

Effects of Abiotic Factors on Macroinvertebrate Drift in the Lower Mississippi River, Louisiana

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ABSTRACT.—We assessed the effects of abiotic factors on invertebrate drift composition in the lower Mississippi River from November 1984 to June 1985. We sampled drift, measured in situ water quality variables and recorded river stage and discharge 1 night each month. Principal component analysis (PCA) and standard multiple regression were used to investigate temporal relationships between drift and abiotic factors in a large river system. Several drifting taxa (Ephemeroptera, Trichoptera) were significantly, negatively related to discharge and positively related to temperature, current and conductivity. In separate analyses, collector, engulfing predator and detritivore feeding groups were significantly, positively related to stage/discharge and negatively related to current velocity. In addition, each trophic component had several prey and one predator highly correlated with it. Seasonal variability in drift was a response to both invertebrate predation and fluctuations in the hydrologic cycle. Our study could not distinguish between two main effects of river discharge on drift: dilution and habitat availability. The possibility that drift may be a separate community apart from the benthos, and thereby affected strongly by seasonal abiotic factors, is discussed.

INTRODUCTION

Invertebrate drift has intrigued stream ecologists for more than 3 decades (Waters, 1972), and has been the basis for much controversy. Causal mechanisms for drift have been divided into passive and active components. Passive (catastrophic) drift was viewed as a result of the normal erosional force of a stream (Kovalak, 1979), or spring run-off scouring (Anderson and Lehmkühl, 1968). Conversely, active drift implied a behavioral element. Invertebrates may enter the drift to avoid overcrowded conditions (*i.e.*, emigration of excess production: *see* Waters, 1961, 1966); seek out unexploited food resources (Brittain and Eikeland, 1988); avoid an unfavorable physicochemical environment (Larimore, 1974; Hall *et al.*, 1980); or elude predators (Allan, 1978; Malmqvist and Sjöström, 1987).

Most theories concerning macroinvertebrate drift were derived from studies conducted on small streams (generally 1st–4th order; *see* Waters, 1972; Brittain and Eikeland, 1988, for reviews). Recently, questions have been raised concerning the validity of applying theories, developed on small lotic systems, to larger rivers (Welcomme, 1979; Junk *et al.*, 1989; Sedell *et al.*, 1989). For example, Allan (1978) had suggested that visually oriented predators may be responsible for the diel periodicity exhibited by drifting stream invertebrates. This may be the case in small, clear-water streams. However, Koetsier and Bryan (1992) found that the turbid waters of the lower Mississippi River (a 12th order system) may nullify the effects of these predators (*sensu* Walde, 1986). Yet, diel periodicity of invertebrate drift still occurred. Clearly, some other mechanism is responsible.

Few drift studies have been performed on large rivers (\geq 9th order; Bingham *et al.*, 1980;

Beckett and Kasul, 1985; Obi and Conner, 1986; Koetsier and Bryan, 1989, 1992). Fewer still have attempted to determine underlying mechanisms responsible for invertebrate drift timing or composition in these large systems. In the present study, we examined the relationship between selected abiotic factors and seasonal macroinvertebrate drift patterns in an attempt to discover underlying relationships between abiotic factors and invertebrate drift in the lower Mississippi River.

MATERIALS AND METHODS

The study site was located on the lower Mississippi River (river km 437.2), a 12th order system, near West Feliciana Parish, Louisiana, approximately 40 km NW of Baton Rouge (91°19'W long, 30°45'N lat) and described in detail elsewhere (Koetsier, 1986). Macroinvertebrate drift was sampled at the surface 1 night each month from November 1984 through June 1985. We restricted our analyses to nocturnal drift because the greatest drift density, biomass and species richness have been collected in the night samples (Brittain and Eikeland, 1988; Koetsier and Bryan, 1989; Waters, 1972). The site was 20 m from shore in fast-flowing current (1.0–1.6 m/sec), where the water was approximately 15 m deep. Each drift collection consisted of six consecutive 2-h samples with conical nets (0.2 m² mouth; 3 m long and mesh of 0.505 mm). To avoid any confounding effect by visually oriented predators, the sampling period began 15 min before dusk and ended 15 min after dawn. Each net was suspended a few centimeters below the water's surface with floats and anchors. Flow meters mounted in each net mouth provided estimates of volume filtered. To facilitate comparisons among replicates, each sample was expressed as mean number of drifting individuals/100 m³ of filtered water. All samples were preserved in the field with 10% formalin.

Every 2 h on each sampling date, water temperature, dissolved oxygen, pH, specific conductance (in situ with a Hydrolab Model 6D Surveyor) were measured. Surface current (measured with a General Oceanics digital flow meter: Model 2035) varied little throughout the night and subsequently, was recorded only at midnight. River stage levels and discharge (recorded daily at 1500 h) were obtained from the U.S. Army Corps of Engineers Talbert Landing (Mississippi) gauging station (river km 492.7).

In the laboratory, macroinvertebrates were separated from the entire sample using a dissecting microscope. Organisms were preserved in 70% ethanol for later identification and enumeration. Slide preparations of critical structures of chironomid larvae and oligochaetes were made for genera-level identifications. Taxa were classified into functional feeding groups using the taxonomic-functional feeding group tables in Cummins (1973) and Merritt and Cummins (1978).

All data were transformed using common statistical transformations (*see* Elliott, 1977; Zar, 1984). Data transformed by $1/x$ best met the assumptions of linearity and homoscedasticity, and this transformed data was used for all parametric analyses. A negative multicollinear relationship existed between water temperature and dissolved oxygen. Therefore, dissolved oxygen was omitted from the analyses. Although stage and current velocity would be expected to exhibit collinearity, our discharge and stage data were macrohabitat measures (daily observations at approximately 1500 h), whereas our current velocity data were in situ, site-specific measurements. Because of these differences, current velocity, stage level and discharge did not always vary together.

We used Principal Components Analysis (PCA: SAS, 1984) to analyze the interrelationships among taxonomic and trophic groups of drifting macroinvertebrates. With PCA, we attempted to explain the observed relationships of variables loading highly on a factor in terms of common underlying mechanisms. Both Varimax (orthogonal) and Promax

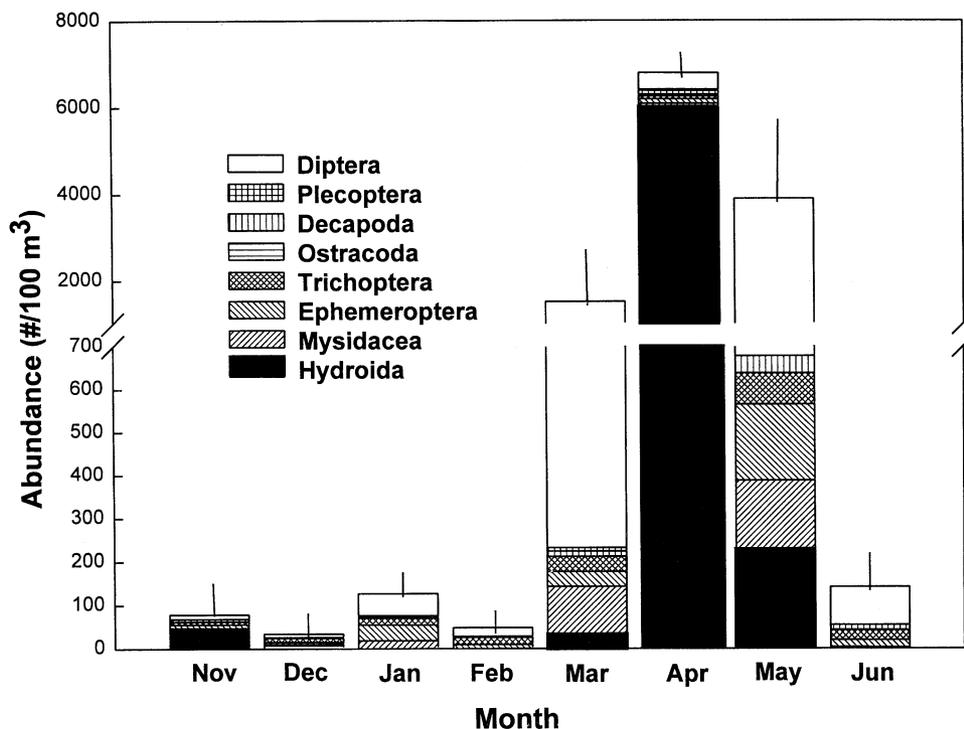


FIG. 1.—Mean abundance of higher invertebrate taxa collected in drift. Vertical bar represents \pm SD from the total abundance mean

(oblique) rotations were used to facilitate fit and interpretation. Variable inclusion in factor interpretation was based on the correlation of the original variable with the factor and the loading value of the variable on the factor. For a variable to be included, a minimal loading value of 0.5 was needed (Tabachnick and Fidell, 1983).

Factor scores for taxonomic and trophic groups were regressed against abiotic variables by standard multiple regression to identify possible relationships between the two variable sets. All dependent variables were entered into the regression model simultaneously (SAS, 1984).

RESULTS

Drift composition.—Invertebrate drift abundance was relatively low in winter ranging from 33/100 m³ in December to 126/100 m³ in January (Fig. 1). In spring, total density increased in March, peaked in April and decreased in May and June (1511, 6787, 3894, 141/100 m³, respectively).

Invertebrate taxa varied each month. Hydroida (*Cordylophora lacustris*, *Hydra*) dominated drift composition in both November and April (56%, 89% of total abundance, respectively). In December, Trichoptera (Psychomyiidae, *Hydropsyche orris*, *Potamyia flava*) was the most abundant taxon in the drift (27% of total abundance). Diptera (*Chaoborus*, Chironomidae) dominated the drift community in March, May and June (85%, 83%, 62%, of total abundance, respectively).

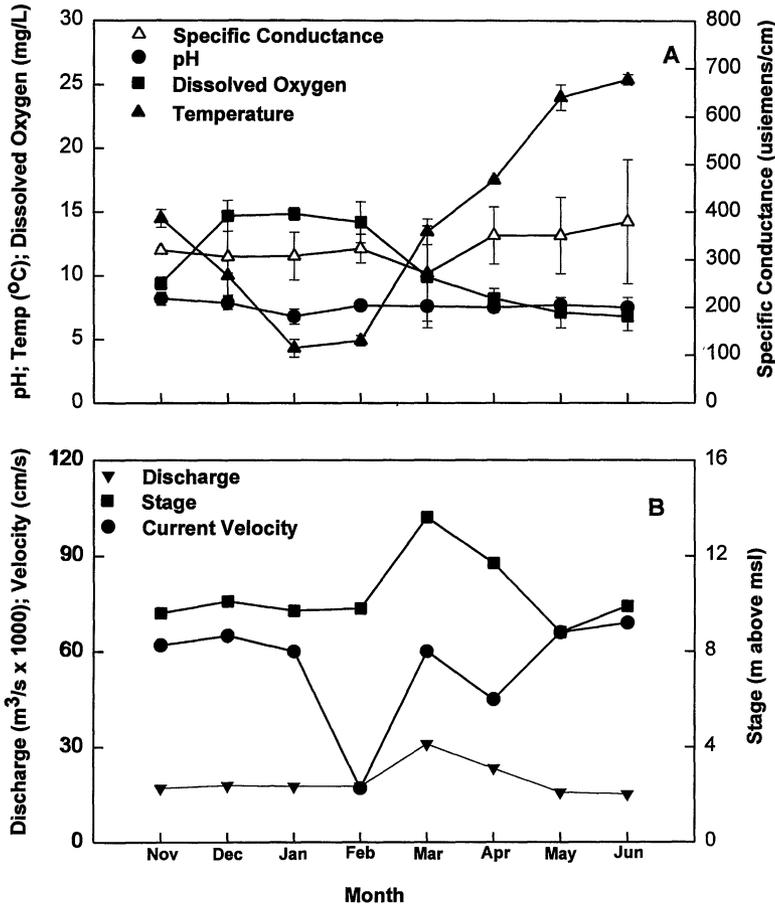


FIG. 2.—(A) Mean values of specific conductance, pH, dissolved oxygen and water temperature measured in the lower Mississippi River during the study period (November 1984 to June 1985). Vertical bars represent 1 SD from the mean. (B) Measured values of discharge and stage level for the lower Mississippi River recorded by U.S. Army Corps of Engineers at Talbert Landing (Mississippi). Current velocity was measured at midnight at the sampling site

Abiotic factors.—Water temperature, pH and specific conductance (Fig. 2) varied within the range reported for the St. Francisville reach of the lower Mississippi River (Hartzog, 1975). Dissolved oxygen and water temperature had a typical inverse relationship for heterotrophic systems (Hynes, 1970; Wetzel, 1975); pH varied throughout the study period, with a low of 6.8 (January) and a high of 8.0 (November). Specific conductance remained constant (323 μ siemens/cm) in the winter (November to February). In spring, conductivity dipped to 240 μ siemens/cm (March), then increased slowly to 380 μ siemens/cm in June.

Discharge and river stage were correlated ($r = 0.83$) during the study. Both remained constant during November through February, increased during spring, and returned to previous levels in May and June (Fig. 2). Current velocity varied little in November through January (62–64 cm/sec) but varied from a low of 57 cm/sec (April) to a high of 67 cm/sec (June).

TABLE 1.—Variable loadings from Principal Components Analysis of macroinvertebrate taxonomic group abundance (#/100 m³) in the drift from the lower Mississippi River during the study period. Varimax and Promax rotations were used to obtain simplest structure. Bold-faced numbers indicate taxa included in the interpretation of the principal component (PC)

Taxa	Loadings		
	PC 1	PC 2	PC 3
Amphipoda	0.884	-0.099	-0.038
Decapoda	0.822	0.165	-0.184
Ephemeroptera	0.701	-0.067	0.064
Hydroida	0.560	-0.009	0.160
Isopoda	0.549	-0.071	-0.181
Trichoptera	0.503	0.161	0.504
Coleoptera	0.197	0.607	-0.078
Megaloptera	-0.031	0.804	-0.126
Diptera	-0.027	0.153	0.602
Odonata	-0.002	0.766	-0.834
Variance explained (%)	32	18	17

Associations of taxa.—Based on inspection of scree plots (eigenvalues vs. number of extracted factors: SAS, 1984) generated by the PCA, five factors were kept. Of these five factors, the first three accounted for 67% of the total variation in drifting invertebrate abundances (Table 1). Taxa principal component (PC) 1 included several taxa that displayed high drift tendencies (Amphipoda, Ephemeroptera, Decapoda, Hydroida, Trichoptera) and one taxon that did not (Isopoda). In contrast, PC 2 was composed of taxa seldom encountered in the drift (Megaloptera, Odonata, Coleoptera). Similar to PC 1, PC 3 contained taxa prone to enter the current (Trichoptera, Diptera: positive loading values) and one taxon that seldom drifts (Odonata: negative loading value).

Regression of the three taxa PC factors against the measured abiotic factors revealed significant ($P < 0.01$) relationships between the variable sets (Table 2). Temperature, specific conductance and current velocity were positively related and explained 61% of the total variation exhibited by the first taxa factor. Specific conductance and pH were also

TABLE 2.—Standard multiple regression of principal components (PC) of drifting macroinvertebrate taxa on abiotic factors. Only significant models and abiotic factors are included

Principal component	Abiotic variable	F value ($P < 0.01$)	R squared
Taxa PC 1 (prone to drift)	-Stage	19.40	0.61
	-Discharge		
	+Temperature		
	+Conductivity		
	+Current		
Taxa PC 2 (not prone to drift)	-pH	3.88	0.20
Taxa PC 3 (prone to drift)	+Conductivity	8.70	0.40
	+pH		
	-Discharge		

+: positively regressed -: negatively regressed

TABLE 3.—Variable loadings from Principal Component Analysis of trophic group abundance (#/100 m³) collected from the drift in the lower Mississippi River during the study period. Varimax and Promax rotations were used to obtain simplest structure. Bold-faced numbers indicate trophic groups included in component interpretation

Trophic groups	Loadings		
	PC 1	PC 2	PC 3
Gatherer	0.982	-0.046	-0.055
Engulfing predator	0.936	-0.162	0.009
Filterer	0.898	0.010	-0.121
Detritovore	0.802	0.204	0.100
Piercing predator	0.420	0.614	0.150
Scraper	0.211	0.761	0.130
Parasite	-0.060	-0.045	0.999
Shredder	-0.155	0.967	-0.109
Variance explained (%)	53	18	14

positively related, whereas discharge was negatively related to taxa grouped on PC 3. River discharge accounted for 40% of the variation displayed by the invertebrate taxa on PC 3. The abundance of organisms comprising PC 1 and PC 3 were significantly affected by the seasonal hydrological cycle of the Mississippi River. Subsequently, only these three factors and their potential underlying structure were interpreted (Table 1). Although the contribution of PC 2 was significant to the regression model overall, abiotic factors only accounted for 20% of PC 2's variability. Because taxa which loaded highly on PC 2 seldom entered the drift, we can only assume that other, unmeasured variables were responsible for their temporal variation in the river.

Trophic associations.—Taxa collected from the drift were placed in one of eight functional feeding groups (detritovore, engulfing predator, collector-filterer, collector-gatherer, parasite, piercing predator, scraper, shredder) following Cummins (1973) and Merritt and Cummins (1978). Scree plots indicated that the first three principal component factors accounted for 85% of the total variation in functional feeding group abundances. Subsequently, these three component factors were used for interpretation. The first factor (PC 1) included both collector subgroups (collector-gatherers: Ephemeroptera—*Hexagenia limbata*, *Stenonema*; collector-filterers: Trichoptera—*Hydropsyche orris*), detritivores (Decapoda: *Macrobrachium ohione*, Mysidacea: *Taphromysis louisianae*) and engulfing predators (Coleoptera: *Pelodytes*, *Amphizoa*, Gyrinidae). The second factor (PC 2) was composed of shredders, scrapers (Coleoptera: *Optioservus*, *Gonielmis*) and a piercing predator (Coleoptera: *Hydroporus*). The third factor (PC 3) was comprised solely of the large (2.5 cm) fish parasite *Argulus* (Crustacea: Branchiura) (Table 3).

Regression analysis revealed that all three factors were significantly related to ($P < 0.01$) abiotic variables (Table 4). Stage and discharge measures and current velocity explained 56% of the variation exhibited by PC 1 trophic groups. Trophic groups on PC 2 were positively related to stage and discharge, and negatively to specific conductance. These abiotic variables accounted for 41% of the total variance displayed by PC 2. Trophic PC 3 related positively to discharge ($r^2 = 0.26$).

DISCUSSION

The present study revealed two possible underlying mechanisms influencing macroinvertebrate drift in the lower Mississippi River. Organisms entering the drift did so to avoid invertebrate predators or unsuitable abiotic conditions.

TABLE 4.—Standard multiple regression of trophic principal components (PC) on abiotic factors. Only significant models and abiotic factors are included

Principal component	Abiotic variable	F value (P < 0.01)	R squared
Trophic PC 1 (gatherer, engulfer, filterer, detritovore)	+Stage	16.03	0.56
	+Discharge		
	–Current		
Trophic PC 2 (shredder, piercer, scraper)	+Conductivity	8.65	0.41
	+Stage		
	+Discharge		
Trophic PC 3 (parasite)	+Discharge	3.73	0.26

+; positively regressed; –: negatively regressed

Predator avoidance.—In the Principal Component analyses, each taxon and trophic factor had at least one predator highly loaded on it. This implies that some shared underlying mechanism had influenced all variables summarized by that component. Prey entering the drift to avoid invertebrate predators (which in turn enter the drift seeking prey) may be one potential mechanism. The high association of an invertebrate predator to several potential prey was surprising but not unexpected. Several studies have shown increased drift rates of potential prey organisms in the presence of predators (Corkum and Pointing, 1979; Corkum and Clifford, 1980; Walton, 1980). Indeed, invertebrate predators can influence both immigration and emigration (via drift) from substrate patches (Lancaster, 1990; Lancaster *et al.*, 1990).

Although Flecker (1992) theorized that drift was an evolutionary consequence of fish predation in small streams, Koetsier and Bryan (1992) suggested that this may not be the case in the lower Mississippi River. They found that, despite high turbidity and large sediment loads, diel periodicity of the macroinvertebrate drift occurred. They advanced the hypothesis that organisms entering the drift did so to avoid invertebrate predation. Tactile invertebrate predators, not dependent on visual location of prey, would not be hindered by high turbidity. Prey organisms may drift on contact by these predators (*e.g.*, Peckarsky, 1980; Walton, 1980; Walde and Davies, 1985). Our data support this contention. A predator, associated (highly loaded) with specific prey on each PCA factor, may cause the prey to enter the drift; and in turn, may enter the drift itself seeking these prey organisms.

Abiotic conditions.—Based on the variance explained by the independent variables in the regressions, stage level and river discharge appeared to be the overriding abiotic factors affecting the drift of taxonomic and trophic groups.

Associations of taxa.—Catastrophic drift (*sensu* Anderson and Lehmkühl, 1968) did not occur during peak stage level or discharge. Taxonomic groups prone to drift (*e.g.*, taxa whose linear combinations were associated with PC 1) were negatively related to stage level and discharge (Table 2). Similar relationships have been noted elsewhere. Several studies in both small streams (Minshall and Winger, 1968; Pearson and Franklin, 1968; LaPerriere, 1983) and large rivers (Conner and Bryan, 1976; Benke *et al.*, 1986; Obi and Conner, 1986) have reported inverse relationships occurring between drift and river discharge.

Two hypotheses have been proposed to explain this apparent contradiction in drift. First, if stream discharge increases but total invertebrate abundance drifting remains constant, the drift numbers per cubic unit would decrease (LaPerriere, 1983). This “dilution effect” assumes that stream drift is not the result of mechanical dislodgment of invertebrates from

the substrate by current. Another assumption of dilution is that a finite percentage of the benthic community will enter the drift regardless of discharge or current velocity. In the second hypothesis, as stage level rises, dry floodplain areas become inundated. Because many drifting invertebrates are rapid colonizers, this potentially 'new' habitat would be attractive to colonizing organisms in the drift. The net result would be a decrease in drift as stage level or discharge increases (Benke *et al.*, 1986). This second hypothesis assumes that drift is not a constant percentage of benthic populations. If drift is a density-dependent phenomenon, it may act as a "release valve" for excess benthic production (*see* Waters, 1961). As productivity from the benthos reaches a resource-limited plateau, competition for food or space would force out less competitive individuals. Thus, resource competition would be the driving force behind the colonization of new habitats.

The answer probably lies between these two extremes. In some stream systems, heavy scouring, as a harsh disturbance event, would prevent community build-up to the point where biotic interactions would regulate community structure. In more stable, benign streams, biotic interactions may greatly influence drift rate, density or composition (*sensu* Poff and Ward, 1989). Our study was not designed to determine where the invertebrate drift of the lower Mississippi River lies on this "harsh-benign" continuum. Although an extensive levee system borders the lower Mississippi River, water levels in spring overflow and usually rupture the levees, inundating floodplain areas (as was the case during our study period). If drift is the result of density-dependent behaviors (*see* Diamond, 1967), then drift rates would decrease as the inhabitable floodplain becomes available. These newly exposed floodplain areas may act as "sinks" removing some drifting invertebrates from the river. In southeastern, blackwater streams, the highest secondary production in riverine ecosystems occurs in the inundated floodplain (Smock *et al.*, 1985; Gladden and Smock, 1990; Smock *et al.*, 1992). The converse is also true. As stage level or discharge decreases, the floodplain acts as a "source" of drifting invertebrates. Indeed, Eckblad *et al.* (1984) found that the density of invertebrate drift flowing out of backwater channels was 10 times greater than drift density in the main channel of the upper Mississippi River.

Within the framework of control set by stage level and discharge, taxa and trophic factors were also influenced by pH, specific conductance and water temperature. Little is known concerning the effects of seasonal variations of pH and specific conductance on drift. Over short periods, sharp decreases in pH have been responsible for large drift increase in small streams (Hall *et al.*, 1980). However, due to the large buffering capacity in the lower Mississippi River, rapid shifts in pH do not occur. In the Mississippi River, adjustments in pH occur over decades (Bryan *et al.*, 1992) and would not be responsible for short-term, annual variations of invertebrate drift found in our study.

Little information exists on the effect of specific conductance (total dissolved solids) on macroinvertebrate drift. As a measure of micronutrient levels, specific conductance does correlate with high levels of benthic biomass and production (Kruger and Waters, 1983). If drift is the migration of excess benthic biomass/production (Waters, 1961), then the relationship between specific conductance and drift would be positive. The positive relationship between the drifting taxa components (PC 1, 3) and specific conductance in our study lends support to this notion. However, more research is needed before firm conclusions are drawn.

Water temperature may influence development and be related to drift in this way. Increasing temperature coincides with incubation of univoltine invertebrate species (\leq one life cycle per year). Waters (1972) noted that invertebrate drift from some streams was composed of younger stages. Most taxa frequently found in the drift of the lower Mississippi

River (PC taxa factors 1 and 3) were multivoltine species (> one life cycle per year) and may not be affected by temperature alone.

Trophic associations.—In our study, trophic components were significantly positively related to stage level and river discharge. During the spring, high densities of engulfing predators accounted for the strength of this relationship. In the lower Mississippi River, the engulfing predator group was composed of sessile (*Hydra*) and stalked colonial (*Cordylophora lacustris*) Hydroida. While heavy scouring, accompanying increased discharge, did not detrimentally affect insect taxa, it did affect hydroid population in two ways. First, heavy discharge disrupted the stalked colonies of *C. lacustris*, allowing fragments to be swept away by the current. Both Koetsier (1986), and Obi and Conner (1986) reported large numbers of *C. lacustris* fragments in the drift during high spring runoff. Second, water flushing out of sloughs and backwater areas had the potential to import large numbers of *Hydra* into the main channel of the lower Mississippi River. Eckblad *et al.* (1984) reported that 85% of the organisms exported from backwater areas to the main channel of the upper Mississippi River were *Hydra*. This may account for the apparent contradictory effects of stage level or discharge on trophic groups.

In synthesis, do the abiotic variables we measured cause macroinvertebrates to drift in the lower Mississippi River? At first it seems that macroinvertebrate drift should operate at a different temporal scale from the abiotic variables we measured. This may be true in small streams. However, too little is known about macroinvertebrate drift and its relationship to abiotic variables in large rivers. Because of the high specific heat of water, coupled with the large water volume and buffering capability of the lower Mississippi River, daily variations in abiotic variables are small (Bryan *et al.*, 1992). Little daily change in abiotic factors has been found at our sampling locations (Hartzog, 1975). Consequently, seasonal changes in abiotic factors may be more meaningful to drifting macroinvertebrates. This would be especially true if the drift community was a separate community from the benthos. Research in large, southeastern rivers by Benke *et al.* (1984, 1986) and Koetsier (1986) showed that species composition in the benthos greatly differed from that of the drift. Circumstantial evidence also supports this idea. For example, both McLay (1970) and Elliott (1971) concluded that the mean distance traveled by drifting, lotic invertebrates is approximately 11 m/night. However, their studies were restricted to small, low-order (≤ 3 rd order) streams. In large rivers (12th order), distances traveled by drifting macroinvertebrates are not known. Considering the width, depth, current velocity and discharge of the lower Mississippi River, 11 m probably is a vast underestimation of the true drifting distance. It is possible that in large rivers a permanent "planktonic" macroinvertebrate community may occur. This notion is based on Müller's (1974) 'colonization cycle' and strengthened by empirical work in arctic systems (Hershey *et al.*, 1993). In small streams, the downstream movement of an organism probably is relatively short, and the total displacement during a night is achieved in a saltatory fashion (Waters, 1972). In large rivers, macroinvertebrates shunted from tributaries, may spend their entire life cycles in the drift. New recruits entering from tributaries during times of high scouring discharge (within the tributaries themselves), would supplement or replace emerging individuals from this planktonic community.

This "planktonic" macroinvertebrate community could be a relic of the presettlement history of the river. While little information exists on presettlement conditions of the lower Mississippi River; its subsequent physical alteration may be similar to the pre-/and post-s snag removal condition of the Willamette River in Oregon (Sedell and Froggatt, 1984). The Mississippi River, like the Willamette River, may have been characterized by several braided channels clogged with large debris dams at close intervals. With the river in this state, an invertebrate drifting 10–15 m from one debris dam would have a high probability of en-

countering another. A genetically fixed behavioral trait (*i.e.*, drift) in macroinvertebrates may not have changed when the river was dredged and de-snagged for transportation and navigation.

River discharge and stage level are the predominant factors affecting macroinvertebrate drift in the lower Mississippi River. Contrary to what we expected, drifting invertebrate abundances decreased with increasing discharge and stage level. Two hypotheses, the dilution effect and colonization of new habitat, have been proposed to explain this relationship. Further, in large river systems we advanced the notion of a "planktonic" drift community, that may be a relic of the river's presettlement condition. Future research is needed to adequately test the validity of these theories.

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