

SPATIAL AND TEMPORAL DIFFERENCES IN
ASSEMBLAGES, CONDITION FACTORS,
AND GROWTH RATES OF WARMWATER
STREAM FISHES IN NORTHCENTRAL
OKLAHOMA

By

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CHAPTER I

INTRODUCTION

The following chapters are written in the format required by manuscripts submitted for publication in Ecology a journal of The Ecological Society of America (Chapter II) and Copeia, journal of the American Society of Ichthyologists and Herpetologists (Chapter III).

CHAPTER II

THE INFLUENCE OF SCALE ON MECHANISMS STRUCTURING FISH
ASSEMBLAGES IN A NORTHCENTRAL OKLAHOMA
WARMWATER STREAM

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INTRODUCTION

What is the appropriate scale of an investigation, and at what scales are specific results applicable? These two questions are of concern to all ecologists, and the answers change depending upon the question asked. For example, small-scale processes such as herbivory and competition play a large role in structuring local plant communities by controlling the number of species and individuals present in a patch of vegetation (Fowler and Rausher 1985). However, at large spatial scales, precipitation, geomorphology, temperature, and dispersal patterns dictate regional plant assemblages (Crawford and Gosz 1982, Neilson 1986, McAuliffe 1994). Thus, at each scale one or more different mechanisms are influencing community structure.

Determining the major controlling mechanism at each scale is difficult because different relationships may be found at different scales or among different studies. For example, large-scale studies ($>10^3$ m²) have found fish communities to be structured according to stream order, with species richness generally increasing in a downstream direction (Harrel et al. 1967, Lotrich 1973). Medium- and small-scale studies, those at the level of a specific stream order or an individual reach or pool (10^1 - 10^3 m), have produced conflicting hypotheses in that different biological (Matthews et al. 1987, Schlosser 1987a and 1987b, Harvey 1991, Prenda et al. 1997) and physicochemical (Matthews and Styron 1979, Stewart et al. 1992) factors, or habitat types (Gorman and Karr 1978, Schlosser 1987a, Meador and Matthews 1992) have been shown to be responsible for regulating stream fish assemblages. This patchwork of results is difficult to apply to any one system, and production of a general model is problematic because few studies have focused on multiple scales within the same community. Therefore,

further insight into fish assemblage structure, and community structure in general, is difficult because the spatial scale at which one controlling factor diminishes and another begins is not clearly defined (or in some cases not investigated). Further compounding the problem is the fact that the mechanisms regulating species interactions at one scale may not be important or as important at other scales (Power et al. 1985).

In this study I identified the dominant mechanisms regulating fish community structure at three spatial scales in a northcentral Oklahoma prairie stream. I used the drainage (the watershed), segment (within a stream order), and reach (within specific habitats) stream-scale classification schemes (Grimm and Fisher 1992) to address three questions: (1) do fish assemblages change as spatial scale changes? (2) if so, do the mechanisms structuring them also change? and, (3) what are the dominant mechanisms at each scale? I use answers to these questions from this study and those from other scale-specific investigations by other researchers to form a general model of scale-dependent controls on fish assemblage structure in warmwater streams.

STUDY SITE--- The Wild Hog Creek watershed is a 12.8 km² basin in northeastern Oklahoma (Fig. 1) located in The Nature Conservancy's Tallgrass Prairie Preserve. The upper basin contains several first order streams and two second order streams that are divided by a series of rolling hills, and are the origin of third order Wild Hog Creek. Most first order streams are ephemeral with poorly developed pools and riffles that fluctuate in size with changing discharge. The second order streams are intermittent, with channels characterized by large riffle areas separated by small to medium size (2 - 20m) pools. Riffles typically desiccate in mid-summer, but 6 pools

persisted throughout the study period. The third order segment, although subject to water loss in drier months, is perennial with well-developed pools, riffles, and raceways that, in wetter years, have at least some flow year-round. Stream substrate is composed of sand, mud, gravel, cobble and some areas with large bedrock outcroppings.

Fishes in the Tallgrass Prairie Preserve are a mixture of upland and prairie species. To date, 23 species have been found in the drainage (Matthews and Gelwick 1993) with the majority (16 of 25) in the genera Notropis, Etheostoma, Lepomis, and Micropterus.

MATERIALS AND METHODS

With the exception of 31 April, when sampling was not possible, fish were collected bi-weekly from each stream order (first, second, and third) from 19 April 1997 to 27 September 1997. Specific sampling sites within each stream varied to obtain a representative estimate of the fish populations in each habitat. Pools were sampled by seining until there was a decrease in the number of fish caught (assuring the majority of fish were sampled). Riffles were sampled by kick seining with a 5 m or 9 m seine, or by using small dipnets in areas where the seines were ineffective. Most fish captured were identified, enumerated, and then returned to the stream unharmed. However, some (<5%) were preserved in 10% formalin for analysis in the laboratory.

For the drainage analysis, 13 environmental variables were measured on each date at all collection sites. Water samples and measurements of discharge, air temperature, and water temperature were taken from fixed sites in each stream order throughout the sampling period. The average of three replicate water samples was used to represent

each date/site combination. Sulfate (SO_4^{2-}), nitrate ($\text{NO}_3\text{-N}$), and chloride (Cl^-) were determined on a Dionex DX-100 ion-chromatograph. Ammonium-nitrogen ($\text{NH}_4\text{-N}$) was determined using the phenolhypochlorite method immediately upon return to the laboratory (Solorzano 1969), and soluble reactive phosphorous (SRP) with the molybdate blue method (Murphy and Riley 1962). Turbidity, pH, and conductivity were assessed in the laboratory using standard probes (conductivity, pH) or meters (turbidity) and atomic N:P ratio was also calculated for each site/date combination. Additional data (rainfall and solar radiation) were obtained from the Foraker site of the Oklahoma Mesonet (located 6.5 km from the stream). In addition to the measured environmental data, nine dummy variables, represented by a 1 or 0, were used to represent the month and stream order sampled.

Fish community structure was investigated using multivariate analysis procedures in CANOCO for Windows (ter Braak and Smilauer 1997). For the drainage analysis a Detrended Correspondence Analysis (DCA) was used to ordinate samples (first, second, and third order streams and their corresponding dates) on the basis of species abundances at those site/date combinations. DCA, an indirect gradient analysis, was used because it reveals patterns in community structure based only on species abundance, not on directly measured environmental variables (ter Braak and Prentice 1988). Prior to the analysis, abundances were square-root transformed to decrease the effects of highly abundant species, rare species (those found in <10% of the samples) were down-weighted

After the DCA, several Canonical Correspondence Analyses (CCA; ter Braak 1986) were performed. CCA is a direct gradient analysis in which both species and environmental data are used to produce the ordination axes. This results in a plot

representing the relationship between species abundances, sites, and environmental variables. The first CCA analysis was used to determine if the CCA axis 1 matched the gradient on DCA axis 1 and to determine if the measured environmental variables had a significant effect on fish community structure within streams. Prior to analysis, values of Cl^- , SO_4^{2-} , $\text{NO}_3\text{-N}$, SRP, and $\text{NH}_4\text{-N}$ were log transformed.

A second CCA was performed to relate the measured environmental variables to the first axis from the DCA ordination. To do this, the variable producing the DCA axis 1 gradient was used as a co-variable in this CCA. This allowed me to factor out the effect of the variable causing the DCA axis 1 gradient and then, using the remaining environmental variables, to interpret the remaining variance in the species-abundance data set. A third CCA was performed using stream order and month as co-variables. This analysis determined if any of the environmental variables had an affect on fish assemblage structure apart from expressing seasonal differences within the fish assemblage. Monte-Carlo tests (199 permutations) were performed on each CCA to determine if the overall analysis and/or the first axis gradient explained a significant amount of the variation in community structure.

Analyses of community structure at the levels of stream segment and stream reach were performed by using species-abundance data from only the third order stream. The third order stream was chosen because it is perennial and species can usually move freely among habitats. Therefore, only mechanisms responsible for structuring assemblages within the third order stream would be detected. Species abundances taken from 25 samples of pools and riffles over the course of the study were used in the segment analysis. For the reach scale analysis I constructed a third species data set using only

samples taken from pools, and a second environmental matrix that consisted of seven environmental variables representing month (as dummy variables) and the number of predators (spotted bass; Micropterus punctulatus) in the sample area.

I used a DCA to examine community structure at the level of stream segment. In this analysis species abundances in the third order data set were square root transformed and rare species (those in <2 samples) were downweighted. To analyze assemblage structure at the reach scale a partial CCA (partial CCA indicates use of co-variables) was performed on the data set for pools. This analysis related the species-abundance data from 25 third order pools to the seven environmental variables aforementioned to identify factors structuring assemblages within pool microhabitats. In this analysis, months were used as co-variables (to factor out temporal differences in abundance of fish due to recruitment, immigration, and emigration), M. punctulatus was made passive in the species data set (so as not to bias the CCA), and species that were found in fewer than two samples were excluded from the analysis. Exclusion of rare species does not affect the overall ordination (Gauch 1982, Capone and Kushlan 1991).

RESULTS

Drainage Analysis.

Within the Wild Hog Creek basin habitat volume and heterogeneity (sensu Schlosser 1987a) varied with season and stream order. Visual assessment of the basin during the study found that habitat volume and heterogeneity of each stream were highest in the wet season and lowest in the dry season (Fig. 1). The third order channel did not cease flowing and riffle and pool habitats persisted throughout the study. In contrast, all

but one first order, and all second order channels experienced times of no flow and resulted in large areas of the stream channel desiccating in the second order, and complete desiccation of the first order channels in the upper basin.

A total of 33 samples (11 at each stream order) containing 8093 fish, and representing 16 species, were taken during this study (see Appendix). The first two DCA axes from the drainage analysis explained 44% (eigenvalue = 0.133) and 9% (eigenvalue = 0.028), respectively, of the variance in species abundance (Fig. 2). Lengths of the gradients were 1.3 SDs for axis 1 and 0.8 SDs for Axis 2, indicating a large amount of overlap (low beta diversity) exists among the assemblages of the three sites (Gauch 1982).

DCA axis 1 produced a clear pattern in that species with high 1st axis scores (Ameiurus natalis, Percina caprodes and Moxostoma erythrurum) were found primarily in the third order stream and the species with the lowest 1st axis score, (Etheostoma whipplei), was most common in the first order sites (Fig. 3). Therefore, DCA axis 1 can be interpreted as a gradient representing stream order, with species being ordinated with respect to their occurrence (or probability of occurrence) in each stream order. DCA axis 2 (Fig. 2) could not be interpreted.

The first drainage-level CCA generated four axes explaining 76% of the variance in species abundance among sites, and 87% of the variance in species abundance among sites with respect to the environmental variables. The first axis produced the same stream order gradient (Fig. 4) seen in the DCA ordination, and accounted for a significant amount of the observed variation (Monte-Carlo test overall analysis, $p = 0.005$). CCA axis 2 represented a 2nd order gradient that was correlated with SO_4^{2-} . However, when the CCA was performed using stream order as a covariable, the strength of this gradient

diminished (Fig. 5). With effects of stream order factored out in the second analysis, 54% of the remaining variance in species abundance among sites, and 78% of the remaining variance in species abundance among sites with respect to the environmental variables was explained. The second CCA also indicated that the remaining variables (those not used as covariables) had a significant effect on community structure (Monte-Carlo for overall analysis, $p= 0.005$), and that there were significant temporal differences in community structure (Monte-Carlo for axis 1, $p= 0.005$). Temporal differences are represented on the first axis where April had the highest score (0.59), and May had the second lowest (-0.45).

The third CCA, using stream order and months as co-variables, found that the remaining environmental variables (e.g., everything but month and stream order) did not significantly contribute to community structure at this scale other than expressing the temporal differences (Monte-Carlo test overall analysis, $p= 0.70$) seen in the preceding CCA. Therefore, the measured environmental variables (shown in Fig. 5) did not directly regulate assemblage structure, but instead they only reflected the temporal differences in monthly assemblages.

Segment Analysis

The segment scale analysis indicated that fish assemblages within the third order stream are influenced by mechanisms other than those operating at the drainage scale. The first two DCA axes for the full data set for the third order stream explained 54% (eigenvalue = 0.462) and 9% (eigenvalue = 0.076) respectively, of the variance in species abundances (Fig. 6). Axis 1 represented a microhabitat gradient (i.e., pool vs. riffle)

occurring within the segment with each species being associated with a specific habitat type within the segment. E. spectabilis and P. caprodes, located on the far left side of the axis, occurred in riffles (P. caprodes was found on the edge of riffles) and M. punctulatus, L. cyanellus, L. sicculus, and L. megalotis, ordinated on the right side of the graph, were found primarily in pools. Therefore, within segments of the stream, fish assemblages were structured mainly by habitat. The second DCA axis appears to be a biological gradient within habitats, as predatory species (M. punctulatus and L. cyanellus) had very high second axis scores, and prey species had lower scores. This relationship is discussed further in the next analysis.

Reach Analysis

The final analysis, performed at the reach scale, was a partial CCA on the data set for fish samples in pools of the third order stream and the seven environmental variables (months and numbers of bass) aforementioned. Partial (with months used as covariables) and full CCAs on these data produced identical gradients on the first and second axes, but because of the temporal differences in fish abundance, the partial CCA produced a more interpretable ordination, and had the same level of significance (Monte-Carlo overall test, $p < 0.035$) as the full CCA. The partial analysis showed a pattern similar to that on axis 2 of the DCA ordination of all samples from the third order stream (Fig. 7) Again, this appears to reflect a biological interaction. The analysis indicated that within pools, interactions between species (in this case the number of bass) significantly affected the fish assemblages (Monte-Carlo overall test, $p < 0.04$). The predatory bass had a very high score on CCA axis 1, whereas scores for the prey species were at the opposite

extreme (Fig. 7). Therefore, the number of predators apparently was important in structuring the fish assemblages in pools.

DISCUSSION

The results of this study indicate that spatial scale is an important determinant of stream fish assemblage structure. To illustrate this spatial dependence, I produced a model for the fish assemblages of Wild Hog Creek that represents each scale and its corresponding primary control mechanism (Fig. 8). However, because habitat changes throughout the year, depending specifically on presence or absence of flow in all three stream orders, I suggest two forms of this model, one applicable to periods when water is present in all streams, and the other for dewatered periods. This separation is necessary because habitat types, volume, and heterogeneity are different under these two regimes, and changes in the models (e.g., the lack of 1st order sites and 2nd order riffles when it is dry) had to be made to incorporate changes in community regulation driven by hydrologic variance typical of warmwater streams (Matthews 1988, Stanley et al. 1997). Therefore, the two versions of this one model represent the endpoints of a highly variable hydrologic spectrum.

Drainage Scale

At the drainage scale, fish assemblages in the Wild Hog Creek watershed were dictated by stream order. The physical and environmental differences between stream orders acted to segregate the communities into order-specific assemblages. Although the same species pool exists for each stream order, autecological differences among species

resulted in distinct assemblage structure among first-, second-, and third- order sites. This is clearly seen in the first DCA (Fig. 2) where sample scores are stratified by stream order. Although assemblages changed over time, assemblage structure remained relatively consistent within each stream order. This consistency has been demonstrated in other studies and can be related to similarities or differences in species habitat requirements, preferences, life history, and specific characteristics of each stream order/channel (Gelwick 1990, Meador and Matthews 1992, Stewart et al. 1992, Matthews et al. 1994).

First order sites in Wild Hog Creek were characterized by poorly-developed pools and riffles with substantial and rapid fluctuations in size and discharge throughout the year. Even when water was present, fish were absent from the majority of the first order channels in the basin because of barriers to colonization (e.g., waterfalls) or the lack of permanent water (personal observation). In areas that did contain fish, habitat predictability and heterogeneity were extremely low and only species tolerant of the fluctuating and at times extreme conditions, and can move into and out of first order channels during wet intervals, were likely to be found there (Ross et al. 1985, Schlosser 1987a). Therefore, community structure within first order sites was based upon the presence or absence of water. If the channel was dry, obviously no communities exist, and if it was wet, rapid colonization occurred but the fine-scale structuring mechanisms seen in higher stream orders (like those found at the reach scale) were difficult to discern because of rapid changes (wetting and drying; immigration and emigration of fish) and lack of distinct pool-riffle physical structure in most first order sites.

Second order Wild Hog Creek channels were intermediate between the first and third orders in that the presence of some large well-developed perennial pools allowed permanent residency of some species. However, because of drying and channel morphology, second order habitat heterogeneity, volume, and predictability were lower, and fluctuated more, than third order channels (personal observation, see also Fig. 1). This resulted in a decrease in species richness and significantly decreased the number of fish that inhabited the stream during the 'dry' periods (Spranza, see chapter 3).

The fish assemblages in the third order stream reflected differences in habitat between the stream orders in that the presence of many well developed perennial pools and riffles, coupled with increased habitat volume and size, allowed fish to occupy this area year-round. This produced a change in the assemblage from one dominated mainly by small minnows and small centrarchids (as seen in the first- and second -order channels) to one that included larger adult centrarchids, catostomids, ictalurids, and an increased density, and types of cyprinids. As was seen in other studies (Power 1984, Capone and Kushlan 1991, Matthews et al. 1994), larger fish species tended to occupy the deeper, more stable habitats (pools) that are common in the third order channel. This produced a very different assemblage compared to those of the first and second order streams, because fish occupying the third order did not have to contend with intermittency (as did fish occupying other stream orders). Although discharge did decrease to almost zero in the third order stream, there was always some flow, and the extreme habitat fragmentation that occurred in the lower stream orders did not occur.

Segment Scale

At this scale, structural features of habitat appeared to be the primary factor controlling fish assemblages with each species being in either a riffle or pool assemblage. The separation of assemblages indicated that habitat preference of individual species dictated community structure at this scale and produced distinct pool and riffle assemblages. For example, large species (M. punctulatus, L. cyanellus and L. megalotis), that were grouped together (Fig. 6), are found primarily in perennial pools. These medium to large pools can buffer seasonal fluctuations in discharge within the stream (Schlosser 1987a), offer protection from terrestrial predators (Power 1984), and provide a relatively stable year round habitat (Meador and Matthews 1992). Cyprinids and other small minnows can be found in any area of the stream, but most are found within pools and raceways in varying densities (Matthews et al. 1994) with some movement into riffles during the summer as a result of increased recruitment (personal observation). Darters (E. spectabile and P. caprodes) were primarily taken in riffles or on the edge of riffles where their primary food, benthic insects, are abundant (Page 1981, Lehtinen 1982). However, this study and others (Lehtinen 1982, Gelwick 1990) found that there are significant temporal differences in the fish communities of riffles which, in part, can be attributed to seasonal fluctuations in discharge and recruitment. For example, Lehtinen (1982) found that in a stream that is similar to Wild Hog Creek, E. spectabile and P. caprodes shifted habitats from riffle areas to shallow (E. spectabile) and deep (P. caprodes) pools during times of decreased discharge. Upon rewetting of riffle habitats, these fish then moved back into riffle areas. This conforms with my finding that seasonality also plays a significant role at this scale by influencing the size, quantity and

availability of preferred habitats. Therefore, the “wet” and ‘dry” versions of the model (Fig. 8) are different at this scale in order to account for the lack of first order habitats and second order riffles and small pools.

Reach Scale

At the reach scale, biotic interactions within pools appear to structure Wild Hog Creek fish assemblages. In this study, prey species tended to occur in pools that did not have bass in them. Similar patterns have been observed in other studies where individuals susceptible to predation tended to avoid or limit their time in habitats that would put them in close association with a predator (Cerri and Frasier 1983, Power et al. 1985, Schlosser 1987b, Harvey 1991, Matthews et al. 1994), or selected habitats on the basis of the ratio between predation risk and food intake (Gilliam and Frasier 1987). Because centrarchids tend to remain in a home pool (Gerking 1959, Berra and Gunning 1972), and production (primary and secondary) and habitats (types available and volume) change seasonally within these systems, other types of biological interactions (competition and resource limitation) may also play a role in structuring microhabitat assemblages within reaches.

Resource limitation and habitat overlap between species can result in high levels of inter- and intraspecific competition (Mittelbach 1981, Werner et al. 1983) and may play a significant role in regulating assemblage structure within habitats. Prenda et al. (1997) found that interspecific habitat overlap was greater at low densities than at high densities, and at high densities there was a trend of ‘mutual avoidance’ between species with the same habitat requirements, effectively partitioning the habitat, and minimizing the overlap between competitors. This mechanism is consistent with the distribution of

L. cyanellus and M. punctulatus within Wild Hog Creek. These two species (both piscivores) prefer similar habitats (deeper pools), and because adult L. cyanellus are too big to be consumed by the bass, they should be found together. However, within Wild Hog Creek these two species tend to be found in different locations or at low densities (of L. cyanellus) when found together. Similar findings by Matthews et al. (1994) suggest that these two species are direct competitors. Thus L. cyanellus may be actively avoiding pools with bass and/or are being actively excluded from primary habitats (pools) by bass.

Competition may also play a role in the pools that have bass in them. Power et al. (1985) found that within isolated pools containing bass, large schools of Campostoma anomalum occupied shallow habitats along the perimeter of the pool. With migration between pools prevented, competition for food in these peripheral areas surely increased as the food supply decreased. Although the study by Power et al. (1985) was done in an artificially isolated pool, the same type of interactions can take place in isolated dry-season pools. Thus, along with presence/absence of a predator, competition and habitat partitioning act secondarily to structure fish assemblages in pools with and without bass.

The role of biological interactions in structuring fish assemblages of riffles in Wild Hog Creek is unresolved by my analysis. However, some relationships can be seen in my data. Unlike pool assemblages, riffle dwelling species do not have to contend with large aquatic piscivores because such predators typically are absent from this habitat. However, microhabitat partitioning by darters has been shown to play a large role in the structuring of riffle assemblages. Stauffer et al. (1996) found that high habitat specialization among ten co-occurring species of darters resulted in a high degree of habitat partitioning. Although the amount of habitat partitioning varies with the number

of co-occurring darter species, partitioning has been found to occur in systems with as few as two species (Kessler and Thorp 1993). Because degree of partitioning increases as number of potential competitors increases (Lehtinen 1982) past and/or present competition between darter species is the likely cause of this partitioning. Past competition would lead to increased specialization, whereas present competition would restrict species to their particular niche, thereby lowering habitat overlap. Therefore, given the similarity of riffles in the second-and third-order streams, I hypothesize that, under wet conditions, species interactions (past or present) that result in habitat partitioning play a large role in the community structure of these riffle areas. When riffle habitat decreases in the dry season, riffle species shift to pool habitats until re-wetting of the riffles occurs. During these times habitat overlap between species increases which results in a decreased partitioning. Additionally, predation by pool-dwelling species may be important in structuring darter assemblages in these suboptimal habitats.

In conclusion, my findings suggest that: 1) fish assemblage structure changes as spatial scale changes; specifically, there are different assemblages at drainage, segment, and reach scales, 2) mechanisms acting to structure assemblages also change as scale changes and, 3) with identification of spatial scales and the different mechanisms acting at each scale, it was possible to produce a model for warmwater prairie-stream fish assemblages that takes into account different spatial scales, and the changing mechanisms within them. However, specific areas of further research are needed to strengthen this model, specifically interactions within first order streams, and what affect competition and predation have in structuring riffle fish assemblages.

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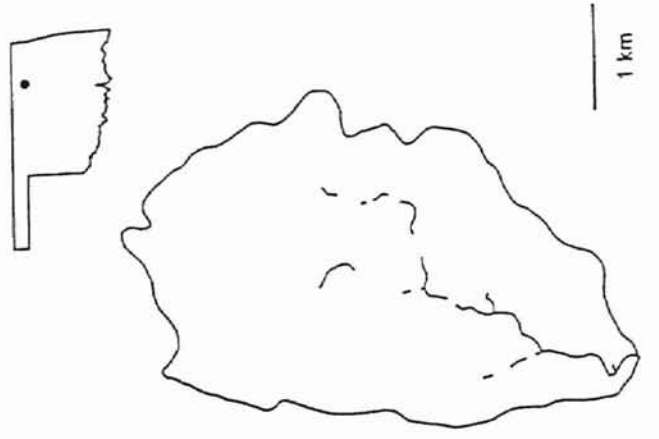
Figure Captions

1. Wild Hog Creek basin showing the first, second, and third order sample streams and the distribution of water during “Wet” and “Dry” periods.
2. Sample scores from a DCA performed on the drainage-wide data set showing clustering of 1st order ●, 2nd order ◆, and 3rd order ■ sites.
3. Species DCA scores plotted as pie charts showing species abundance in each stream order. Species found in higher stream orders have higher first axis scores.
See Appendix for key to abbreviations.
4. CCA results from ordination of all stream orders and environmental variables. All sample site scores fall within the designated stream order envelope. See Appendix for key to species abbreviations.
5. Ordination of the environmental variables from a partial CCA with stream order used as co-variables. Length of vector indicates magnitude of influence that each variable has on the ordination with the effect of stream order factored out of the analysis. Temporal differences in assemblages are indicated by separation on axis 1. See Appendix for key to species abbreviations.

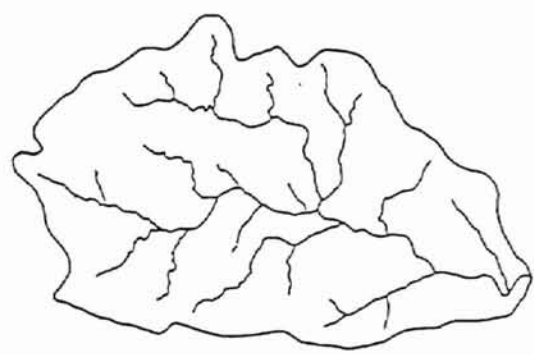
6. Species scores from a DCA on the data set for the third order indicating distinct pool and riffle assemblages. See Appendix for key to species abbreviations.

7. Results of a partial CCA from the reach analysis. Predator and prey separation is seen on the first axis where predator species have high first axis scores and prey species have low scores. See Appendix for key to species abbreviations.

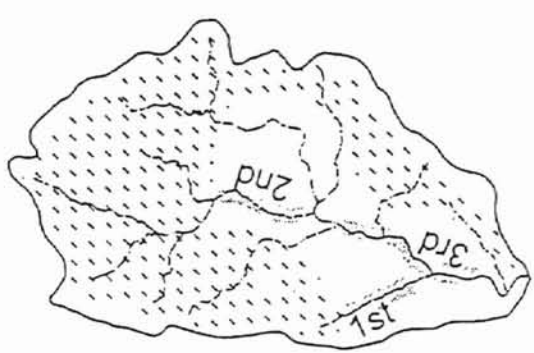
8. A model representing each scale and its corresponding control mechanisms during wet and dry periods. Differences between wet and dry models are due to changing discharge within each stream. See Figure 1 for habitat size during each period.



minimum surface water extent (October 1997)

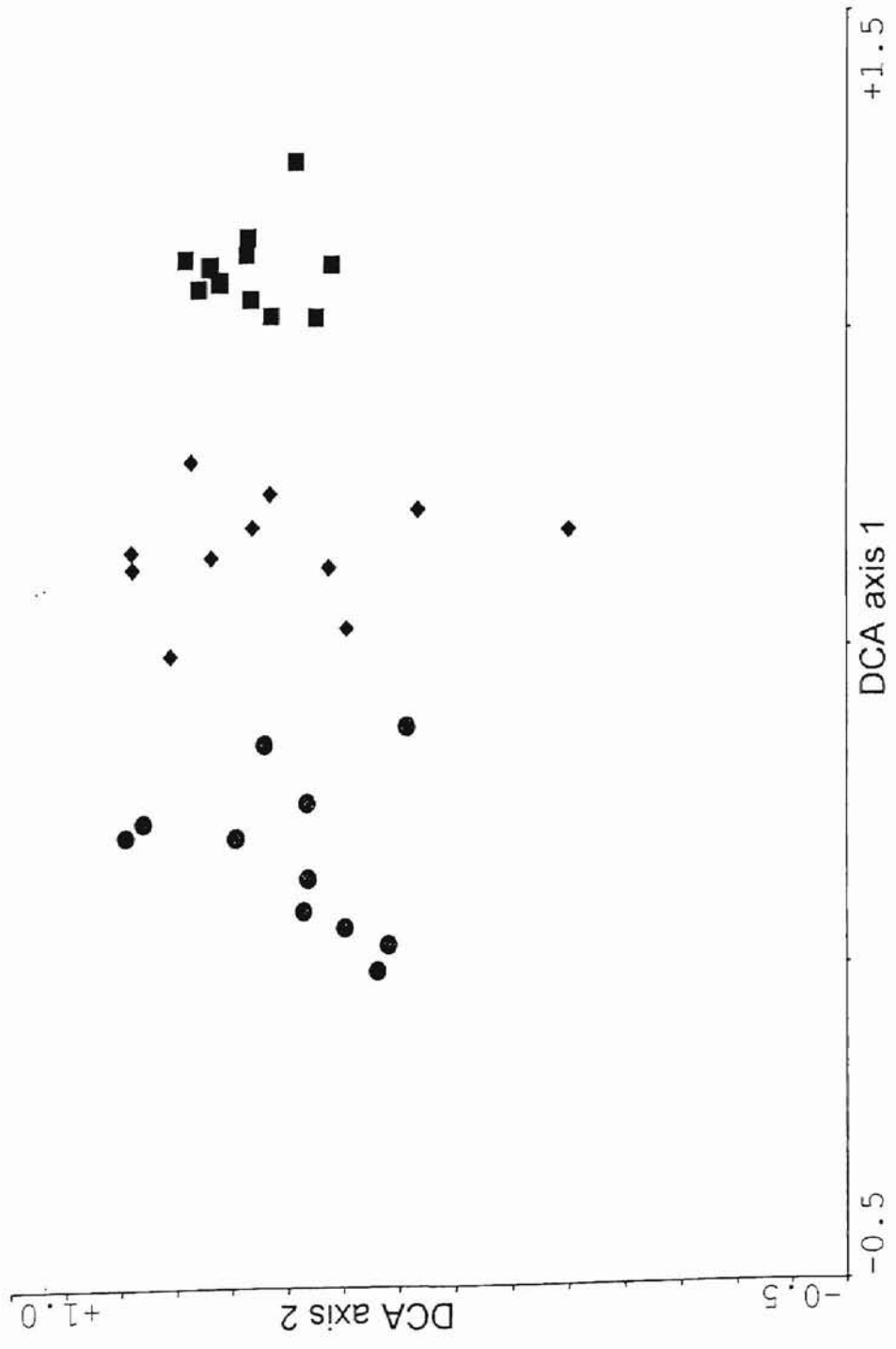


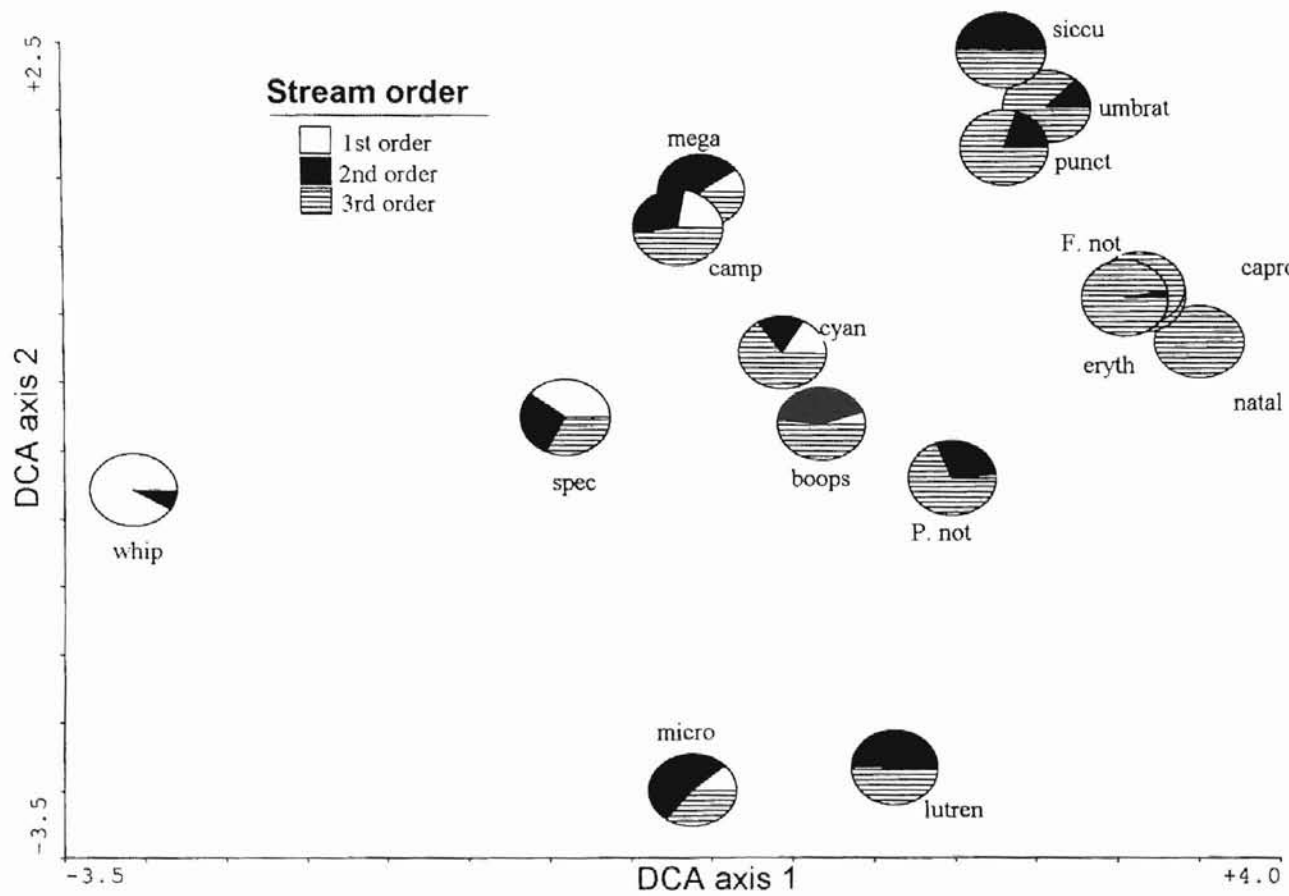
maximum surface water extent (March 1997)

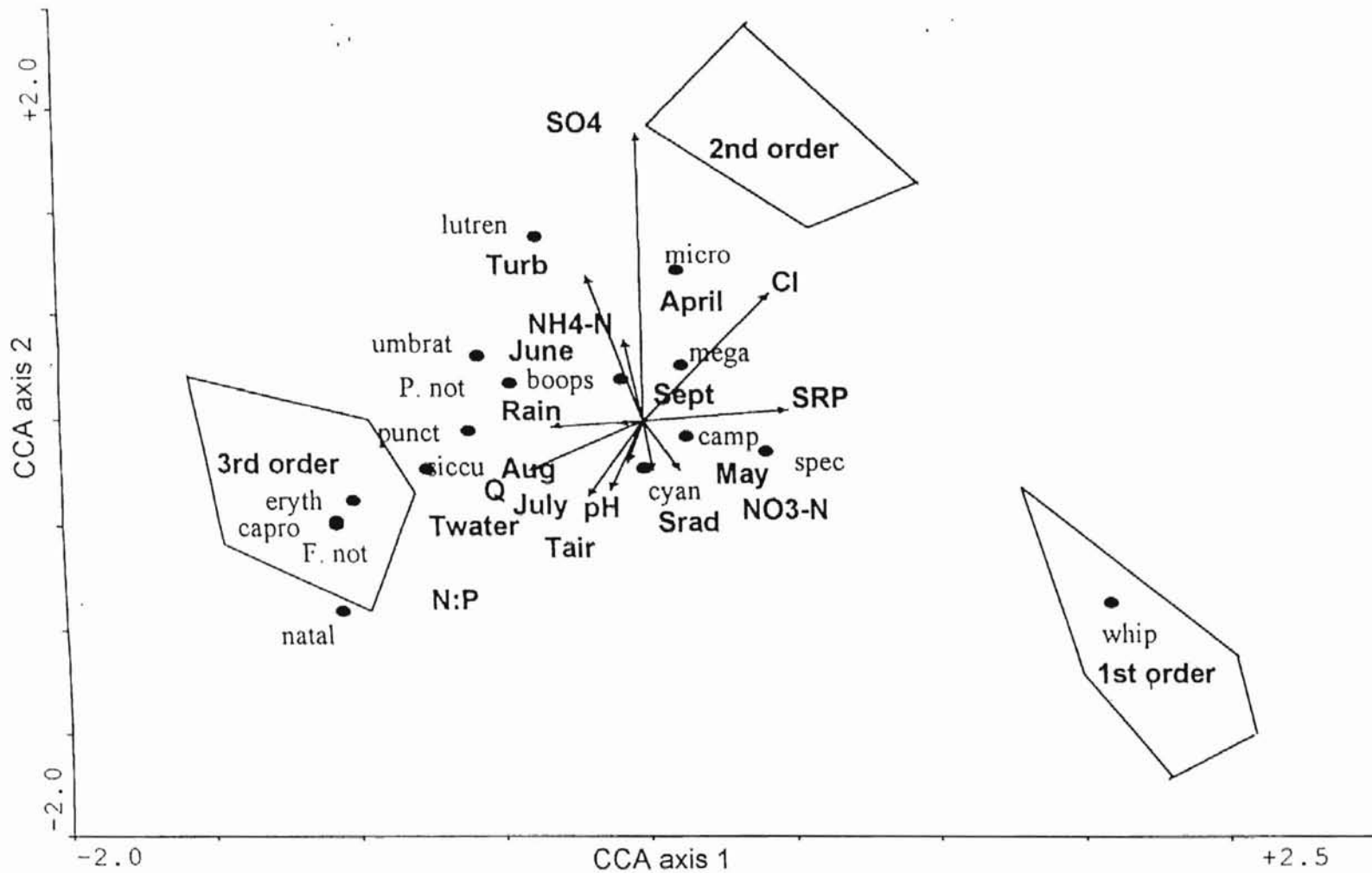


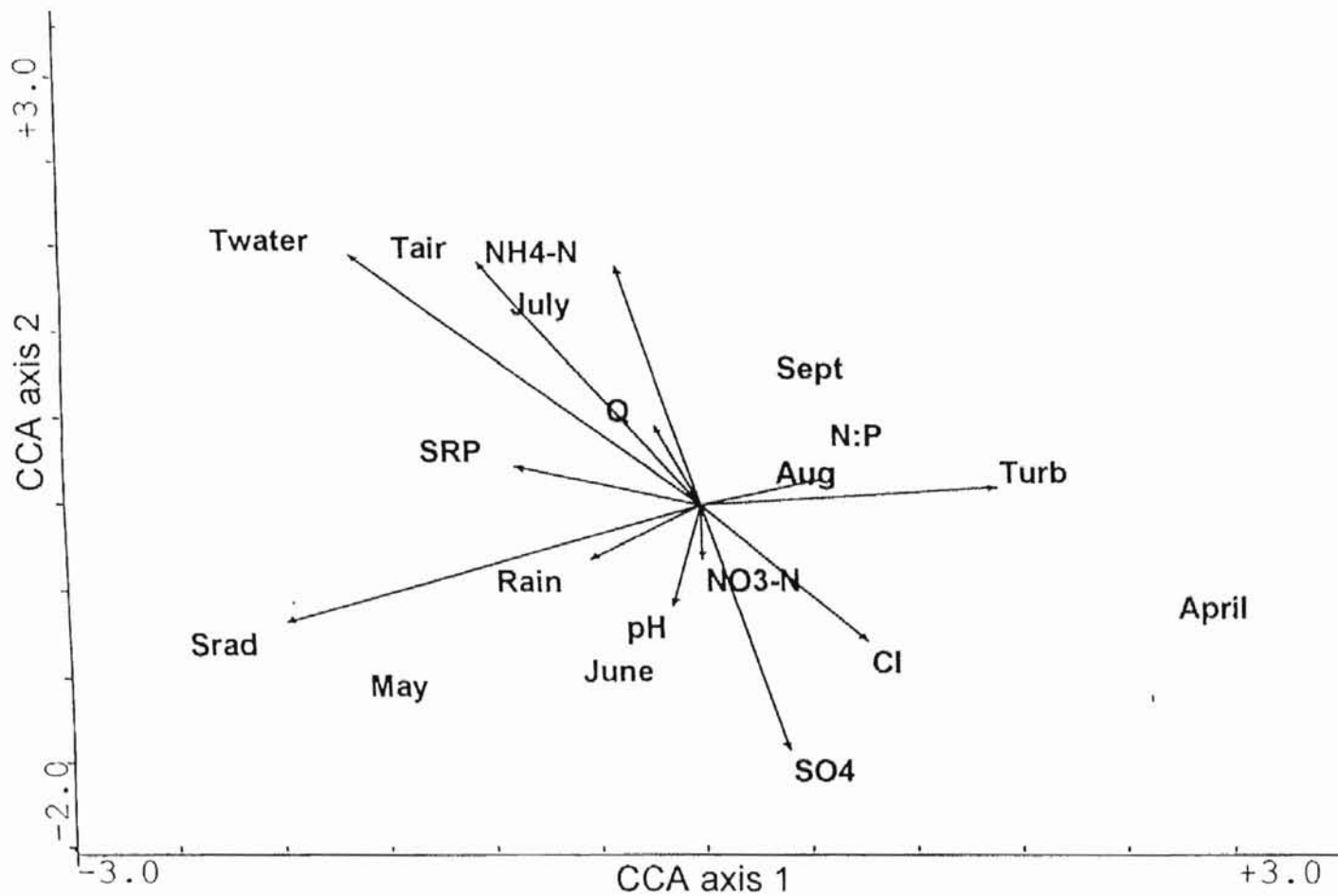
sampling regions
channels lacking fish

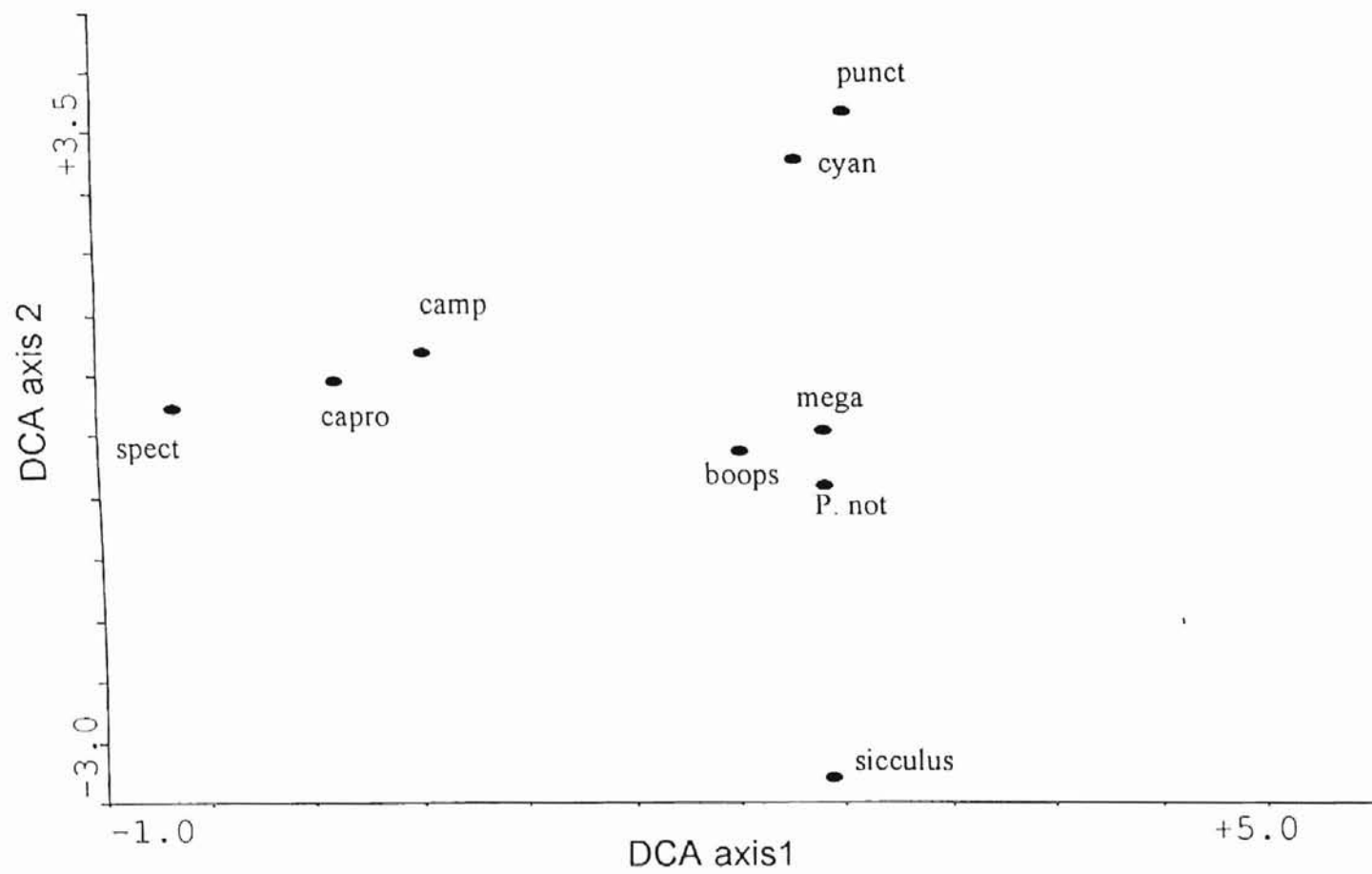
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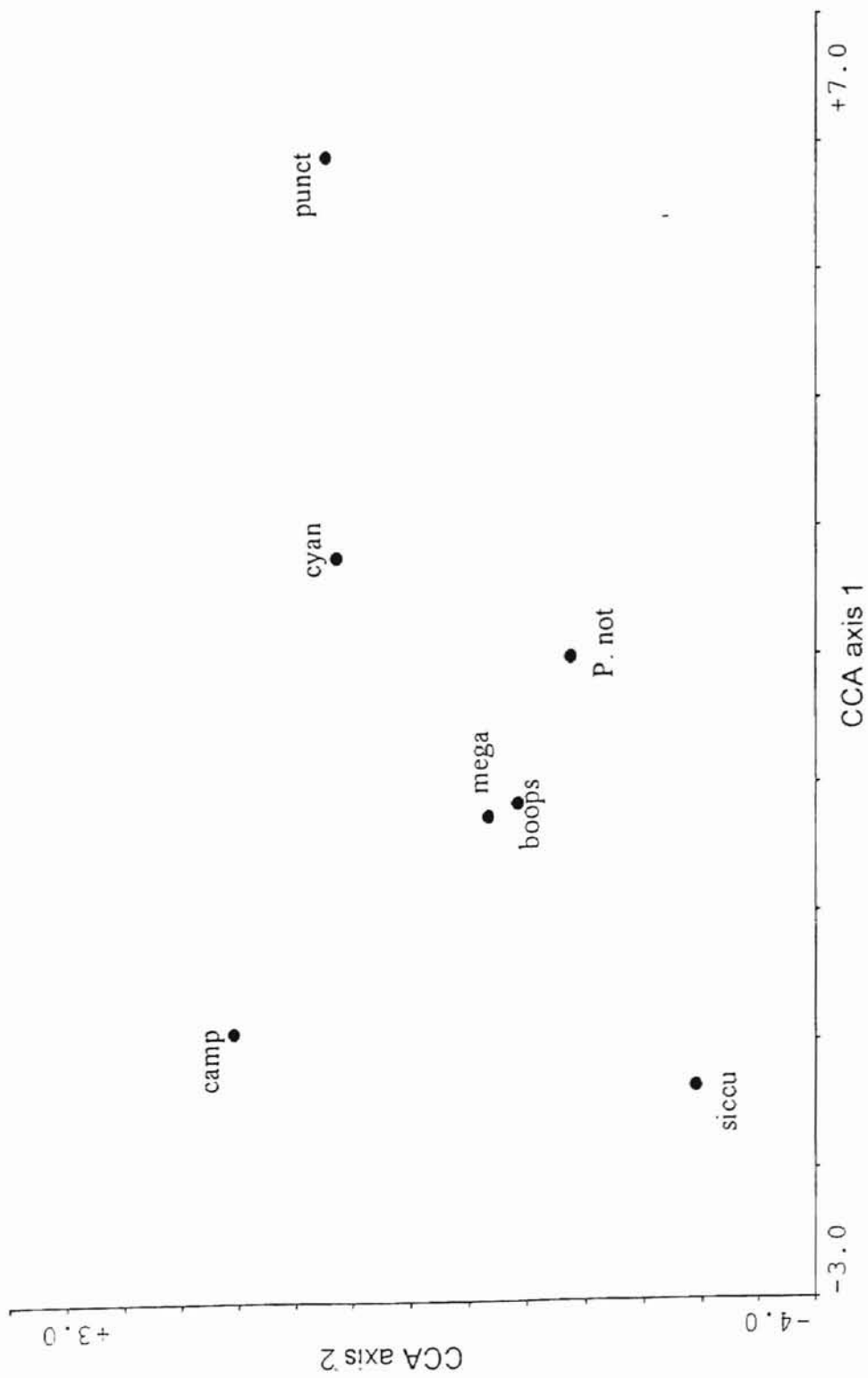












SYSTEM SCALE (m)

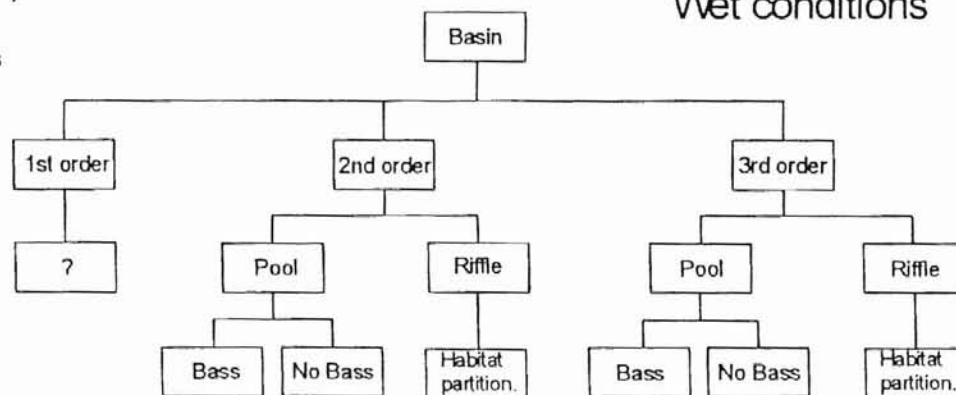
Drainage 10_4-10_5

Segment 10_3

Reach 10_1-10_2

Microhabitat 10_0

Wet conditions



34

SYSTEM SCALE (m)

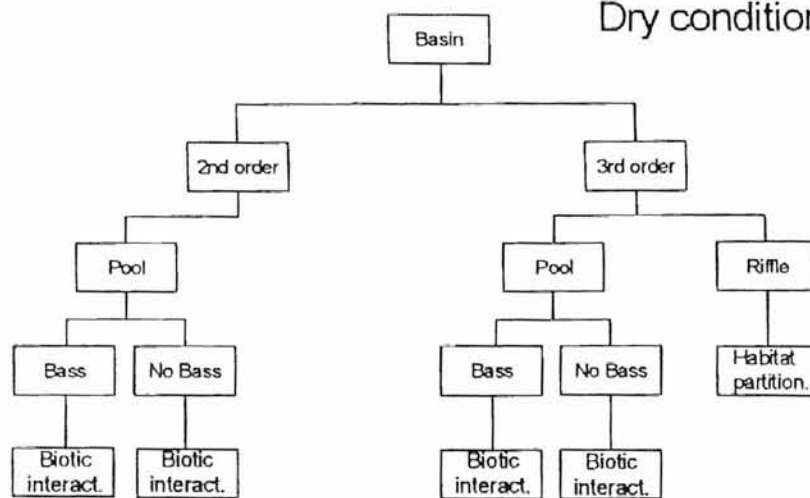
Drainage 10_4-10_5

Segment 10_3

Reach 10_1-10_2

Microhabitat 10_0

Dry conditions



Appendix

Appendix . Species and abundances for each sample date and stream order and abbreviation for species names.

Species and order	Sample date											Abbreviation
	4-19	5-18	5-30	6-13	6-27	7-10	7-23	8-14	8-30	9-1	9-27	
First order												
<u>Camptostoma anomalum</u>	52	250	164	153	147	43	38	35	52	23	20	camp
<u>Etheostoma spectabile</u>	30	14	6	5	11	22	24	26	23	27	24	spec
<u>Etheostoma whipplei</u>	1	1	1	1	1	1	1	1	1	1	1	whip
<u>Notropis boops</u>	18	10	3	5	9	6	5	4	9	4	2	boops
<u>Pimephales notatus</u>	5	3	0	0	0	0	0	0	0	0	0	P. not
<u>Lepomis cyanellus</u>	3	4	2	2	2	3	1	2	3	2	2	cyan
<u>Lepomis megalotis</u>	29	20	15	12	1	7	8	3	2	2	2	mega
<u>Lepomis microlophus</u>	1	1	0	0	0	0	0	0	0	0	0	micro
<u>Micropterus punctulatus</u>	0	0	0	0	0	0	0	0	1	0	0	punct
<u>Labidesthes sicculus</u>	0	0	0	0	0	0	0	0	0	0	0	siccu
<u>Fundulus notatus</u>	0	0	0	0	0	0	0	0	0	0	0	F. not
<u>Moxostoma erythrurum</u>	0	0	0	0	0	0	0	0	0	0	0	eryth
<u>Percina caprodes</u>	0	0	0	0	0	0	0	0	0	0	0	capro
<u>Ameiurus natalis</u>	0	0	0	0	0	0	0	0	0	0	0	natal
<u>Lythrurus umbratilis</u>	0	0	0	0	0	0	0	0	0	0	0	umbrat
<u>Cyprinella lutrensis</u>	0	0	0	0	0	0	0	0	0	0	0	lutren

Appendix 1 cont.

	Sample date										
	4-19	5-18	5-30	6-13	6-27	7-10	7-23	8-14	8-30	9-1	9-27
<u>Second order</u>											
<u>Campostoma anomalum</u>	40	134	265	141	116	170	184	78	82	97	63
<u>Etheostoma spectabile</u>	27	15	6	14	15	19	16	12	12	13	7
<u>Etheostoma whipplei</u>	1	0	1	0	0	0	0	0	0	0	0
<u>Notropis boops</u>	110	30	55	141	22	18	18	21	23	38	115
<u>Pimephales notatus</u>	35	4	0	16	15	3	7	3	6	4	2
<u>Lepomis cyanellus</u>	3	2	1	2	2	7	2	2	2	1	1
<u>Lepomis megalotis</u>	18	24	23	34	132	76	80	33	37	52	56
<u>Lepomis microlophus</u>	2	2	0	1	1	0	0	1	2	0	0
<u>Micropterus punctulatus</u>	0	0	0	0	5	3	3	2	1	2	2
<u>Labidesthes sicculus</u>	0	0	0	0	1	1	1	1	0	0	0
<u>Fundulus notatus</u>	0	0	0	0	0	0	0	0	0	0	0
<u>Moxostoma erythrurum</u>	0	0	0	0	1	0	0	0	0	0	0
<u>Percina caprodes</u>	0	0	0	0	0	0	0	0	0	0	0
<u>Ameiurus natalis</u>	0	0	0	0	0	0	0	0	0	0	0
<u>Lyturus umbratilis</u>	0	0	0	0	1	0	0	0	0	0	0
<u>Cyprinella lutrensis</u>	0	0	0	1	0	0	0	0	0	0	0

Appendix 1 cont.

Third order	Sample date										
	4-19	5-18	5-30	6-13	6-27	7-10	7-23	8-14	8-30	9-1	9-27
<u>Campostoma anomalum</u>	25	176	256	201	198	192	203	194	210	196	199
<u>Etheostoma spectabile</u>	4	3	4	23	14	12	22	19	14	30	27
<u>Etheostoma whipplei</u>	0	0	0	0	0	0	0	0	0	0	0
<u>Notropis boops</u>	33	35	67	53	57	54	40	57	40	138	129
<u>Pimephales notatus</u>	9	10	9	17	24	18	39	39	19	17	15
<u>Lepomis cyanellus</u>	5	6	5	5	14	14	10	13	7	11	9
<u>Lepomis megalotis</u>	15	17	18	20	13	37	19	22	27	32	38
<u>Lepomis microlophus</u>	0	0	0	2	0	0	0	4	0	0	0
<u>Micropterus punctulatus</u>	4	4	5	4	7	6	10	11	5	8	8
<u>Labidesthes sicculus</u>	0	2	2	2	2	2	3	3	3	3	4
<u>Fundulus notatus</u>	3	3	3	3	4	3	3	3	4	3	4
<u>Moxostoma erythrum</u>	2	2	2	4	3	3	4	3	3	2	3
<u>Percina caprodes</u>	2	2	3	2	2	3	4	3	4	2	2
<u>Ameiurus natalis</u>	0	0	0	0	0	0	1	0	0	0	0
<u>Lythrurus umbratilis</u>	0	0	0	0	1	0	0	0	0	0	0
<u>Cyprinella lutrensis</u>	0	0	0	1	0	0	0	0	0	0	0

CHAPTER III

SPATIAL AND TEMPORAL VARIATION IN CONDITION FACTORS AND
GROWTH RATES OF NORTHCENTRAL OKLAHOMA
WARMWATER STREAM FISHES

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INTRODUCTION

The extreme fluctuations in habitat, water volume, and physicochemical conditions that warmwater intermittent streams undergo play a large role in the ecology of the fish populations inhabiting these areas (Paloumpis, 1958, Matthews, 1987; Schlosser, 1987). Within the stream, there is spatial variation in the types and magnitudes of fluctuations, with each stream order having its own characteristics. The middle (second order) and upper (first order) reaches of drainages are the most environmentally unstable (Hall, 1972; Ross et al., 1985), and flow can change depending upon amount of precipitation received and length of time between rainfall events. Heavy precipitation can produce large floods that scour the stream altering channel morphology, as well as fish, invertebrate, and algal assemblages (Schlosser, 1982; Fisher et al. 1982; Power and Stewart, 1987; Chapman and Kramer, 1991). Long periods with little or no precipitation are also common and can cause stream discharge to decline or cease. At times of extremely low discharge, or no discharge, riffles may completely dry, leaving a series of isolated pools scattered from the headwaters to the lower parts of the stream (Larimore et al., 1959; Ross et al., 1985). In these isolated pools, physical and chemical fluctuations are common and at times extreme. Seasonal temperature fluctuations from 1.5°C to 33.5°C (personal observation) and daily fluctuations as much as 9.5°C in 24 hours (Mundahl, 1990) are not uncommon. Diel and seasonal fluctuations in dissolved oxygen within these pools are another factor that can lead to fish kills, particularly when the pools are small and have a high density of fish respiring in them (Mundahl, 1990).

Many headwater species have adaptations (behavioral or physiological) to help them deal with the extreme conditions experienced in these areas. Some species, by adjusting their physiology and/or by producing heat shock proteins, can increase their maximum thermal tolerance (Matthews and Maness, 1979; Fader et al., 1994), while other species actively seek out and occupy cooler areas within the pools (Mundahl, 1990). These and other similar adaptations may limit the distribution and type of species that inhabit intermittent streams by selecting for species tolerant to the type and magnitude of environmental fluctuations found in a specific stream or reach of stream (Matthews, 1987). Therefore, those species having higher tolerances can migrate farther upstream into the headwaters. As a result, fish occupying these highly variable areas are able to exploit habitat that may be lethal and/or inaccessible to other species.

These areas have been commonly referred to as 'harsh' (sensu Peckarsky 1983, Matthews, 1987) environments in that they undergo large unpredictable changes in physical and/or chemical environment and that can potentially cause stressful or lethal conditions for the species occupying them. This contrasts with 'benign' areas where physicochemical conditions and fluxes do not normally exceed physiological tolerances of the species occupying them. However, many species that occupy these intermittent streams have survival strategies for dealing with extreme environmental variations that occur there, and the question of whether warmwater streams should be considered a 'harsh' environment is debatable (Meador and Matthews, 1992). Do these extreme fluctuations, or conditions, truly have a negative impact on fish that inhabit these areas, or do they simply represent normal changes that are within the tolerances of the species that

occupy these areas? If the former is true, then they can be considered to be a harsh environment, if the latter is true, then these areas should not be considered to be any harsher (on species) than the normal ranges of fluctuations within 'benign' streams.

This study attempts to resolve this question of harshness by documenting temporal changes in species diversity, condition factors, and juvenile growth rates of fish species occupying three different stream orders (each having different magnitudes of environmental fluctuations) of an intermittent stream. Condition factors allow quantification of the effects that summer intermittency and habitat fragmentation (e.g., harsh conditions) have on fish. If fish occupying 'harsh' areas have significantly lower condition factors and growth rates than fish occupying the more 'benign' areas, then physical processes within intermittent streams may in fact have a detrimental effect on the species occupying them and should be considered 'harsh'. If they do not, then these areas can not be considered to be any harsher than other, more benign, environments within the basin.

MATERIALS AND METHODS

Study Site --- The Wild Hog Creek watershed is a 12.8 km² basin in Northeastern Oklahoma (Fig. 1) located in The Nature Conservancy's Tallgrass Prairie Preserve. The upper basin contains several first order streams and two second order streams that are divided by a series of rolling hills, and are the origin of third order Wild Hog Creek. Most first order streams are ephemeral with poorly developed pools and riffles that fluctuate in size with changing discharge. The second order streams are intermittent with channels

characterized by large riffle areas separated by small to medium size (2 - 20m) pools. Riffles typically desiccate in mid-summer, but 6 pools persisted throughout the study period. The third order segment, although subject to water loss in drier months, is perennial with well-developed pools, riffles, and raceways that, in wetter years, have at least some flow year-round. Stream substrate is composed of sand, mud, gravel, cobble and some areas with large bedrock outcroppings.

Fishes in the Tallgrass Prairie Preserve are a mixture of upland and prairie species. To date, 23 species have been found in the drainage (Matthews and Gelwick 1993) with the majority (16 of 25) in the genera Notropis, Etheostoma, Lepomis, and Micropterus.

Collection---Fish, temperature, and discharge data were collected bi-weekly from the third order from 19 April 1997 to 12 October 1997 and from 9 March 1997 to 12 October 1997 in the first and second orders. Temperature was taken at the bottom of three designated pools in each stream order; with the average of these three readings used to represent that date/site. Discharge was determined for each stream order by calculating the cross-sectional area and current velocity of a 1m section of the stream. Specific sampling sites within each stream varied to obtain a representative estimate of the fish populations in each habitat, however, as a result of desiccation, some first and second order streams could not be sampled on every date. Pools were sampled by seining until there was a decrease in the number of fish caught (assuring the majority of fish were sampled). Riffles were sampled by kick seining with a standard (5 or 9 m) seine, or by using small dipnets in areas where the seines were ineffective. Most fish captured were

identified, enumerated, and then returned to the stream unharmed. However, some were preserved in a 10% formalin solution for analysis in the laboratory. Species diversity (Shannon-Wiener) was calculated for each stream order and sample date to determine how diversity changed throughout the year. Differences in species diversity were evaluated by a 1-way ANOVA (SAS (PROC GLM), Version 6.12, SAS Institute Inc., Cary, NC, USA.) and means were tested with Student-Newman-Keuls test.

Condition factors---To evaluate changes in fish condition, and differences among stream orders, condition factors of one algivore (Campostoma anomolum), one benthic insectivore (Etheostoma spectabile), and one water-column insectivore/omnivore (Notropis boops) were measured from each stream order over the course of the study. These three species were chosen because of differences in resource use (algivore vs. benthic insectivore vs. omnivore) and habitat preferences (pool vs. riffle). Thus, a broad range of environmental effects could be evaluated by using these different species. The condition factor (**K**) is a general relationship between weight and length and is a measure of the robustness of a fish. A more robust fish is assumed to be in a better state of health (condition). The equation for condition factor, $K = W/L^3$, is from Ricker (1975) where W is the wet weight of the eviscerated fish, and L is the standard length. Condition factors were determined by preserving individuals from all three stream orders in 10% formalin in the field, and transferring them into 70% ethanol in the laboratory. Fish taken from the ethanol were allowed to dry for 7 min (to control for evaporation of ethanol), measured to the nearest 0.01 cm (standard length) with dial calipers, and weighed to the nearest 0.001

g. To control for differences in stomach contents and gonadal state of the fish, individuals were eviscerated prior to weighing. Because juveniles grow differently from adults, juveniles (< 30 mm SL) were analyzed separately. Beginning with the 19 April sample date, differences in condition factors of each species for each sample date and site were assessed using a 2-way ANOVA (SAS (PROC GLM), Version 6.12, SAS Institute Inc., Cary, NC, USA.).

Juvenile condition and growth rates---Growth rates of juvenile *C. anomalum* were calculated to determine how different stream conditions (e.g., harsh vs. benign) affect fish growth. Juveniles were collected bi-weekly from each stream order with a 10 m seine and then transferred to a holding container. From this container, 10-20 fish were removed and placed into a 1-gallon bucket that contained only enough stream water to cover the fish, and a ruler for scale (mm). The fish in the bucket were photographed and returned to the stream at approximately the same location from which they were taken. However, approximately 10% of the juveniles caught were preserved in 10% formalin for later analysis. From the photographs, fish length was determined by using calipers to measure the length of the fish and the ruler in the photo, and length/frequency histograms were produced for each date/site combination.

Length-frequency histograms allowed a single cohort to be followed throughout this part of the study, and enabled absolute (mg / day) growth rates of that cohort to be calculated for each sample date and site. To do this, the range of cohort lengths was identified from the histogram, and then, using the preserved juveniles, condition factors

and the average weight of individuals from only the cohort's size class were calculated. Additionally, a length-weight regression (using the values from the preserved juveniles) was produced to determine weights of the juveniles in the photographs from lengths taken from the photographs. All length-weight regressions were highly significant with all $r^2 > 0.79$ and $p < 0.005$. The weights were then combined with those of the preserved individuals and used to calculate growth. Overall sample sizes used to calculate growth rates varied from 80 to 300 individuals per site/date combination. Condition factors of juveniles were also calculated (with the methods described in the preceding section) for the cohort on each site/date combination and were tested for differences via a 2-way ANOVA (SAS (PROC GLM), Version 6.12, SAS Institute Inc., Cary, NC, USA.).

RESULTS

Temperature and Hydrology--- With the exception of three spring and early summer spates, discharge was < 20 l/s for all stream orders, with several dates at (or close to) zero (Fig. 1). The decrease in discharge during the summer months caused large changes in, and habitat differences among, stream orders. First order streams desiccated earliest and remained dry throughout most of the late spring and summer, only rewetting briefly after precipitation. However, one first order site, because of its position in the basin, did not completely dry. This site was sampled regularly, and these data were used to represent first order streams in all analyses. Thus, it allowed comparisons (diversity, condition, and growth) among the three stream orders well after the other first order streams had desiccated. Second order streams also desiccated, resulting in all second

order riffles and all but six pools drying up. The third order stream, although severely reduced in volume, never experienced cessation of flow. This allowed fish capable of traversing shallow riffles to freely move between habitats. Temperature of all three stream orders exhibited normal seasonal fluctuation, increasing in the summer months and gradually decreasing as cooler seasons approached; second order streams had the highest range and maxima (Fig. 2).

Species Diversity --- Significant differences were found among species diversities for each stream order (ANOVA, $F = 8.27$, $p < 0.002$) with mean third and second order diversities being significantly different from the first order ($p < 0.05$) but not from each other ($p > 0.05$; Fig. 3). Seasonal fluctuations in fish diversity occurred in each stream order (Fig. 3), resulting in the lowest diversity in late spring and early summer when large numbers of juveniles emerged in each stream order.

Adult condition factors---- Changes in condition factors for each species showed similar trends in that the mean condition factors of each species was greatest in the second order (Table 1). Unfortunately, abundances of E. spectabile were extremely variable, with only three sample dates producing individuals from all three stream orders. To compensate for this, E. spectabile was grouped for analysis (via 2-way ANOVA) by month (April, June, and September) which increased the sample size for each date/site combination (that had individuals from each stream order) and resulted in a more accurate 2-way ANOVA (with the increased degrees of freedom). Condition factors for C.

C. anomalum, N. boops and E. spectabile are shown in Figures 4, 5, and 6 respectively, and although a large amount of variation occurred, there were significant date x site interactions among all three species and stream orders (Table 2). Listing all the significant interactions between dates and sites is not practical (due to the quantity). However, the graphs of condition factors and their corresponding SE's (Figs. 4, 5, and 6) provide a good indication of the differences detected in the ANOVA (overlapping error bars indicating no significant difference).

Juvenile condition and growth rates---Condition factors for juvenile C. anomalum were determined for fish from all three stream orders from 7 May to 28 June. After 28 June, identification of the cohort was not possible due to large amounts of overlap between different cohorts, therefore, juvenile sampling was ended. Condition factors of the juveniles showed the same spatial trends as the adults; second order condition was the highest, and first order condition was the lowest. Table 1 shows mean condition factors for each site excluding the 7 May sample. This date was excluded because there was no corresponding condition factor for the third order stream for that date's cohort, and inclusion of these very low first and second order scores (seen in Fig. 5) would produce an inaccurate comparison of overall site means. As with the adult condition factors, a significant site x date interaction was detected in the juveniles ($F = 12.59$, $p < 0.0001$; Table 2). Differences between dates and sites can be seen in Figure 5 where overlapping error bars indicate no significant differences in condition factors. Overall trends in juvenile condition indicates that individuals from second- and third-order streams rapidly increase to

levels above those of first order juveniles, with the second order stream producing fishes with the highest mean condition factor.

Juvenile growth rates were calculated from 7 May through 28 June. Throughout the study, growth rates were highest in the second order stream (Fig. 6), with rates being as much as three times those of the third and four times those of the first order streams. These data, coupled with the condition factor data, give a strong indication that the second order streams, despite their intermittency and apparently harsh environment, produce very robust fish.

DISCUSSION

Environmental fluctuations produce large physicochemical and morphological changes in intermittent streams. Conventional wisdom would dictate that the extreme decreases in habitat volume coupled with increases in temperature and number of competitors would result in a very unproductive environment for individuals occupying these areas. This line of thinking holds for species that have not evolved in areas similar to warmwater intermittent streams (Meffe and Minkley, 1987). For these species, extreme fluctuations in temperature, discharge, habitat and dissolved oxygen can produce very stressful, if not lethal conditions. Therefore, from the point of reference of non-adapted species, intermittent streams would be a 'harsh' environment. However, the effects that these fluctuations have on fish that have evolved in these types of streams appears to be contrary to what would be expected. Fluctuations (non-lethal) in the environment do not appear to affect the ability of these fish to reproduce, grow and thrive in these areas. In

fact, they appear to increase the productivity of the species occupying the most widely fluctuating ('harsh') environments.

First order streams are traditionally considered to be the most variable, both hydrologically and chemically. However, in this study, fish in the second-order channel were subjected to the largest fluctuations in habitat, discharge, and temperature. If these types of fluctuations are truly detrimental to fish, second order streams would have the lowest growth rates and condition factors of the three sites. However, second order sites usually had the highest condition factors, and although differences in juvenile condition were not as pronounced as those of the adults, the overall trend of fish in second order streams having the highest condition factors suggests that a highly variable environment may actually have some type of benefit for species that are able to deal with the environmental fluctuations.

One benefit for fish occupying the second order channel is the increased solar radiation (compared to the first and third orders) that this areas receives. Although increasing solar radiation will increase the temperature fluctuations experienced by the fish, Johnson et al. (1986) found that when compared to streams with old-growth (canopied) forest, deforested streams with open canopies had greater solar radiation, primary production, and increased density and/or size of salmonid fry. Wild Hog Creek has a similar situation in that the second order stream is an open canopy prairie stream, whereas the first and third order sites are located in a well-developed gallery forest. Therefore, increased solar radiation in the second order stream may have resulted in greater primary production, which in turn increased condition factors and growth rates of

the fish in the second order.

Other benefits of residence in the second order channel may be related to biological interactions (predator/prey and competition) that play a role in structuring stream fish assemblages. The third order stream had the highest density of piscivorous species (followed by second and then the first order streams). These species tended to occupy the larger pools and can effectively exclude small prey species (e.g., Campostoma and Notropis) from these areas through either active predation or by altering the behavior of the prey species. Power et al. (1985) found that within isolated pools predatory bass caused Campostoma to shift to less productive feeding areas and to decrease their feeding rates. These types of shifts may significantly reduce the condition factors and growth rates of these fish by; (1) increasing the activity (avoiding the predator) of prey in areas where there are no refuges (Power et al., 1985; Gorman and Karr, 1988), (2) forcing them into less productive refugia habitats (Werner et al., 1983; McDonald et al., 1992) (3) altering feeding rates (Power et al., 1985), or (4) increasing competition (inter-and intra-specific) within refugia habitats (Mittlebach, 1986). Thus, as a result of occupying a less variable environment, there is an energetic cost resulting from predation and/or predator-induced competition.

These costs are not as pronounced in the first and second order streams where the lack of suitable habitat restricts the distribution and number piscivorous species. Very few bass were taken within these areas, and only juveniles were taken in pools that had large numbers of other species. As the habitat began to fragment (as discharge decreased) the number of juvenile bass decreased (probably due to downstream emigration) until none

were present in the first order streams, and only three were in the second order stream. Within the second order, one pool did contain a resident adult bass, however, there were rarely any small fish (centrarchids or cyprinids) occupying the pool. Therefore, the lack of large predators, and the negative effects associated with them, gives the fish occupying the first and second orders an energetic advantage over individuals in the third order. This advantage is seen (in the form of higher condition factors) in three trophically distinct species, and when it is coupled with the higher primary production within the second order, an even greater energetic advantage is produced. These combined advantages are most likely responsible for producing the majority of the higher growth rates and condition factors seen in fish occupying the second order stream.

These results suggest that, with respect to the species that occupy them, the upper reaches of intermittent streams that have habitat capable of sustaining fish populations year-round should not necessarily be considered a harsh environment. For as long as there is suitable habitat, and fluctuations do not reach lethality, the energetic gains (that result in higher condition and growth rates) associated with these areas are greater than the more 'benign' areas. Thus, conditions producing an environment that is beneficial to the individuals inhabiting it cannot be considered harsh, and Meador and Matthews (1992) suggestion that these areas should not be considered "a priori" a harsh environment with respect to the species occupying them appears correct.

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Table 1. Stream order specific mean condition factor and SE for each fish species sampled. Data for E. spectabile (unlike that of the ANOVA analysis) includes all individuals sampled. Juvenile C. anomalum only includes 18 and 30 April and 14 and 28 June dates.

Species	Stream order	Mean	SE
<u>C. anomalum</u> (adult)	1	1.111	0.0184
	2	1.200	0.0110
	3	1.175	0.0083
<u>N. boops</u>	1	1.011	0.0178
	2	1.150	0.0129
	3	0.981	0.0081
<u>E. spectabile</u>	1	1.061	0.0241
	2	1.183	0.0266
	3	1.031	0.0127
<u>C. anomalum</u> (juv.)	1	1.040	0.0120
	2	1.168	0.0162
	3	1.128	0.0129

Table 2. Results of a 2-way ANOVA on condition factors of the three species of fish sampled.

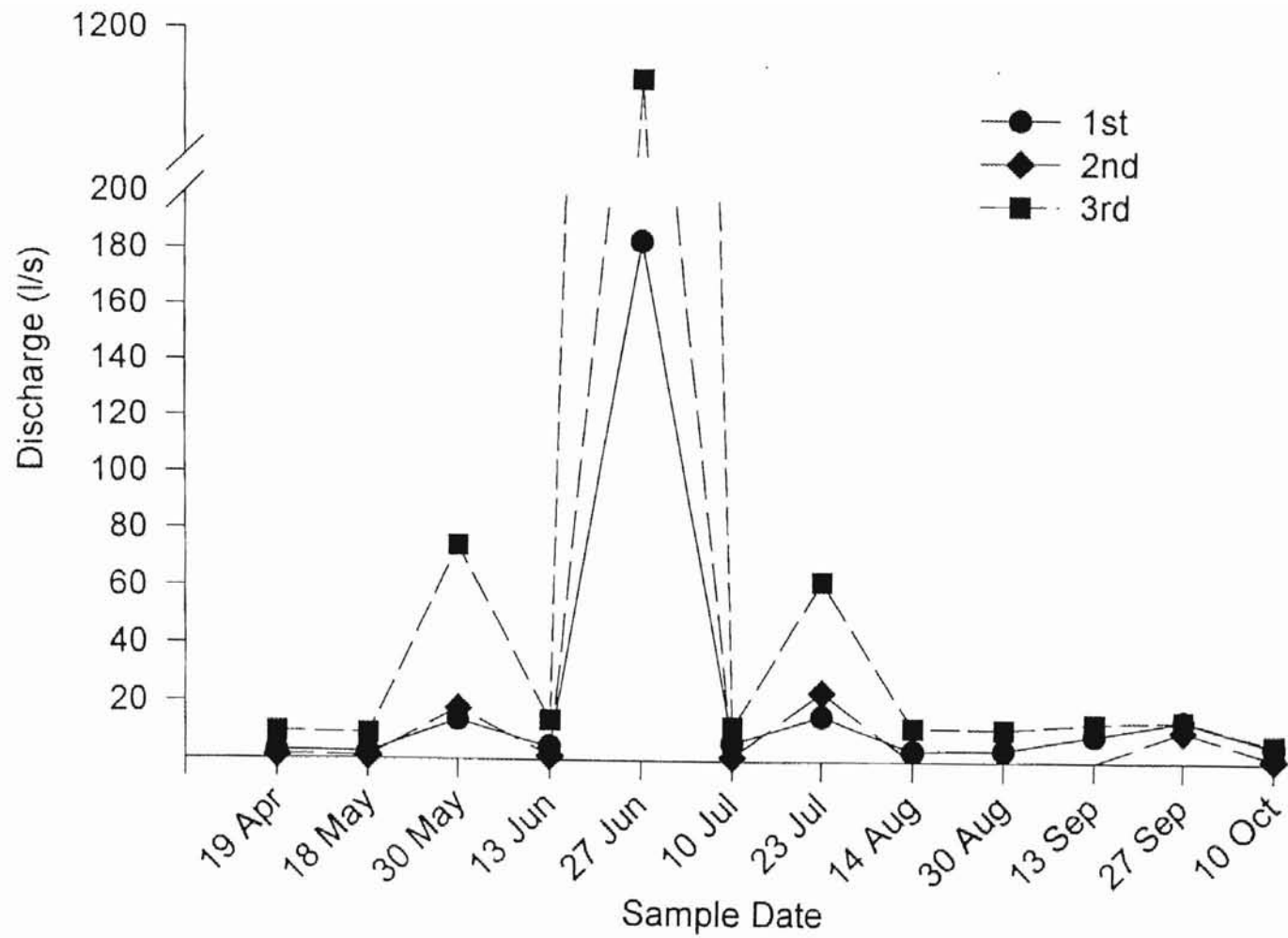
Source	df	F	P
<u>C. anomalum</u> (adult)			
site	2	6.36	0.0001
date	11	13.57	0.0001
date x site	18	5.36	0.0001
<u>E. spectabile</u>			
site	2	5.84	0.0037
date	2	3.35	0.0380
date x site	4	2.77	0.0296
<u>N. boops</u>			
site	2	6.48	0.0001
date	11	64.83	0.0001
date x site	19	6.51	0.0001
<u>C. anomalum</u> (juv)			
site	2	32.41	0.0001
date	3	35.02	0.0001
date x site	6	12.59	0.0001

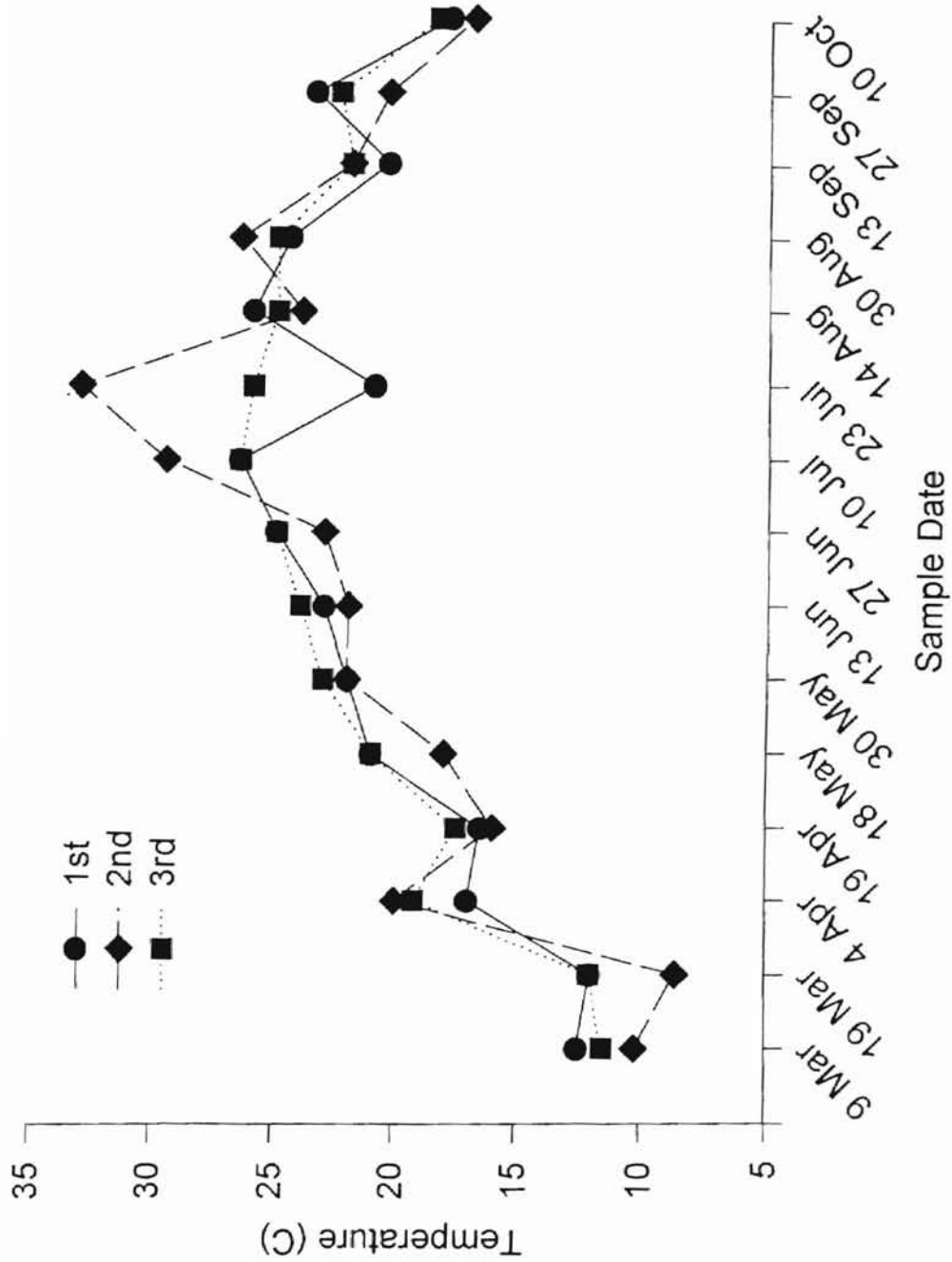
Figure Captions

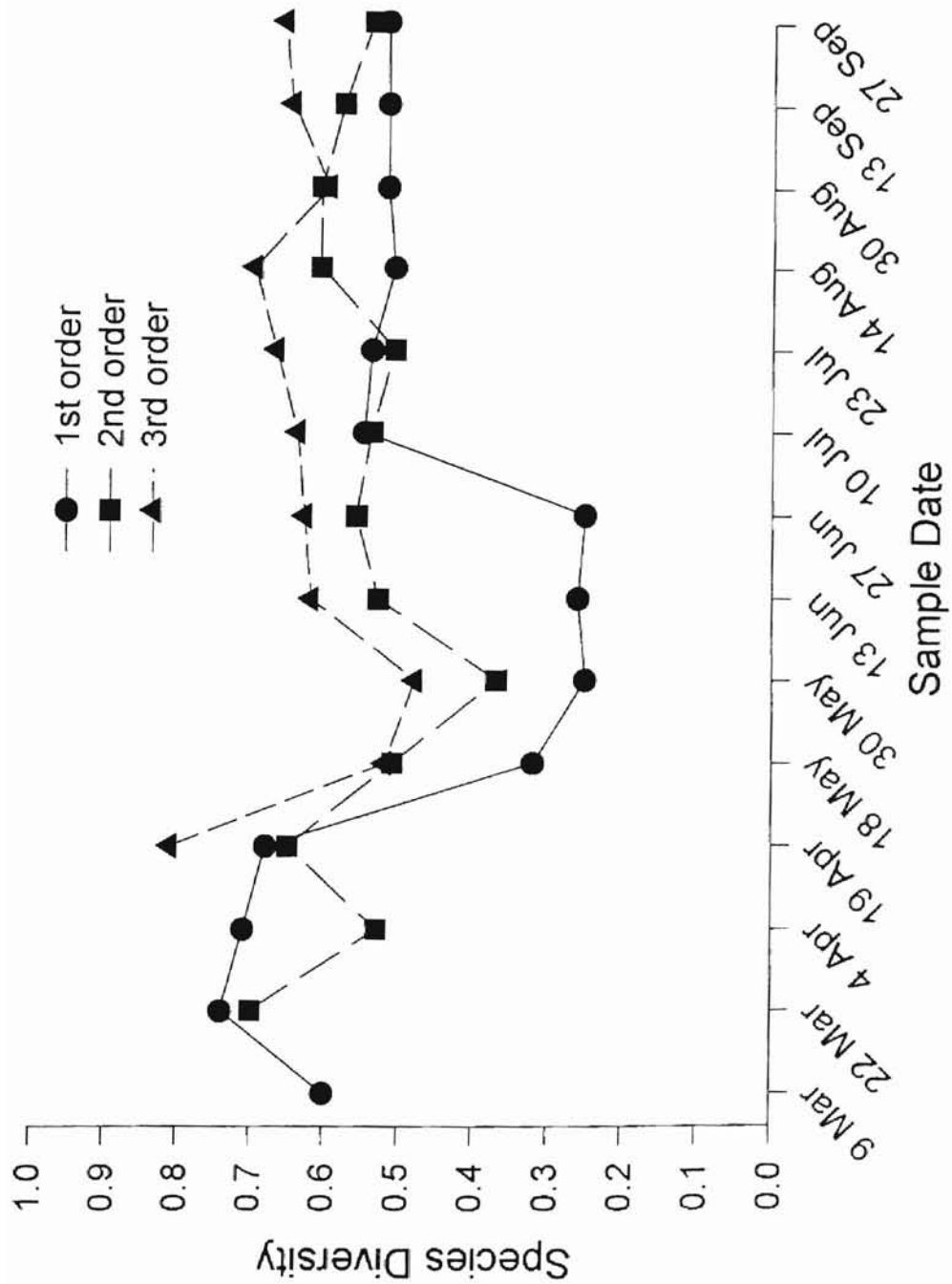
1. Discharge for each stream order from April – October 1997. Maximum discharge was 1163 l/s (third order), 309l/s (second order), and 183 l/s (first order).
2. Temperature (degrees C) of each stream order from March – October 1997.
3. Species diversity of fish communities within each stream order for each sample date.
4. Condition factors for adult C. anomalum from each sample date and stream order.
Missing values indicate no individuals were taken from that site on that date.
Error bars represent 1 SE.
5. Condition factors for N. boops from each sample date and stream order. Missing values indicate no individuals were taken from that site on that date. Error bars represent 1 SE.
6. Condition factors for E. spectabile from each sample date and stream order. Missing values indicate no individuals were taken from that site on that date. Error bars represent 1 SE.
7. Juvenile C. anomalum condition factors for each stream order from 7 May to 28 June 1997. Error bars represent 1 SE.

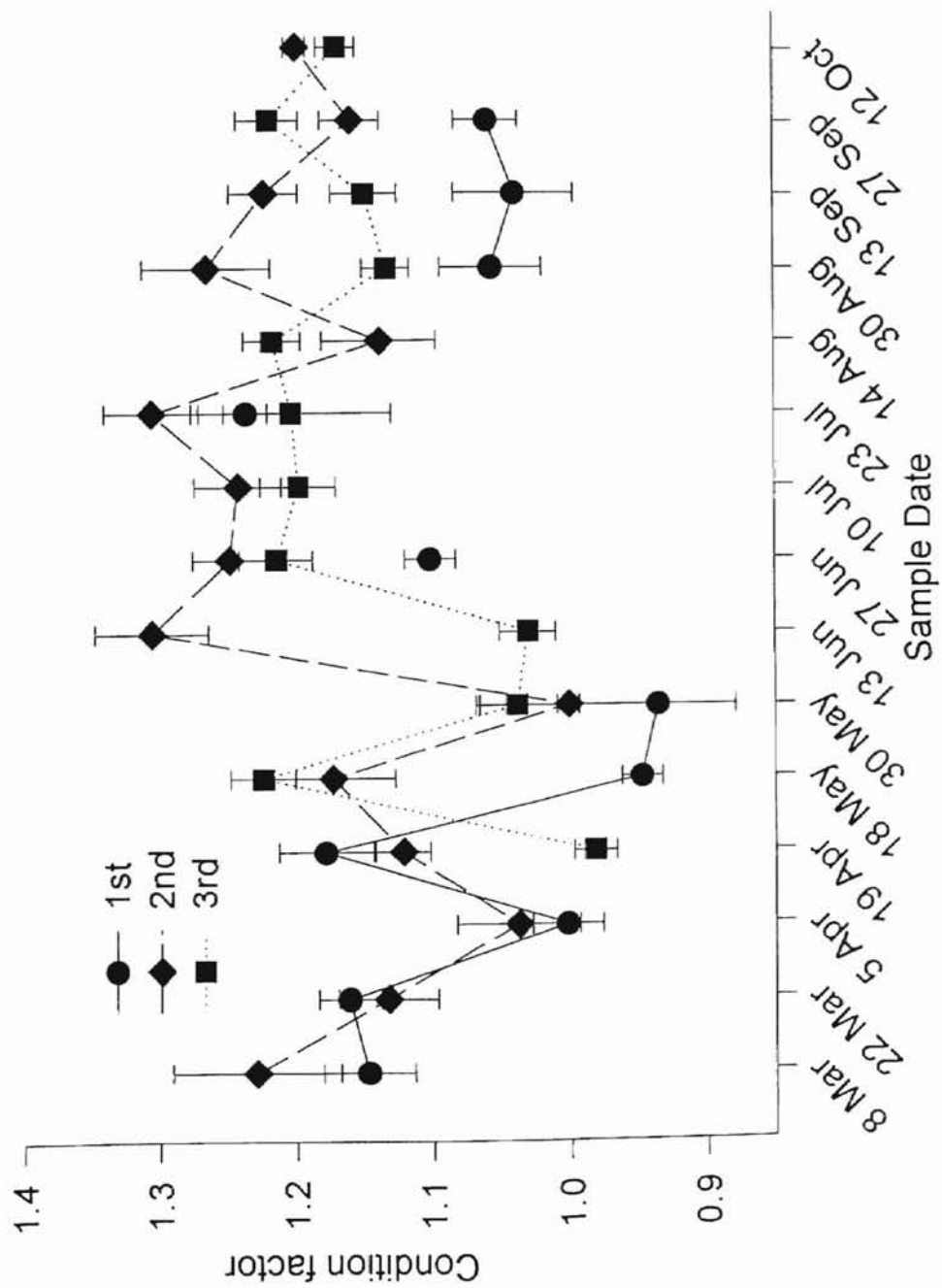
8. Growth rates of juvenile C. anomalum in first, second, and third order streams.

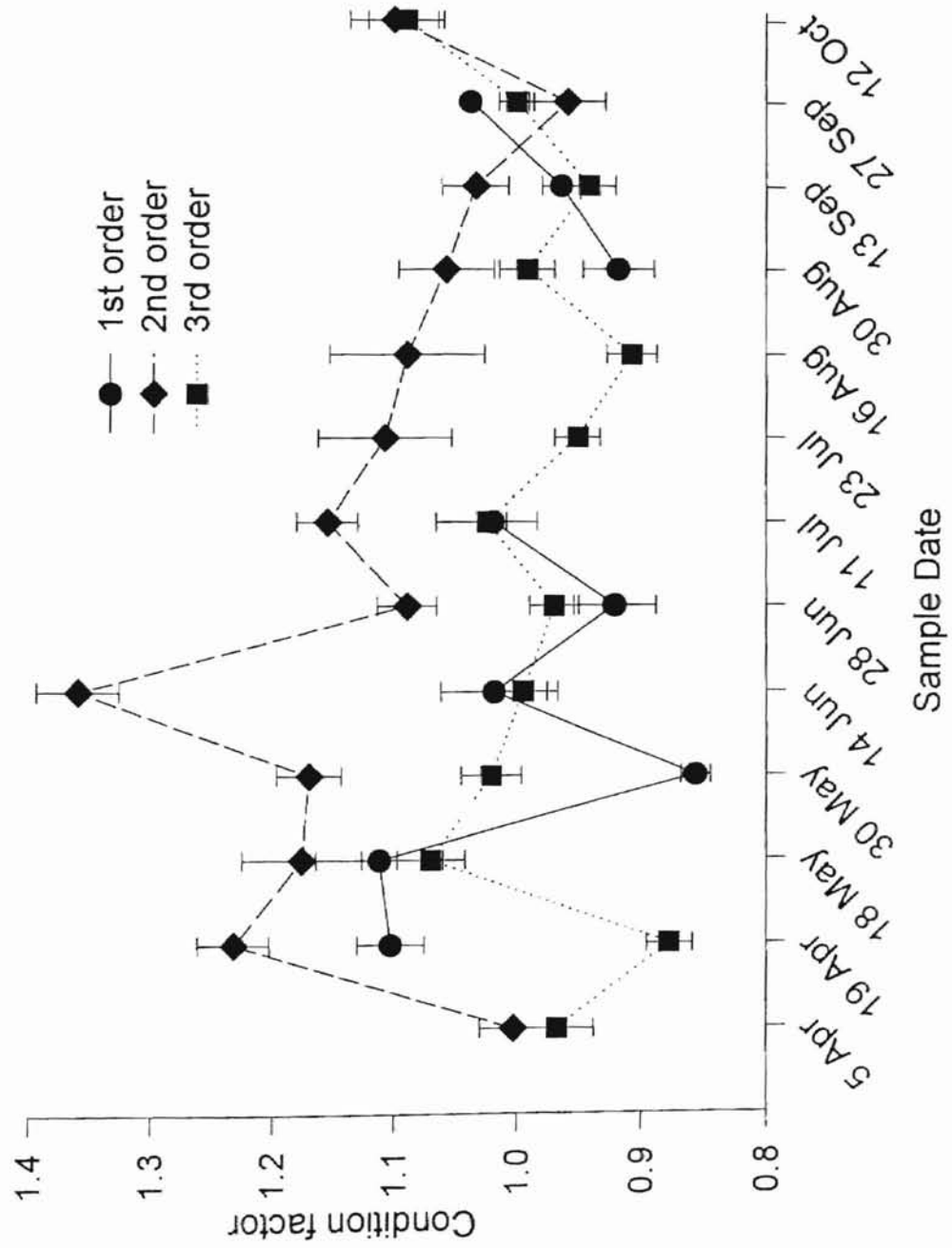
Error bars represent 1 SE.

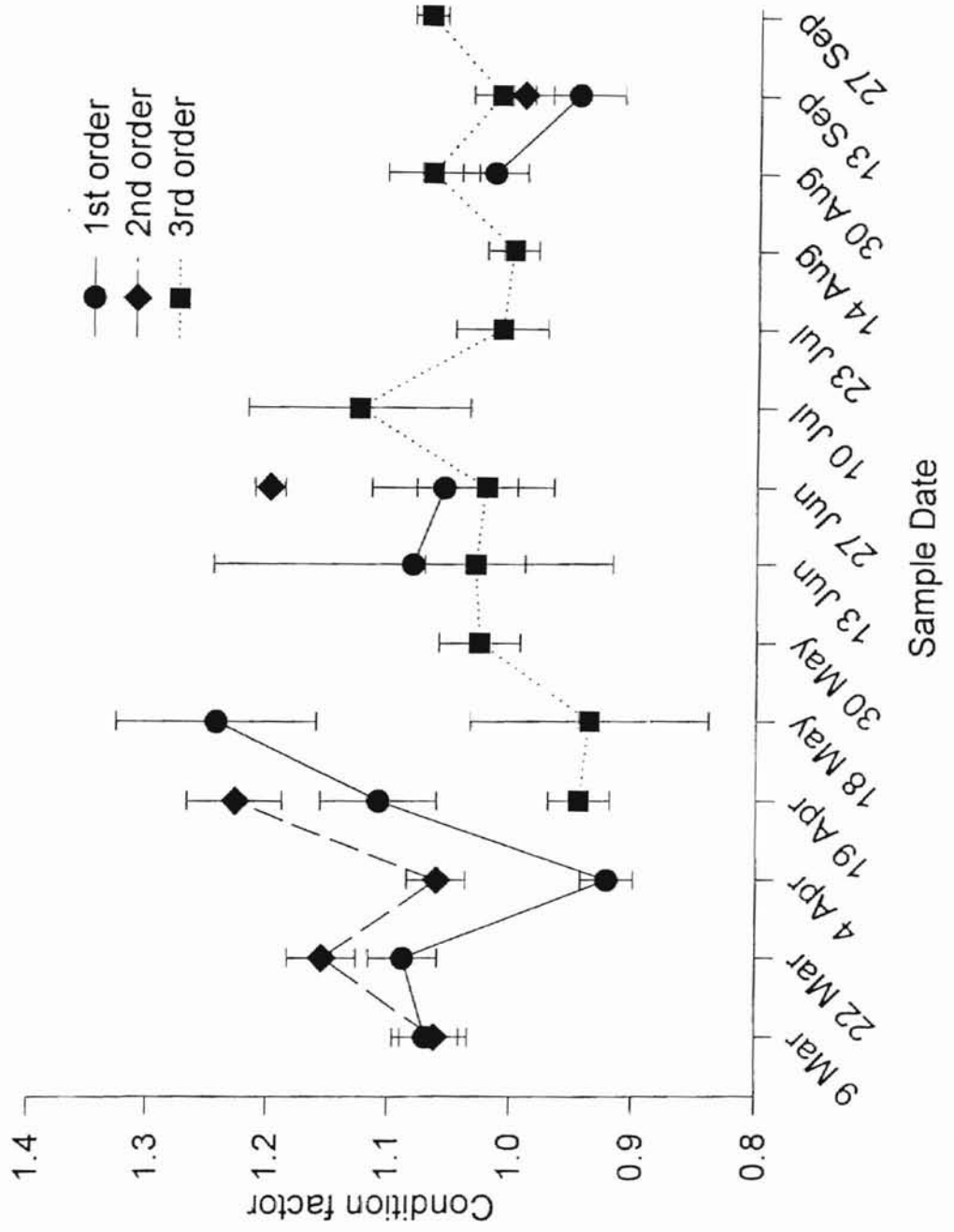


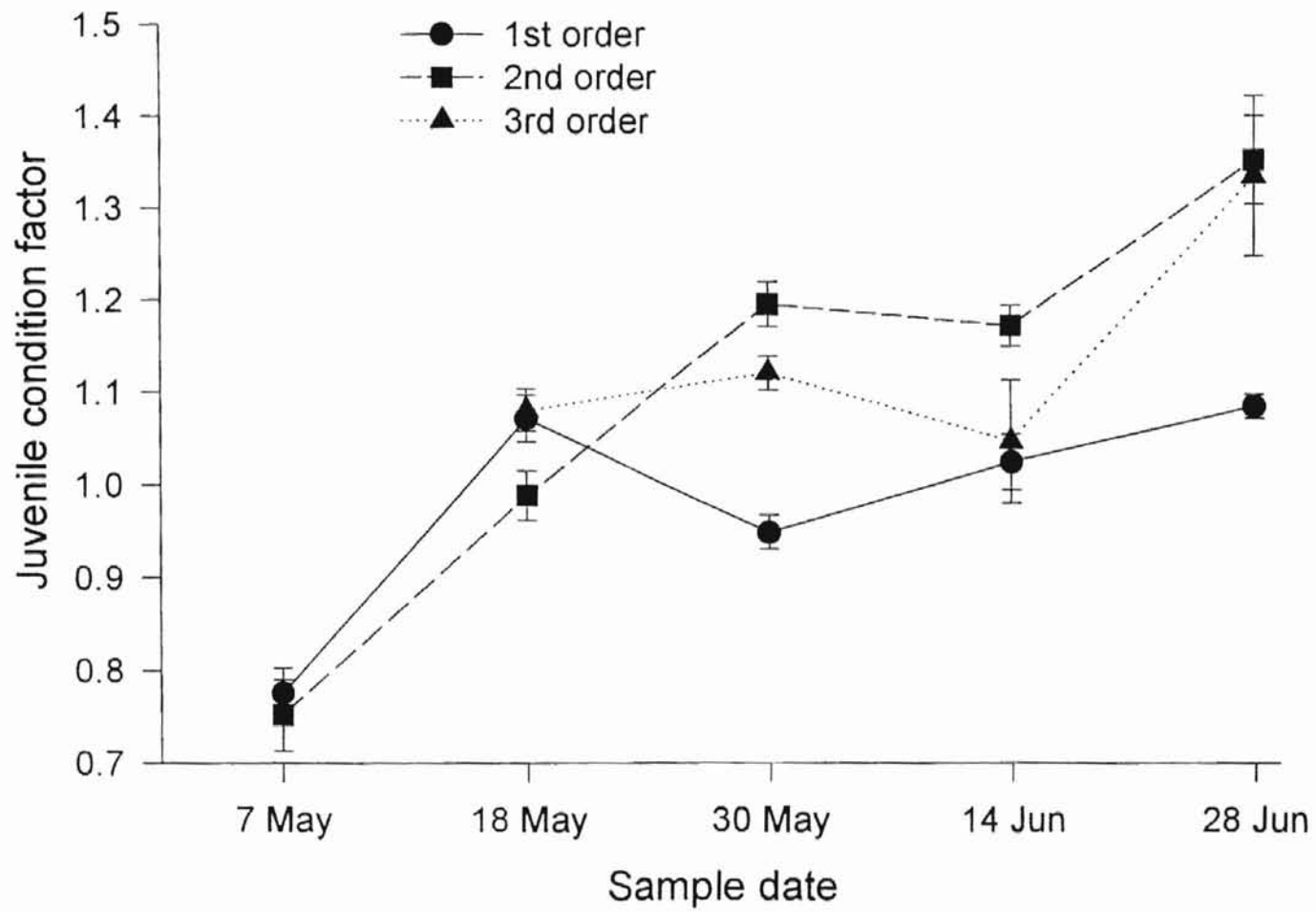


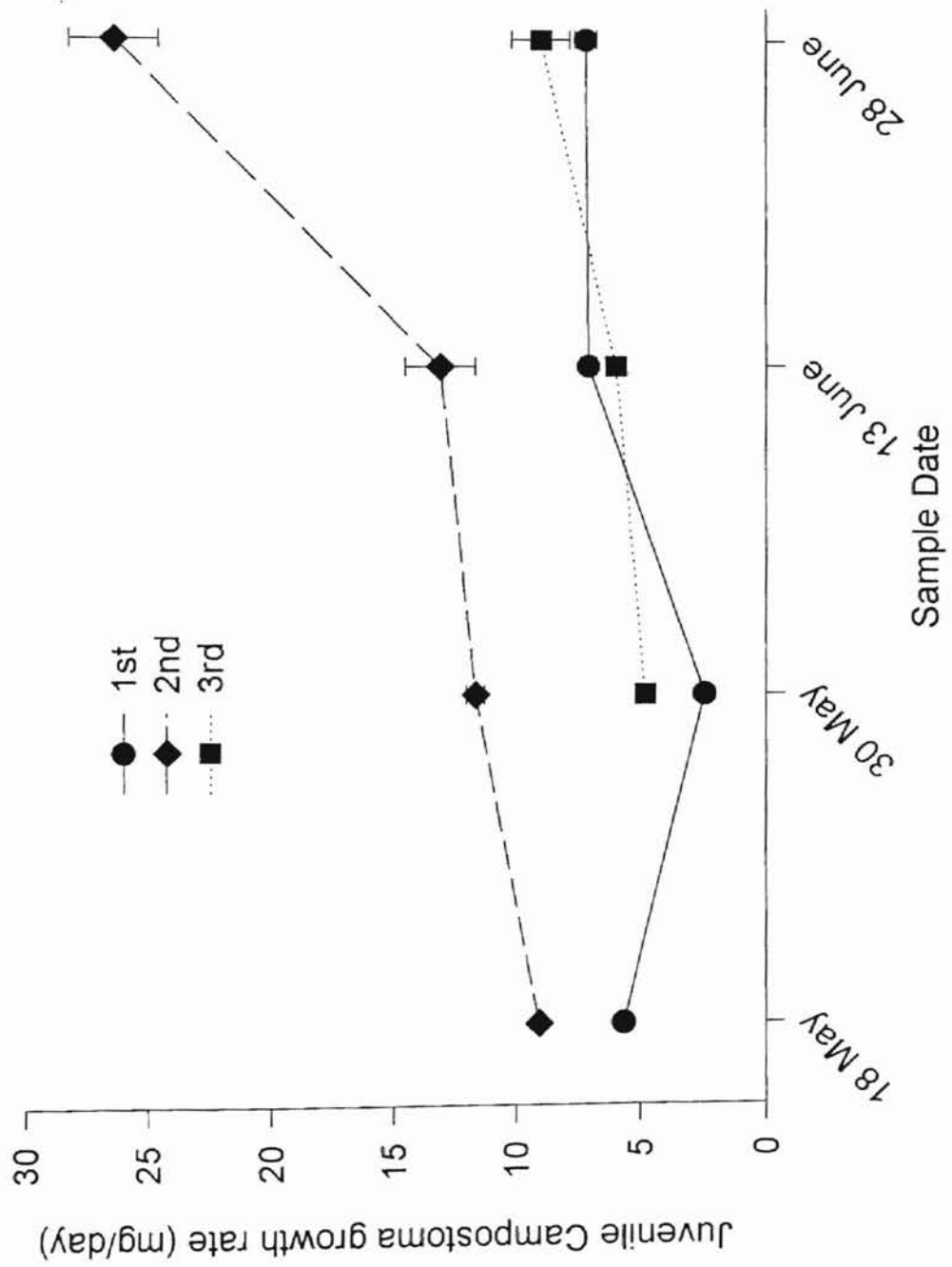












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