	0.519	0.057	0.646
<i>Aeshna multicolor</i>	0.195	-0.342	0.329
<i>Aeshna palmata</i>	0.467	0.064	0.662
<i>Aeshna umbrosa</i>	-0.383	-0.263	0.409
<i>Anax junius</i>	-0.307	0.720	-0.551
<i>Enallagma civile</i>	-0.420	0.609	-0.127
<i>Enallagma cyathigerum</i>	0.039	0.659	-0.190
<i>Enallagma spp.</i>	0.584	0.208	0.672
<i>Erythemis collocata</i>	-0.750	0.604	-0.056
<i>Gomphus kurilis</i>	-0.053	-0.359	0.411
<i>Ishnura spp.</i>	-0.243	-0.735	0.053
<i>Lestes congener</i>	0.299	0.129	0.154
<i>Lestes disjunctus</i>	0.449	-0.649	-0.603
<i>Lestes dryas</i>	0.547	-0.572	-0.517
<i>Lestes spp.</i>	-0.691	0.719	-0.341
<i>Libellula forensis</i>	-0.042	0.017	-0.074
<i>Libellula pulchella</i>	0.522	-0.365	-0.371
<i>Libellula spp.</i>	0.293	0.406	-0.370
<i>Pachydiplax longipennis</i>	-0.791	0.243	0.031
<i>Sympetrum corruptum</i>	-0.367	-0.302	-0.721
<i>Sympetrum ilotum</i>	-0.780	0.112	-0.350
<i>Sympetrum madidum</i>	0.039	0.659	-0.190
<i>Sympetrum pallipes</i>	0.330	-0.677	-0.613
<i>Sympetrum spp.</i>	0.081	-0.439	-0.745
<i>Sympetrum vicinum</i>	-0.347	0.802	-0.340
<i>Tramea lacerata</i>	-0.591	0.614	-0.237

Table A.2.5: r-Values for NMS ordination of adult species

Axis:	1	2	3
	r	r	r
<i>Aeshna californica</i>	0.182	0.151	0.154
<i>Aeshna multicolor</i>	0.108	0.362	0.189
<i>Aeshna palmata</i>	-0.073	0.265	0.232
<i>Aeshna spp.</i>	0.024	0.267	0.213
<i>Aeshna umbrosa</i>	-0.214	-0.707	-0.334
<i>Anax junius</i>	0.343	0.274	-0.110
<i>Archilestes californica</i>	0.168	0.089	0.084
<i>Enallagma cyathigerum</i>	0.674	0.143	0.146
<i>Enallagma spp.</i>	0.536	-0.103	-0.042
<i>Erythemis collocata</i>	0.386	0.277	0.049
<i>Ishnura cervula</i>	0.257	0.099	-0.372
<i>Ishnura spp.</i>	0.254	0.422	-0.062
<i>Lestes disjunctus</i>	0.130	0.262	-0.141
<i>Lestes dryas</i>	0.137	0.141	-0.176
<i>Lestes spp.</i>	0.044	0.078	-0.579
<i>Libellula forensis</i>	0.480	0.282	0.243
<i>Libellula luctuosa</i>	0.437	0.224	0.293
<i>Libellula pulchella</i>	0.200	0.156	-0.354
<i>Pachydiplax longipennis</i>	0.276	0.178	-0.083
<i>Plathemis lydia</i>	0.438	0.198	0.058
<i>Sympetrum corruptum</i>	0.312	0.202	-0.019
<i>Sympetrum danae</i>	0.168	0.089	0.084
<i>Sympetrum ilotum</i>	0.290	0.085	0.192
<i>Sympetrum occidentale</i>	-0.266	0.341	-0.305
<i>Sympetrum pallipes</i>	-0.359	0.547	-0.138
<i>Sympetrum spp.</i>	0.262	0.334	-0.447
<i>Tramea lacerata</i>	0.373	0.228	0.336

Table A.3.1: Annotated Odonate life-history data

SPECIES	EGG			NYMPH			FLIGHTCODE	REF	OVILOC	REF
	DRYRESEGG	REF	OVERWNT	REF	FORAGSTR	REF				
<i>Aeshna californica</i>	0	5	1	1	1	3	Ap	1	2	1
<i>Aeshna multicolor</i>	0	5	1	1	1	3	M	1	5	1
<i>Aeshna palmata</i>	0	5	1	1	1	3	Ju	1	5	1
<i>Aeshna umbrosa</i>	0	5	1	1	1	3	Ju	1	3	1
<i>Anax junius</i>	0	5	0	3	1	3	M	1	4	1
<i>Archilestes californica</i>	0	5	1	2	1	3	Ag	2	6	2
<i>Enallagma civile</i>	0	5	0	3	1	3	Ju	1	2	1
<i>Enallagma cyathigerum</i>	0	5	0	3	1	3	M	1	2	1
<i>Erythemis collocata</i>	0	5	0	3	0	3	Jn	1	4	1
<i>Gomphus kurilis</i>	0	5	0	3	0	3	M	4	1	4
<i>Ishnura cervula</i>	0	5	0	3	0	3	M	1	2	2
<i>Lestes congener</i>	1	5	1	1	1	3	Ag	1	6	1
<i>Lestes disjunctus</i>	1	5	1	1	1	3	Ju	1	5	1
<i>Lestes dryas</i>	1	5	1	1	1	3	Jn	1	6	1

1=resistant

1=egg

0=ambush

Ap=April

1=water or sediments

0=non-resistant

0=nymph

1=stalking

M=May

2=submerged veg

Reference (for full reference, see Literature Cited):

1. Walker, 1956

2. Kennedy 1913

3: Corbet 1999

4: Dunkle 2000

5: S. Valley, pers. comm.

Jn=June

3=submerged wood

Ju=July

4=floating veg

Ag=August

5=emergent veg near water

6=emergent veg away from water

Table A.3.1: Annotated Odonate life-history data (continued)

<i>Libellula forensis</i>	0	5	0	3	0	3	Jn	1	1	1
<i>Libellula luctuosa</i>	0	5	0	1	0	3	Jn	1	1	1
<i>Libellula lydia</i>	0	5	0	1	0	3	M	1	1	1
<i>Libellula pulchella</i>	0	5	0	1	0	3	Ju	1	1	1
<i>Pachydiplax longipennis</i>	0	5	0	3	0	3	Jn	1	1	1
<i>Sympetrum corruptum</i>	0	5	1	3	1	3	Jn	1	1	5
<i>Sympetrum danae</i>	0	5	1	3	1	3	Jn	1	1	1
<i>Sympetrum ilotum</i>	0	5	1	3	1	3	M	1	1	1, po
<i>Sympetrum madidum</i>	1	5	1	3	1	3	Jn	1	1	5
<i>Sympetrum occidentale</i>	1	5	1	3	1	3	Jn	4	1	5
<i>Sympetrum pallipes</i>	1	5	1	3	1	3	Ju	1	1	5
<i>Sympetrum vicinum</i>	1	5	1	3	1	3	Ju	1	1	1
<i>Tramea lacerata</i>	0	5	0	3	0	3	Jn	4	4	5

1=resistant

1=egg

0=ambush

Ap=April

1=water or sediments

0=non-resistant

0=nymph

1=stalking

M=May

2=submerged veg

Reference (for full reference, see Literature Cited):

1. Walker, 1956

2. Kennedy 1913

3: Corbet 1999

4: Dunkle 2000

5: S. Valley, pers. comm.

Jn=June

3=submerged wood

Ju=July

4=floating veg

Ag=August

5=emergent veg near water

6=emergent veg away from water