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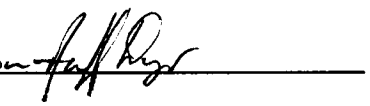
Signature 

Date 5/14/90

DISPERSION AND FACTORS INFLUENCING DRIFT OF PREDATORY STONEFLY NYMPHS (PLECOPTERA: PERLIDAE)

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Susan Acuff Dyer

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ABSTRACT

Natural dispersion patterns of several predatory stonefly nymphs (Plecoptera: Perlidae) and associated prey items were examined. Dispersion was documented on natural snag material retrieved from the research site and similarly constructed into snag bundles as the experimental habitat units. Nymph dispersion was determined to be uniform and the associated prey items were significantly clumped.

I considered two factors which may influence the drift of predatory stonefly nymphs--hunger state of the nymphs and initial nymph density. The previously constructed snag bundles were the experimental units from which drift response of satiated and starved nymphs; and high, medium, and low initial density snags were documented. There was no significant difference in drift response between starved and satiated nymphs ($p = 0.3131$). However, drift response varied significantly among days ($p = 0.0001$). An increase in drift occurred with increasing density between low, medium, and high initial density snags.

Behavioral observations were conducted in an artificial stream mesocosm to determine if density-related drift was due to active or passive means, varied with time of day (day or night), and whether it was, in part, due to behavior modifications. Modifications investigated were differences

in amount of time spent in movement, number of encounters, and types of competition encounters or modifications in the number of encounters. All drift phenomena observed were active detachment and not the immediate result of an intraspecific encounter. Differences in movement and number of encounters on the snag were documented for day and night. There was an increase in movement with increasing density (medium and high) with respect to the number of encounters. There was an increase in movement with increasing density during night-time runs and a decrease in movement with increasing density during day-time runs. Also, the type of interactions were much more aggressive during day-time runs.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

I. INTRODUCTION

Stream systems are dynamic. Substrate character is a major factor in stream system dynamics. Rocky bottom streams present a comparatively stable substrate for inhabiting benthos. In sandy bottom streams which dominate the southeastern coastal plain, wood appears to be a major structural feature. This woody "snag" material, provides a correspondingly stable habitat over shifting substrates (Benke et al., 1984). High aquatic insect/invertebrate diversity and productivity is most often found within these snag habitats (Benke et al., 1984; Wallace and Benke, 1984).

Stonefly (Plecopteran) nymphs are a major component of invertebrate inhabitants of snag habitats (Benke et al., 1984). The life cycle range of stoneflies is 1-3 years with most of that time spent in the nymphal stage. Developmental instar numbers may vary from 3-28 depending on species (Merritt and Cummins, 1984). Specifically in the southeastern Coastal Plain, the stonefly genera Acroneuria and Paragnetina have a 2-3 year nymphal stage and generally 23 developmental instar stages (Merritt and Cummins, 1984). Stonefly nymphs play an important role in the food web for many fishes (Pennak, 1982). Food preferences of stonefly nymphs may vary depending on species, life history stategies, or food availability. Within the Plecoptera, families such as

Pteronarcyidae, may be strictly detritivorous. The Perlid nymphs, however, are carnivorous predators.

Stoneflies lay their eggs in masses which attach to aquatic substrates either by sticky gel or with the use of anchoring devices (Merritt and Cummins, 1984). Once immediate resources are depleted, dispersal of newly hatched nymphs is the only vehicle for increasing the foraging range.

Dispersion (the spatial pattern of distribution of organisms or populations), a fundamental aspect of stream communities, may result from several different mechanisms (Walde and Davies, 1984; Drake, 1984). However, an investigation of the distribution can contribute to the understanding of causal mechanisms. There are three statistical types of spatial patterns: random, clumped, or uniform (Ludwig and Reynolds, 1988). The type of pattern observed may offer insight to the causal factors which influence the pattern. Random dispersion patterns have been suggested to be rare in nature (Peckarsky, 1988). It has also been suggested that regulatory mechanisms may influence dispersion patterns. Several investigators have developed the use of contributing causal mechanisms to observed community patterns (Pemberton and Frey, 1984; Meire et al., 1989). For example, random patterns may imply environmental homogeneity or nonselective behavioral patterns whereas clumped or

uniform population patterns may imply environmental heterogeneity or competition, respectively.

Walde and Davies (1984) showed that predaceous stoneflies were randomly distributed in selected streams. Associated prey items were found to be significantly clumped. Foraging theory suggests that when prey distribution is clumped, predators should aggregate in those high density patches (Pyke et al., 1977). Predator and prey densities investigated by Walde and Davies (1984) were uncorrelated. Walde and Davies suggested the predators were responding to other factors, such as other predators (competition) rather than prey dispersion. That is, predators may be responding to intraspecific competition rather than to prey densities. A random distribution may also be produced by unstable prey patches, or the complete absence of any foraging strategy. It is beneficial to investigate the pattern of dispersion of prey items as well as the focal predators in studying behavior and stream drift mechanisms. Biotic or abiotic processes or pressures may influence the spatial pattern of a population and hence their dispersion within the system. Dispersal is the movement of organisms into or out of an area (Williams, 1981), and drift is one means of dispersal. Drift refers to the downstream transport of stream invertebrates and has been the focus of research endeavors since the late 1920's (Needham, 1928). Early research focused on

the composition, density, or periodicity of drift. Several studies indicate that in some species, different size classes may influence drift to different degrees (Hall et al., 1980; Allan, 1978). Anderson (1966) found an increase in drift at night was due to an increase of drift in the larger size class of organisms such as Ephemeroptera, Plecoptera, and Simuliidae (Hall et al., 1980; Allan, 1978). This size class characteristic, as well as other drift-response phenomenon, may be related to life history strategies.

Recently, drift investigations have centered on the behavioral aspect as to whether drift results from passive or active means (Elliot, 1967; Kohler, 1985; Mueller, 1963, 1974; and Waters, 1972). Passive drift often tends to result from an increase in current velocity/sediment load, i.e., catastrophic drift (Anderson and Lehmkuhl, 1968; Ciborowski et al., 1977) or displacement during periods of increased nocturnal activity resulting in detachment (Waters, 1972). Active drift results from behavior-induced controls, such as light stimulus, density, predator/prey interactions, or hunger state (Bishop, 1969; Dimond, 1967; Walton, 1980; Williams, 1988). Some organisms/life stages seem to be more liable to passive drift while others play a more active role in their propensity to become unattached and drift.

Previous research has suggested that hunger state may contribute to stream invertebrate drift (Williams and

Levens, 1988). They investigated the gut fullness of benthic and drifting invertebrates (caddisfly larvae, Gammarus, and Baetis) to determine if drifting invertebrates were significantly less full than their attached benthic counterparts. In the case of these invertebrates, a significant difference in gut fullness was determined as the drifting invertebrates were significantly less full. However, Hildebrand (1974) found that the drift of Tricorythodes sp. was not influenced by food level (possibly due to differing food preferences than those available). Similarly, Ploskey (1979) found that drifting Baetis nymphs had similar gut-content weights and caloric contents as their benthic counterparts.

Kohler (1985) suggested that Baetis nymphs may employ a "giving-up" strategy while foraging in patchy habitats. This strategy involves a criteria in which the mayfly may decide a foraging habitat is low quality, gives up in the food search, and actively enters the water column. Kohler (1985) found that when periphyton was uniformly distributed on top surfaces, there was zero to nearly zero drift. Corresponding patchy distributions resulted in greater than zero drift response. It was also suggested that Baetis may experience an expected distribution of food and if moved from a high density to lower density patch, the nymphs may respond as if it were low quality and again enter the drift. There appear to be conflicting results and conclusions with

the research conducted on drift response to hunger level and prey density. Perhaps there are multiple factors, which singly or in association, may contribute to drift initiation. Further research is required to determine whether drift may be hunger mediated, species-specific, prey-density related, and/or a behavior-motivated response.

Mueller (1954) suggested competition for space may result in increased drift and subsequent colonization of downstream habitats. In this sense, drift may act as a density-dependent regulatory agent. This may reveal itself as competition for space, food, or both (Hildebrand, 1974). Hildebrand (1974) found drift of all taxa examined (including Ephemerella, Tricorythodes, Simuliidae, and Hydropsychidae) to be a linear function of population density (density independent). Hildebrand suggested that intraspecific competition for space was not a factor which resulted in drift. For these organisms, drift appeared to be the result of a probability of dislodgment from the substrate and not affected by density. Walton (1977) also found a linear relation of increasing drift with increasing density of Acroneuria abnormis. He did suggest, however, that density-dependent drift may be species-specific phenomena occurring from particular substrates only. The increase in drift from higher densities may be related to both probability and behavior. Both factors could also be species-specific,

further complicating interpretation. Behavioral studies are becoming more common in stream ecology. Peckarsky and Penton (1985) investigated competition-affected behavior in predaceous stoneflies. She showed that aggressive interactions may increase with added density and when this occurred, it most commonly resulted in submissive or evasive behavior which led to avoidance. A continuance of avoidance in a lotic system may in itself result in drift.

Lehmkuhl and Anderson (1972) suggested that the occurrence in drift is determined by a species-specific complex of interdependent factors including micro-distribution, life cycle, and behavioral characteristics. In order to define the intrinsic mechanisms of drift, further research must be conducted dealing with the source of individuals which drift and the biotic and abiotic factors which may cause drift. Also, further behavioral investigation is required to determine whether invertebrate drift is due to active detachment or passive dislodgment.

In this investigation, I examined patterns of dispersion and mechanisms resulting in dispersion of predatory stonefly nymphs (Plecoptera: Perlidae). This research focused on two genera, Acroneuria spp. and Paragnetina spp. Preliminary in situ investigation indicated similar behavior, morphology, and life history characteristics of the species within these genera. Preliminary investigation

indicated similar rapid response and good maneuverability in response to stimuli in these stoneflies. Both genera exhibit a strong clinging ability and are less likely than other inhabitants to be passively dislodged from snag habitats (Stewart and Stark, 1988).

First, I determined the pattern of dispersion of these nymphs among 20 snag habitat units comprised of artificially bundled snag material. This provided a base-line for the following research. Dispersion of stonefly nymph prey items (Ephemeroptera, Trichoptera, and Chironomidae (Walton, 1977)) was examined to investigate the possibility that the previously determined pattern of stonefly dispersion may be in response to prey dispersion (similar dispersion patterns may indicate predator response, dissimilar patterns indicate no response of the predator to the prey dispersion).

Two factors which may influence drift of Perlidae nymphs, hunger state and density within snag habitats, were investigated concurrently. This research continues to build on the foundation of hunger level and drift response by physically manipulating the hunger state of stonefly nymphs and examining differences in the propensity to drift. Density was manipulated for 3 levels (low, medium, and high) on the snag habitats to examine differences in the propensity to drift.

This study continues to advance the foundation of behavioral drift controversy by conducting behavioral observations in an artificial stream mesocosm. The mesocosm allowed the video taping of behavior to determine if density-related drift was due to active or passive means; varied with time of day; or was due to behavior modifications (modifications in time spent in movement, encounter rates, or in the types of encounters).

Specific objectives were to:

1. Determine the natural dispersion of stonefly nymphs and associated prey items within artificially bundled snag units.

2. Determine whether hunger state of the nymphs is a factor contributing to the propensity for drift.

3. Determine whether an increase in density within the snag habitat is related to a subsequent increase in drift from that habitat.

4. Determine through behavioral observations whether density induced drift is due to behavioral modifications which lead to active detachment or passive dislodgment and consequential drift.

II. MATERIALS AND METHODS

1. STUDY SITE

The study site, Upper Three Runs Creek (UTR), is a second order coastal plain stream system located on the Savannah River Site in Aiken County, South Carolina (figure 1). UTR creek has received numerous nonthermal discharges from several Savannah River Site operating areas since the 1950's. Through tributary streams, UTR creek has received small amounts of noncontact cooling water, treated sanitary wastewater, and other low-impact effluents (Keyes, 1989).

UTR creek is a sandy-bottom stream, part of the UTR flood plain, which experiences seasonal flooding. As of July 1989, 240 macroinvertebrate taxa have been collected from the stream as part of the F/H ETF monitoring program (Enwright, 1989). The dominant taxa, numerically, are the chirinomids accounting for 66.3% (Enwright, 1989). The most common stoneflies are Acroneuria, Paragnetina, Pteronarcys, and Perlesta, comprising up to 11.5% of the total taxa (Enwright, 1989). Mean density of macroinvertebrate organisms collected on multiplate samplers was 633/m2 (Enwright, 1989).

Research dates corresponded to base flow conditions. Channel width at the research site during base flow

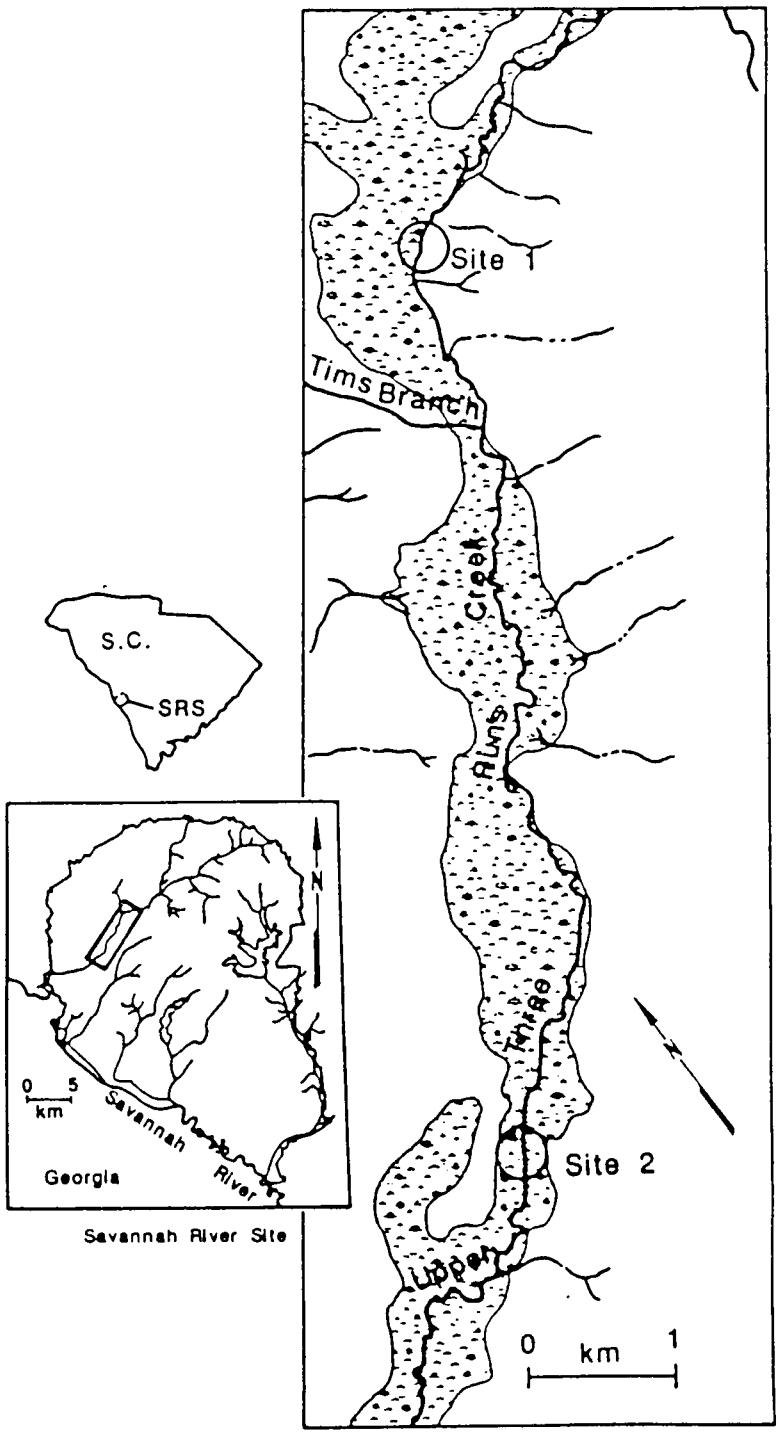

Figure 1. Schematic drawing of the study area. Site 1 represents the snag locations and Site 2 represents stream-side location of artificial stream mesocosm.

conditions (figure 1, site 2) averaged 15.5 m with a mean depth of 42.8 cm. Mean velocity at snag locations was 0.21 m/sec with a standard deviation of 0.05.

2. FIELD MANIPULATIONS

Twenty natural substrate snags were constructed using branches of approximately 20 cm maximum circumference retrieved from the stream site, cut to approximately 40 cm in length, and bundled in groups of three. The total surface area mean of the 20 snags was 0.120 m2 with a standard deviation of 0.021. The snags were cable tied 10 cm under the surface of the water to the tops of PVC pipes previously set within the stream bed. This design was chosen based on preliminary research, (trial and error in the field), and represented as closely as possible, 20 replicate snags. Snags were placed across the stream in sets of four. Each snag was placed at least 1.5 m from adjacent snags. Each snag was placed perpendicular to the stream current and had an unobstructed area toward the bank. Stream placement resulted in slightly different positions of the snags with respect to the bank and adjacent snags. Each experiment required a random selection of treatment for each snag to decrease the variability associated with a position effect. The snags were allowed to naturally colonize prior to subsequent manipulation. Each snag constituted one experimental unit from

which (a) the natural dispersion of nymphs and prey items was determined, (b) hunger state of the nymphs was controlled and subsequent drift was determined, and (c) density of the nymphs was manipulated and subsequent drift was determined.

A modified version of the above procedures was implemented for use in the artificial stream for behavioral observations.

2.1 Dispersion of Plecopteran nymphs and associated prey items

The twenty replicate snags were allowed to naturally colonize for 14 days. Preliminary investigation indicated that a 2 week colonization period was sufficient to allow adequate foraging. After the 14 day colonization period, each snag was placed into a 250 μm net and cut from the PVC pipe. Each snag was rinsed to remove nymphs and prey items. The contents of the net were rinsed into a zip-loc bag and preserved with formalin. The snags were measured for area estimations using length and maximum circumference. The snags were reassembled and cable-tied back onto the PVC pipes which remained set within the stream bed.

2.2 Hunger state of the nymphs and consequential drift

The 20 previously manipulated snags were used. Several decades of phenologically similar stonefly nymphs were collected from the research site. Each nymph was tagged with a copper wire collar, red marked (red nail polish added) or plain to indicate treatment. Nymph tagging was accomplished by first sedating the nymph in a holding container containing dissolving Alka Seltzer (1/4 tablet or less). This sedation lasted approximately 2 minutes. The nymph was then held on one hand while a section of 24 gauge copper wire (approximately 5 mm in length) was manipulated around the nymph between the pronotum and mesothoracic wing pad with the use of tweezers. The nymph was placed into a second holding jar for recovery. Previous observations (conducted prior to research by direct observation in the field) have shown that the collar does not appear to affect behavior. The red tagged nymphs (satiated) and plain (starved) were placed in several holding jars mounted within the stream. The satiated nymphs were fed oligocheates and the starved nymphs received no food additions for 24 hours (Peckarsky and Penton, 1985). Ten nymphs (five starved and five satiated) were placed directly from the holding jars into zip-loc bags and preserved to establish the validity of hunger-state differences between the two treatments.

Snags were checked prior to nymph placement to remove nymphs which naturally colonized prior to manipulation. Random numbers were generated to designate treatment placement for each snag (starved/satiated) and each snag was numbered. The pvc pipes supporting the snags had Tangle-foot applied to the upper portion (below the snag) in order to prevent the escape of nymphs down the pipe. Preliminary investigation showed the nymphs did not enter the Tangle-foot areas.

Three nymphs (3 starved or 3 fed) were placed on each snag. Nymphs were individually placed by hand on their designated snag. A total of 10 replicates was run, 10 starved snags (n = 10) and 10 fed snags (n = 10), for a total of 60 nymphs. On the second run a total of 19 replicates was run, 9 starved and 10 fed snags for a total of 57 nymphs. Drift nets were placed down stream from each snag to retrieve the nymphs which drifted. The nymphs were allowed one diel drift period (24 hour period) before snag retrieval. After the 24 hour drift period, each snag was placed into a 250 µm net and cut from the pvc pipe. Each snag was then rinsed to remove nymphs. The contents of the net from each snag rinsing were rinsed into a zip-loc bag and preserved with formalin. The retrieval nets were rinsed and the contents placed into zip-loc bags and preserved with formalin.

2.3 Nymph density within the snag habitat and consequential drift

The nymph density phase required two runs to check for similar responses between the early instars (small nymphs; head capsule width range 4.6-5.5 mm) and late instars (large nymphs; head capsule width range 6.3-7.4 mm). Instar considerations were made due to the possibility that different life history stategies may exist for different size classes. It has been suggested that late instar nymphs may have higher drift responses due to the proximity in time of emergence (Hall et al., 1980). Both runs tested stonefly drift response with high, medium, and low density. The 20 previously manipulated snags were used. Several decades of phenologically similar stonefly nymphs were collected from the research site. The nymphs were placed in several holding jars mounted within the stream to ensure similar handling among the nymphs. Snags were checked prior to nymph placement to remove nymphs which naturally colonized prior to manipulation. Random numbers were generated to designate treatment for each snag (high/medium/low density) and each snag was numbered. The pvc pipes supporting the snags had Tanglefoot applied to the upper portion in order to prevent the escape of nymphs down the pipe.

Each snag received one of three treatments:

i. High density snags: 6 early instar nymphs (run 2, 5 late instar nymphs)

ii. Medium density snags: 3 early instar nymphs (run 2, 3 late instar nymphs)

iii. Low density snags: 1 early instar nymphs (run 2, 1 late instar nymph).

Nymphs were individually placed on their designated snags. For the small nymphs, the number of replicates are as follows: high (7), medium (6), and low (7). For the large nymphs, the replicates consisted of three replicates for each density. Retrieval nets were placed down stream from each snag to retrieve the nymphs which drifted. The nymphs were allowed 24 hours before snag retrieval. After the 24 hour drift period, each snag was cut from the pvc pipe and placed into a 250 μm net. Each snag was then rinsed to remove nymphs. The contents of the net from each snag rinsing were rinsed into a zip-loc bag and preserved with formalin. The retrieval nets were rinsed and the contents placed into zip-loc bags and preserved with formalin.

2.4 Behavioral Observations

Behavioral observations were carried out stream side (figure 1, site 2) in a Plexiglas-base artificial stream mesocosm in order to increase the visibility of the stonefly nymphs and any interactions. These observations were filmed

using two Panasonic video cameras during both day and night under red light conditions which are undetected by aquatic insects (Casey, 1987; Allan et al., 1986). The behavioral observations were based on classifications characterized by Peckarsky and Penton (1985).

One snag, approximately 20 cm in length, was suspended parallel to the flow in the artificial stream. Water flow was accomplished with the use of a Little Giant sump pump (Model 6-CIM). Velocity similar to Upper Three Runs creek was maintained by a swivel-regulated dam located on the down-stream end of the artificial stream which was incorporated in the design. The system was a one-time-through system using water directly from UTR creek. Two cameras were used, one directed toward the snag from each side of the artificial stream.

The snag was allowed to naturally colonize in UTR creek before use. Phenologically similar stonefly nymphs were collected from the research site. The nymphs were placed in several holding jars mounted within the stream to ensure similar handling among the nymphs. Random numbers were generated to designate the order of the behavioral observations.

Each observation consisted of one of three densities:

i. High density snag observation: 5 nymphs

ii. Medium density snag observation: 3 nymphs

iii. Low density snag observation: 1 nymph

Nymphs were randomly chosen from the holding jars for each run. Same individuals were not used for consecutive runs. Three 30 minute observational replicate runs were video taped for each snag density. Three replicates of complete sets of runs (high, medium, low density) were run during day and night.

3. LABORATORY PROCESSING

3.1 Dispersion

Nymphs were identified to genus and counted. Prey items were sorted and counted.

3.2 Hunger State

Nymphs from the snags (nondrifters) were identified to genus and counted. Nymphs from the retrieval nets were sorted, identified to genus, and counted. Gut analysis (% fullness) was performed on nymphs that were removed from holding jars and preserved. The analysis determined whether the guts from starved nymphs were proportionately less full than those of satiated nymphs, an indication of hunger level (Williams and Levens, 1988).

3.3 Nymph Density

Nymphs from the snags (nondrifters) were identified to genus and counted. Nymphs from the retrieval nets were sorted, identified to genus, and counted.

3.4 Behavioral Observations

Video tapes were analyzed for the following:

1. Total time spent in movement (seconds)
2. Behavior (table 1)
3. Drift (active or passive and due to encounter or not due to encounter

4. STATISTICAL ANALYSIS

Prior to statistical analysis, the input data were tested for normality with univariate procedures (SAS, 1985).

4.1 Dispersion

The distribution of Acroneuria spp. and Paragnetina spp. and associated prey items (Chironomidae, Trichoptera, Ephemeroptera) among the 20 snags was tested for fit against a Poisson distribution using the s2 goodness of fit test. The variance (s2) to mean ($\bar{x}$) ratio was used as a measure of contagion, where a distribution is uniform for $s2/\bar{x} < 1$, random for $s2/\bar{x} = 1$, and clumped for $s2/x > 1$ (Ludwig and Reynolds, 1988). The dimensions of the snags

Table 1. Stonefly behavioral repertoire.

Behavior Class	Description
Initial Contact	
Antennae:	Contact with antennae
Running into:	Actual running into another nymph
Type of Contact	
Turning toward:	Turning to face competitor
Crawl on top:	Crawling on top of another nymph
Bite head:	Biting the head region of another
Bite cerci:	Biting the cerci of another
Bite leg:	Biting the leg
Response to Contact	
Stay:	Remain in position
Move:	Adjust position
Leave:	Find other location
Run:	Abrupt departure
Chase:	Running after departing nymph, often with biting

were converted to total area (m) per snag and the mean and standard deviation calculated.

4.2 Hunger State

Analysis was based on the number of nondrifters (nymphs remaining on the snag at snag retrieval). Results were analyzed by analysis of variance (ANOVA) on log transformed data. A two-way analysis of variance (SAS, 1985) was used to test two main effects (hunger state and day) to drift response. There are 2 hunger levels (starved and satiated) and 2 days (day1 and day2).

Null hypotheses 1: There is no significant difference between the drift response of satiated and starved nymphs.

Null hypotheses 2: There is no significant difference in drift response between day1 and day2.

It is expected that the effect of day is independent of effect of hunger level. Null hypotheses were rejected at $\alpha = 0.005$.

4.3 Nymph Density

Analysis was based on the number of nondrifters. Comparisons were made of drift response in large and small nymphs between high, medium, and low initial density snags. The comparisons were based on proportion

remaining on the snags and the percentage of drifters from each density.

4.4 Behavioral Observations

A comparison of movement (between low, medium and high) and encounters (between medium and high) density snag placements during day- and night-time was made based on the averages (n = 3) of each behavior run. These comparisons were made to evaluate if an increase in movement and/or encounters occurred with an increase in density, and if there was a difference in total time of movement or the number of encounters between day- and night-time runs.

A comparison of behavior between day- and night-time runs was made based on the number and percent of encounters of each behavior type (table 2). This comparison was made to evaluate if the observed aggressiveness of encounters changed between day- and night-time runs.

Table 2. Summary of behavioral observations showing number of specific events and percent of each event by category compared as difference in time of day.

BEHAVIORAL REPERTOIRE SUMMARY				
	NUMBER OBSERVED		PERCENT	
	DAY	NIGHT	DAY	NIGHT
INITIAL CONTACT				
Anntenae	95	25	81.9	89.3
Running into	21	3	18.1	10.7
CONTACT				
Back away	3	1	2.7	3.6
Turn toward	16	8	14.5	28.6
Crawl on top	7	0	6.5	0
Bite cerci	12	3	10.9	10.7
Bite leg	5	3	4.5	10.7
Bite head	67	13	60.9	46.4
RESPONSE				
Stay	79	19	33.3	38
Move	51	22	21.6	44
Leave	87	8	36.7	16
Run	10	1	4.2	1
Chase	10	0	4.2	0

III. RESULTS AND DISCUSSION

1. DISPERSION

Walde and Davies (1984) observed a random dispersion of Acroneuria abnormis. I expected that the predator field dispersion of Acroneuria spp. and Paragnetina spp. to be consistent with their findings. However, these predators were found to be distributed uniformly ($s2/\bar{x}$ = .405, 14 day colonization; $s2/\bar{x}$ = .491, 24 hour colonization). The significance of departure from randomness was assessed using a t-test ($t = 2.00$, $df = 19$, $\alpha = 0.05$). The uniform dispersion I observed suggests that some mechanism or process is affecting the distribution.

I observed that the dispersion of potential prey species was significantly clumped ($s2/\bar{x}$ = 10.17, 14 day colonization; $s2/\bar{x}$ = 2.28, 24 hour colonization). This observation indicates that the dispersion of stoneflies is not responding to the prey dispersion but some other factor.

Meire et al. (1989) suggested that random patterns, as observed by Walde and Davies (1984) for Acroneuria abnormis, result if the occupied space is independent of the space occupied by others. The space provided on the constructed snag units used for my experiments represent distinct area restrictions (mean surface area of experimental snags was 0.120 m2 with a standard deviation of 0.021). A limited

amount of space in conjunction with aggressive stonefly nymphs would not be an accurate description of space independence. Meire et al. (1989) suggested that uniform patterns may result from interference competition. This appears to be the force acting here. Walton et al. (1977) observed increased activity in Acroneuria abnormis in laboratory pans when individuals contacted each other. In concurrence, I found an increase in movement, encounters, and aggressive interactions with increased density in the behavioral experiments. Walton et al. (1977) further postulated that A. abnormis occupied and defended refuges and intraspecific competition for space lead to active desertion of the substrates.

This leads to the conclusion that limited space may be dictating distribution and therefore carrying capacity of the snag units (Walton et al., 1977). Waters (1972) suggested that drift may be a function of the degree to which the carrying capacity is exceeded. This implies intraspecific competition leading to density-related drift to maintain a uniform distribution.

2. HUNGER STATE

Hunger state is a factor which has been suggested to influence drift. The input data was determined to be a random sample from a normal distribution (SAS, 1985). With

direct manipulation of hunger level, no significant difference in the drift responses of satiated and starved stonefly nymphs was observed ($p = 0.3131$, table 3). However, there was a significant difference in drift response among days ($p = 0.0001$). Thus I accepted null hypothesis 1 (there is no significant difference in drift response between starved and satiated nymphs) and rejected null hypothesis 2 (there is no significant difference among day). There was no significant interaction between hunger state and day ($p = 0.3131$). Therefore, fluctuation in drift may vary significantly from day to day, but the difference in drift responses between satiated and starved nymphs remains insignificant.

This finding seems to support the work of Hildebrand (1974) and Ploskey (1979) indicating that hunger state alone is not a factor which influences drift. It is possible that an "expected distribution" and "giving up strategy" suggested by Kohler (1985) may be acting with Acroneuria and Paragnetina. Perhaps the fed stoneflies responded as if moving from a high density prey patch to low density (surplus of oligocheates in the holding jars to a lower natural density of prey items in the field) and experienced the "giving up strategy" by initiating drift. The starved stoneflies may actually have a higher drift response, but it may be masked by the "giving up strategy" of the fed nymphs.

Table 3. Analysis of the effect of hunger state and day on stonefly drift reponse. A two factor Analysis of Variance was used with hunger state and day as main effects.

Source	SS	DF	F	Pr > F
Hunger State	0.7810	1	1.05	0.3131
Day	13.6243	1	18.27	0.0001
Hunger*Day	0.7810	1	1.05	0.3131
Error	26.1000	35		
	Rsq = 0.3622			

Gut fullness differed significantly between 24 hr fed nymphs and 24 hr starved nymphs ($t = 6.812$, $df = 17$, $\alpha = 0.05$). The 24 hr fed nymphs were an average of 55.5% full. The 24 hr starved nymphs were an average of 5.5% full. Perhaps the amount of food in the gut is less significant than the quality of the material. Suboptimal food types may stimulate organisms to drift in the same manner expected with low gut fullness.

Clearly there is room for further research here. Hunger state may be best determined by caloric content rather than gut fullness (Williams and Levens, 1988). One approach would appear to be field manipulations. Animals sampled directly from the water column may have been passively/actively dislodged due to a number of events including predator-prey interactions or current interruptions. Williams and Levens (1988) found no differences in activity level between starved and fed animals. Perhaps hunger state investigations should best begin with behavioral studies.

3. DENSITY

Insights into the workings of competition appear in the density-related drift experiments. The result of the data for total drift at each density appears in figure 2. Waters (1972) reported that a direct relationship between benthic population density and drift density has not been found. I

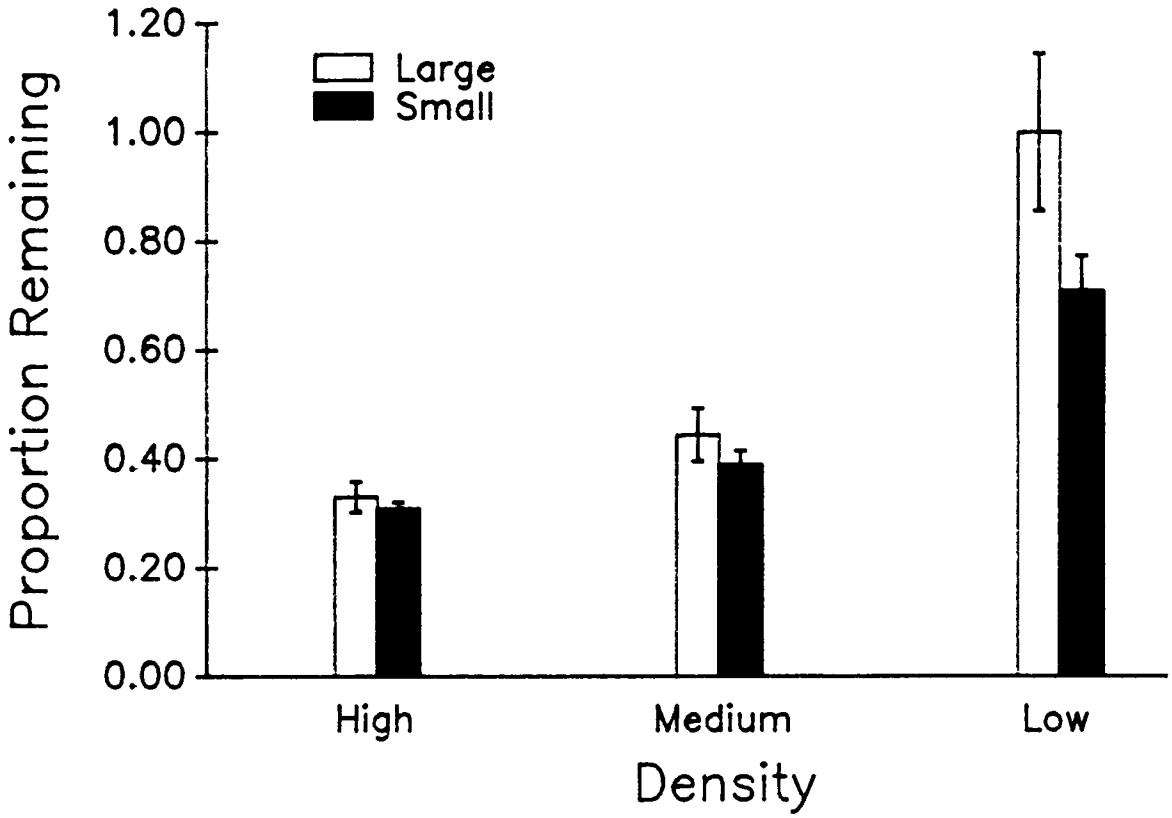

Figure 2. Comparison of drift response in large and small Plecopteran nymphs for proportion remaining on snag habitat (nondrifters) between high, medium, and low initial density snags.

found that the response of drift of the stonefly nymphs increased with an increase in nymph density. There was greatest drift off the high density snags, less from the medium, and very little off the low. Combining large and small nymphs, 67% of the nymphs on high density snags drifted, 59% of the nymphs on medium density snags drifted, and 20% of the nymphs on low density snags drifted. If drift, in this instance were density-dependent (a linear increase of drift with increasing density), one would expect the same percentage of drifters from each snag density and this was not the case. Also, all nymphs that drifted from low density snags were small nymphs. I feel that this occurred because the clinging ability of the small nymphs is less than that of the larger size classes. This was observed during nymph handling. It was difficult to remove a large nymph from the snag or from any area from which a nymph could cling.

Walton (1980) suggested in his research that intraspecific competition interactions may increase with increasing density. Peckarsky (1985) supported this finding with her competition-affected behavioral study. She found an increase in aggressive interactions with an increase in density which lead to avoidance or submissive behavior.

4. BEHAVIORAL OBSERVATIONS

Due to the limited sample size, a problem of independence may exist. While same individuals were not used for consecutive runs, individuals were randomly selected from the "population sample" (consisted of 16 nymphs) used during the experiment. The random selection process was employed to reduce any variability caused by a limited sample size. I observed a general increase in encounters with increasing density in the behavioral observations (figure 3). I found an increase in movement with increasing density during the night-time runs, and a decrease in movement with density in day-time runs (figure 4). The significant difference occurs with a comparison of day- and night-time (time of day). In comparing day- and night-time runs, there is a marked increase in the number of encounters and time spent in movement during day-time runs (figure 3 and 4).

Figure 5 is a representation of number of encounters with movement showing time of day difference. Again, a marked increase in encounters and movement occurred during the day-time runs. The combined day- and night-time runs showed a trend between encounters and movement, but it did not appear to be medium and high density dependent.

A dramatic increase in movement and the initiation of drift response was observed with the addition of direct white light during both day- and night-time runs. This

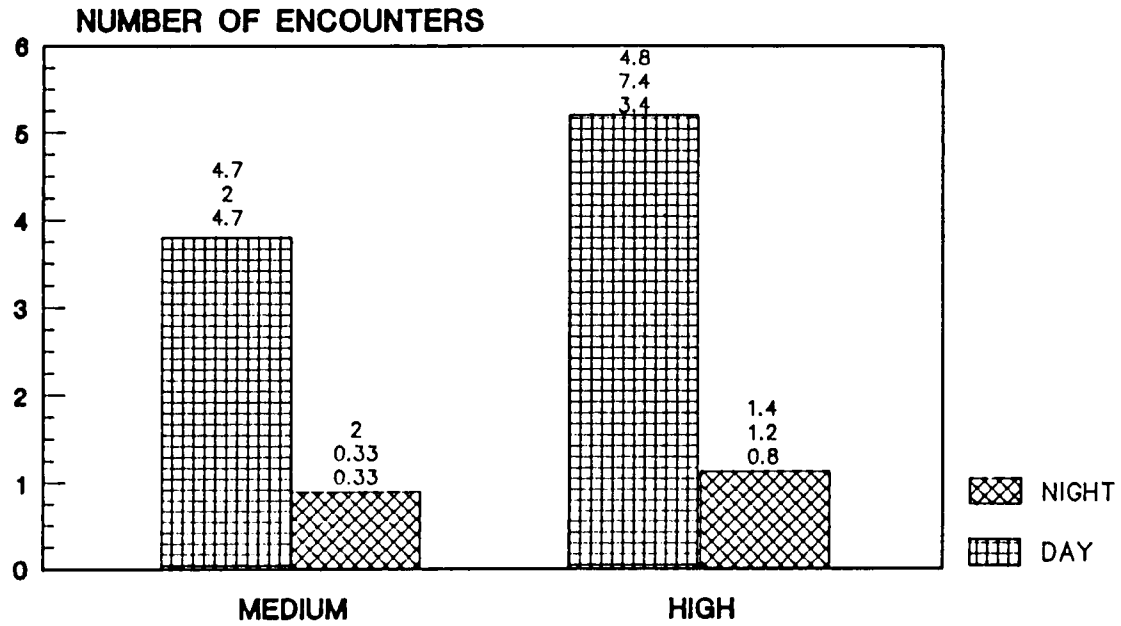

Figure 3. Comparison of total movement (seconds) per stonefly nymph between low, medium, and high density snag placements in behavioral runs showing time of day difference.

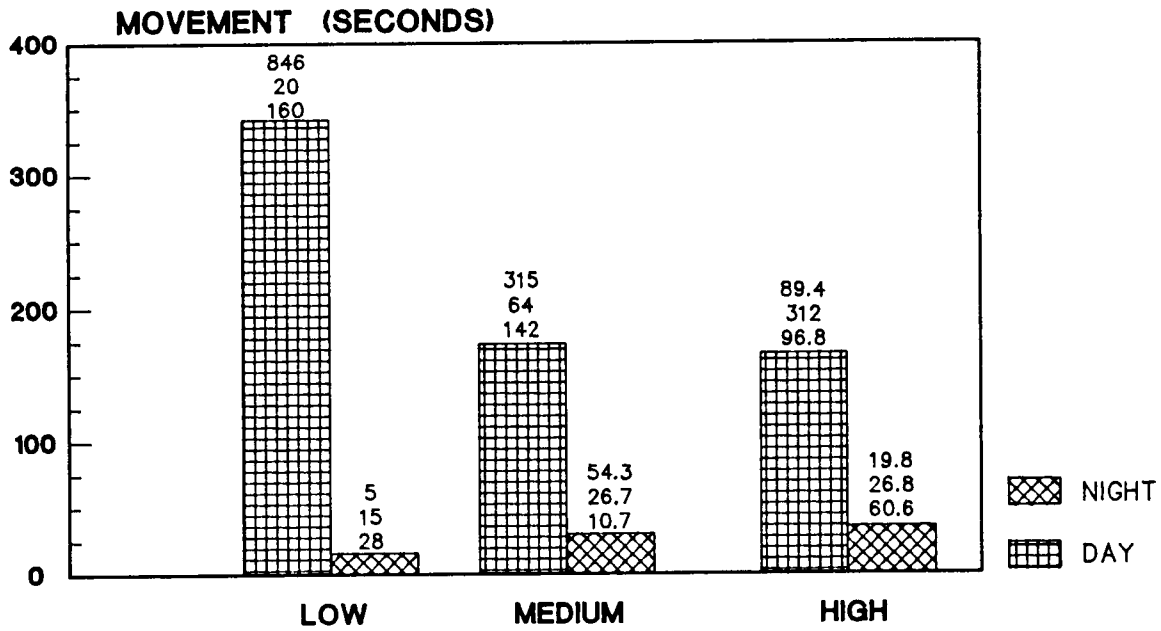

Figure 4. Comparison of number of encounters per stonefly nymph between medium and high density snag placements in behavioral runs showing time of day difference.

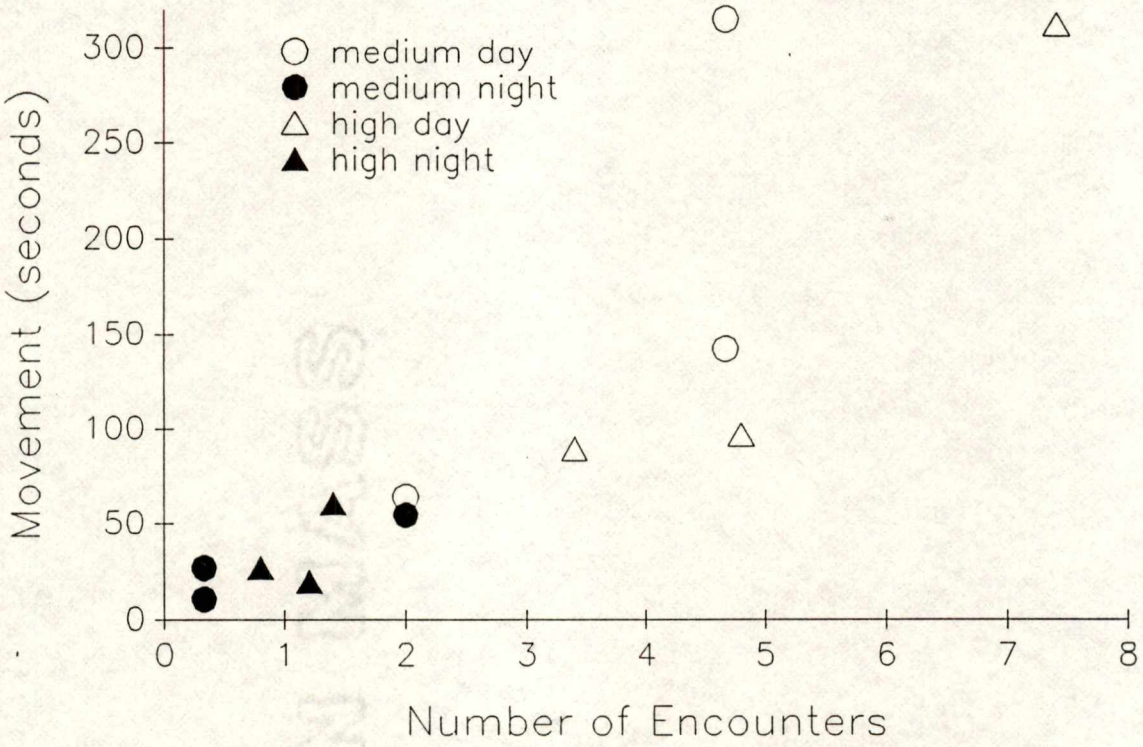

Figure 5. Representation of number of encounters with movement (seconds) showing time of day difference.

suggests that during day-time runs, the nymphs are responding to density as well as light controls. This finding is consistent with Bishop (1969) who found accidental exposures of white light caused marked changes in drift responses.

The types of competition interactions I observed reveal highly aggressive encounters. Episodes of head-to-head biting may last for up to 4 seconds. The behavioral repertoire summary (table 2) indicates more aggressive movement and interactions during day-time runs. In respect to initial contact, a marked increase in "running into" another nymph occurred during the day. With respect to actual contact, there was a marked increase in biting (head, cerci, and leg combined) during the day. In the contact response category, the most common response to an encounter during the day-time was to leave (36.7%); during the night-time, the most common response was to move (44%). No chasing was observed at night, and more run responses occurred during the day-time. An increase in running into another nymph (initial contact), biting (type of contact), and running (response to contact) occurred during the day-time runs. This increase in day-time activity may support the claim that light controls become important in the behavioral aspect of stonefly interactions and perhaps drift as well.

Results from these experiments suggest that intraspecific competition (and light) may interact to influence

substantially the behavior and drift responses of stream invertebrates. Aggressive interactions suggest that the resultant active avoidance of other predators might be responsible for the observed spacing patterns in the field (lack of aggregation). Since aggressive encounters occur with most contacts, the result may demonstrate itself as drift.

In summary, I have demonstrated a dynamic interplay of factors influencing aquatic invertebrate drift. In general, intraspecific competition appears to be a driving force in the drift initiation and natural field dispersion of Acroneuria spp. and Paragnetina spp. Behavioral observations are becoming increasingly vital to the understanding of such processes. The information gained from actual physical observation should stimulate further research in this area. The controversy of hunger state initiated drift continues. A significant contribution in density relating to intraspecific competition, basic behavior, and drift has been made. This research provides further evidence which suggests that density-dependent dispersion may be a significant aspect of population regulation in stream systems.

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