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Diel, size-differential drift patterns of three macroinvertebrate species in the lower Mississippi River, Louisiana (USA)

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Abstract

We explored macroinvertebrate size-differential drift in the lower Mississippi River (a 9th order system). Because this river system is highly turbid, we hypothesized that visually-dependent vertebrate predators feeding on drifting organisms would be at a disadvantage. Thus, size-differential drift should not occur.

For one 24-hour period in both January and April, six drift nets were used to sample surface drift. Nets were emptied once every four hours. Individual intra-ocular distances of three macroinvertebrate species (*Hydropsyche orris*: Trichoptera, *Hexagenia limbata*: Ephemeroptera, *Macrobrachium ohione*: Crustacea) were measured. Percentages of size classes in the drift were determined. In both months, large individuals of *H. orris* and *H. limbata* were prevalent in the nocturnal but scarce in the diurnal drift. In January, large *M. ohione* drifted regardless of time. In April, large *M. ohione* predominated the nocturnal drift. Our results could not be attributed solely to vertebrate predator avoidance. Other mechanisms such as diel micro-habitat migration and current velocity may have accounted for the results.

Introduction

Invertebrate drift has intrigued lotic ecologists for more than three decades (see Waters 1972 and Müller 1974 for reviews). During this time, different schools of thought developed in an effort to explain this phenomenon. Drift of the organism was viewed as active entry into the water column, or as passive entry due to the erosional force of the water current (Waters, 1972). This mechanical debate continues in the literature (Allan *et al.*, 1986). However, it is clear that drift has a behavioral component (Minshall & Winger, 1968; Müller, 1974; Wiley & Kohler, 1984; Rader & Ward, 1990). One such component may be predator avoidance (Walton, 1980). Allan (1978) noted that comparatively large aquatic insects were predominant in the nocturnal and seldom found in the diurnal drift. He hypothesized that larger individuals were exposed to a higher predation risk from visually-oriented vertebrate predators during the day. Given this, they would avoid entry into the water column until after dark. Conversely, smaller organisms, at lower risk, should show no (or little) periodic drift patterns.

Vertebrate predators influencing the drift through size-selective predation has been confirmed in both laboratory (Andersson *et al.*, 1986) and field (Newman & Waters, 1984; Skinner, 1985) experiments. Invertebrate predators can also elicit a size-differential drift response in prey (Walton, 1980; Malmqvist & Sjöström, 1987).

However, some lotic systems may not favor visually-oriented predators. Systems with high bed-load movement or increased turbidity should hinder any type of predator relying on sight as a means of prey location. If visually-oriented predators are present in a high-turbidity system, would there still be a size-differential drift of macroinvertebrate prey?

The lower Mississippi River could be such a system. Nocturnal, bigeminus drift patterns were previously noted (Koetsier & Bryan, 1989). Rutherford & Bryan (1986) recorded monthly Secchi disc readings between 11 and 24 cm on the lower Mississippi River. Visually-oriented predators such as Black Crappie (*Pomoxis nigromaclatus*), White Crappie (*P. annularis*), Largemouth Bass (*Micropterus salmoides*) and other centrarchids are abundant in the river, especially near tributaries (Bryan *et al.*, 1973). Few published drift studies to date have been conducted in high-turbidity, low-visibility streams (but see Obi & Conner, 1986; Koetsier & Bryan, 1989). Therefore, the objective of our study was to determine if size-differential drift of macroinvertebrates does occur in a highly turbid system like the lower Mississippi river. This was accomplished by collecting 24 hr drift samples and measuring individuals of selected species.

Table 1. Physical parameters of the lower Mississippi River taken during the study period.

Parameter	January	April
Current velocity (cm sec^{-1})	60.0	57.0
Stage (m msl)	9.7	11.7
Discharge (× 10000 cfs)	615.0	820.0
Temperature (°C)	4.4	17.5
Secchi reading (cm)	21.0	11.0

Materials and methods

The study site was located on the lower Mississippi River (river km 437.2), a 9th order system, near W. Feliciana Parish, Louisiana (USA), approximately 40 km NW of Baton Rouge (91° 19′ W. longitude, 30° 45′ N. latitude). For one 24-hour period on 25–26 January and 26–27 April 1985 macroinvertebrate drift was sampled with six conical nets. The nets were 3 m in length, had mouth diameters of 0.25 m^2 and were constructed of 0.505 mm mesh. Each net was suspended a few centimeters below the water's surface using floats and anchors. Flow meters mounted in each net mouth provided for estimates of the volume of water filtered. The nets were located 20 m perpendicular to the shore (depth 15 m). To facilitate comparisons between replicates, each sample was standardized to number of drifting individuals/100 m^3. Physical parameters of the study site were measured at the end of each 24-hour period (Table 1). In January sunset was at 18 : 00 while sunrise occurred at 06 : 19. In April, sunset occurred at 18 : 35 and sunrise at 05 : 14. See Koetsier (1986) for a complete description of the study site.

In the laboratory, drift samples were examined using a dissecting microscope. Sorted organisms were preserved in 70% ethanol and later identified and enumerated. The intra-ocular distances of three macroinvertebrate species were measured using an ocular micrometer mounted in a dissecting microscope. Species were chosen based on functional feeding group and habitat preference: i) *Hydropsyche orris* (Insecta: O. Trichoptera) a net-spinning, filter-feeder predominantly found in sand-gravel areas, ii) *Hexagenia limbata* (Insecta: O. Ephemeroptera) a large, burrowing collector found in the sediment banks of the river, and iii) *Macrobrachium ohione* (Crustacea: O. Decapoda) a large free-ranging detrivore found in riverine snag habitats.

For each species, individuals were sorted into size categories. The percentage of individuals in a particular category collected from the drift during each 4-hour sampling period was calculated.

Results

Individuals of all three species appeared in the drift at all times (Table 2). During both months, large and small individuals of *Hydropsyche orris* were encountered during the night (Fig. 1). In January, 100% of the smallest size class drifted immediately after sunset, and the largest individuals drifted near midnight. In April, the largest and smallest individuals favored times between 18 : 00 and 22 : 00.

Hexagenia limbata drifted at night with little or no drift during the daylight hours (Fig. 2). In January, less than 5% of any size class drifted during the daylight hours. Large percentages drifted at night with the peak occurring between the hours 22 : 00 to 02 : 00. In April, this large peak occurred four hours earlier. However, over 50% of the middle size class individuals (1.5–1.9 mm intra-ocular distance) were encountered in the drift during the 14 : 00 to 18 : 00 hour period.

Macrobrachium ohione tended toward more uniform diel drift in the small to medium size classes (0.0–1.9 mm intra-ocular distance) during January (Fig. 3). However, 100% of the largest individuals were in the drift during the hours from 02 : 00 to 06 : 00. In April, a nocturnal drift of larger size classes was displayed; all size classes were depressed during April's daylight hours. Large size classes were found in the drift between

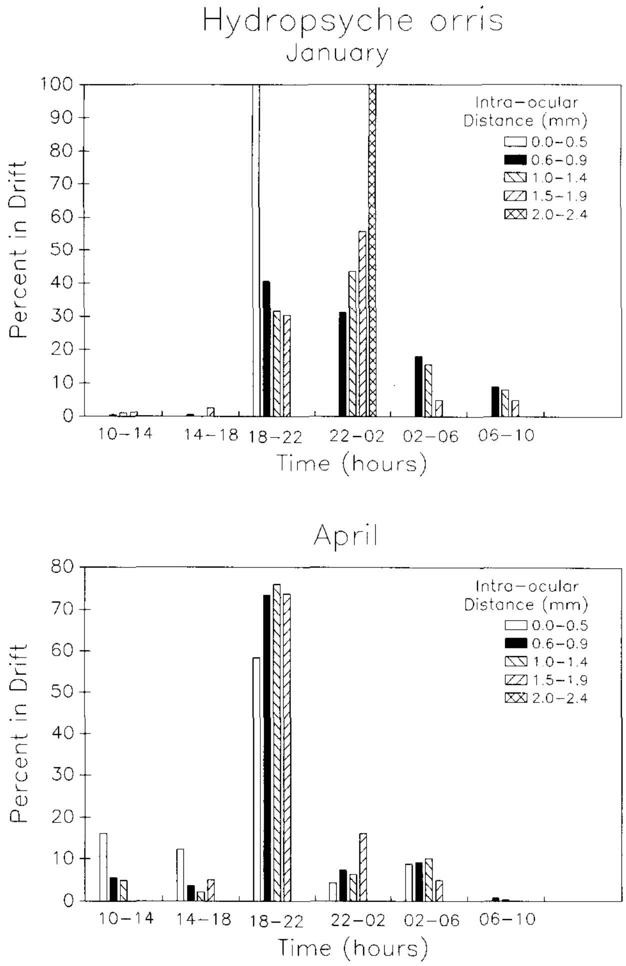

Fig. 1. Percentage of the various size classes of *Hydropsyche orris* in the diel drift.

Table 2. Total density (#/100 m³) of study species caught in drift nets during the collecting period.

Species	*Hydropsyche orris*		*Hexagenia limbata*		*Macrobrachium ohione*	
Month	Jan	Apr	Jan	Apr	Jan	Apr
Time (Hrs)						
10 : 00–14 : 00	0.72	23.51	0.63	1.43	2.00	2.50
14 : 00–18 : 00	0.71	5.53	0.71	30.57	1.90	2.50
18 : 00–22 : 00	30.69	267.59	29.87	124.01	5.25	18.90
22 : 00–02 : 00	33.77	5.74	93.17	18.79	6.82	9.01
02 : 00–06 : 00	10.81	34.31	47.57	14.87	4.05	9.51
06 : 00–10 : 00	6.00	1.82	1.34	0.71	2.70	2.50
Total	82.70	368.50	173.29	190.18	22.72	44.92

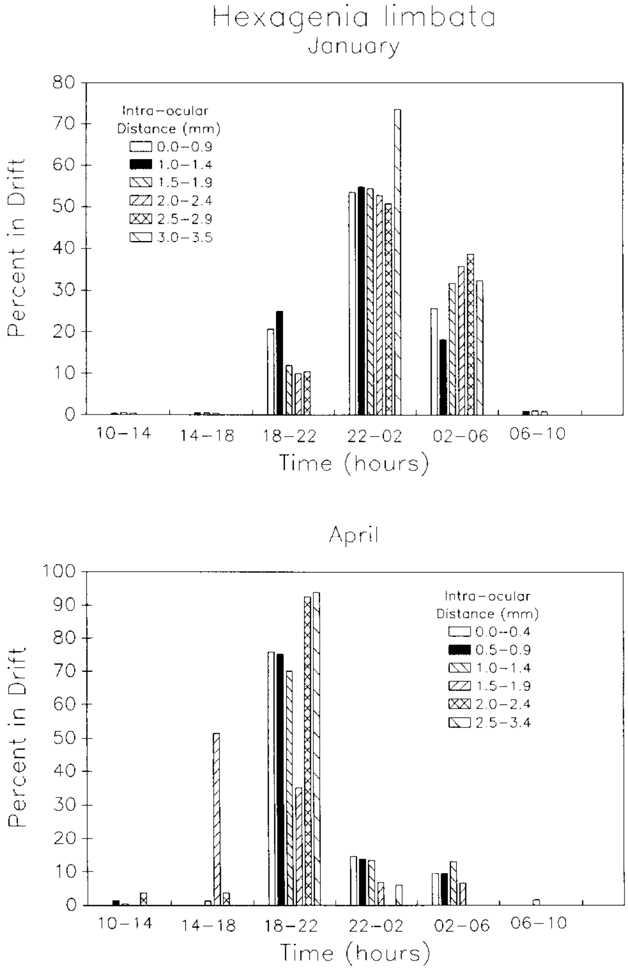

Fig. 2. Percentage of the various size classes of *Hexagenia limbata* in the diel drift.

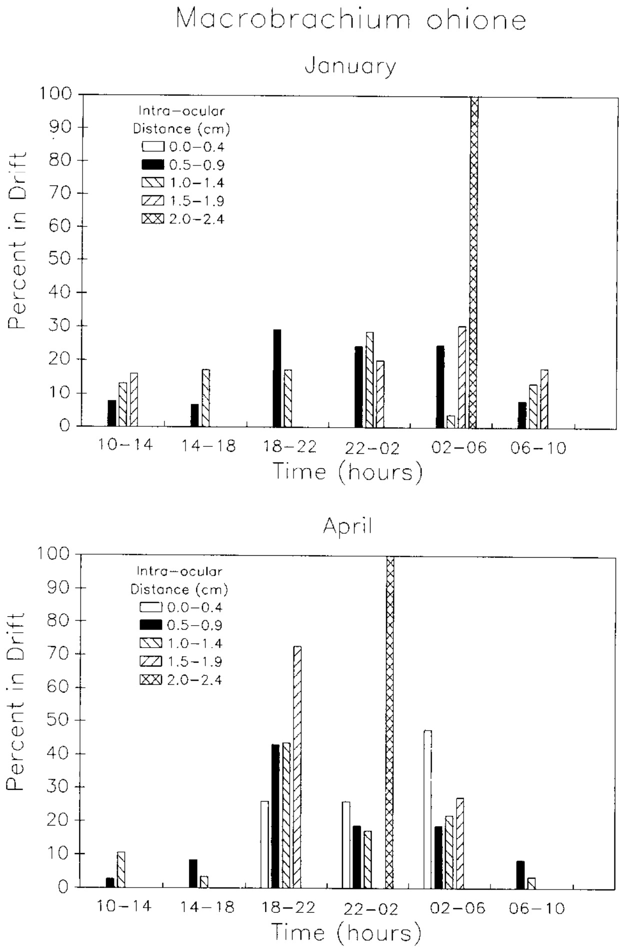

Fig. 3. Percentage of the various size classes of *Macrobrachium ohione* in the diel drift.

the hours of 18 : 00 and 02 : 00, with the largest size encountered near midnight.

Discussion

Allan's hypothesis (1978) that predator avoidance by larger-sized (or larger growth stage) invertebrates is responsible for size-differential drift, has been confirmed by other researchers in both laboratory and field settings. Newman & Waters (1984) reported that mean size *Gammarus pseudolimnaeus* found in the drift was greater at night than during the day. In their test stream, stomachs of the vertebrate predators always contained larger *G. pseudolimnaeus* individuals relative to those normally found in the benthos. Skinner (1985), testing Allan's hypothesis in a clear-water Idaho stream, found that *Baetis tricaudatus* (but not chironomid larvae) displayed size-differential drift. Andersson *et al.* (1986) found that in streams with sculpin, *Gammarus pulex* reduced its diurnal drift rate. However, the drift rate and the mean size *G. pulex* individuals increased in the nocturnal drift.

An alternative to invertebrate prey avoiding sight-dependent predators may be that predators are selectively removing larger invertebrate prey (Brooks & Dodson, 1965). Absence of a diel periodic cycle may result from a failure of fish to visually detect prey organisms and not prey suppression due to increased risk (Zaret, 1972; Ware, 1973).

If size-differential invertebrate drift results from avoidance of visually-oriented predators, any factor hindering predators' sight should decrease the risk of predation. If this risk is lowered, invertebrate prey of all sizes should drift irrespective of the photoperiod. One factor that may hinder visually-dependent predators is high turbidity. The lower Mississippi River is a highly turbid system. Yearly Secchi disc readings range from 11 cm to 24 cm (Rutherford & Bryan, 1986). Yet we found a size-differential invertebrate drift cycle in three prominent invertebrates.

However, *M. ohione* displayed a fairly even diel distribution of size classes in January (with exception of large individuals 2.0–2.4 cm intra-ocular distance occurring in the drift shortly before dawn). This would be expected from a relatively larger-bodied taxon released from visually-dependent predators, as Allan (1978) predicted.

Although size-differential drift occurs in clear lotic systems, alternative mechanisms need to be explored in highly turbid systems. We propose two possible explanations that may account specifically for our data from the lower Mississippi River, and generally for other exceptions to the predator-avoidance hypothesis.

Possibly some drifting organisms in the lower Mississippi River were derived from the connecting black-water bayous. Indeed, several species of Odonata not usually found in rivers were collected in the drift samples (Koetsier, 1986). Invertebrates in these clear bayous would still be subject to size-selective predation. The size-differential drift pattern as a predator avoidance strategy may be genetically fixed in these organisms. This would not change over a short generation time; the comparatively sudden release from predation in the turbid receiving stream would not affect their drift cycle (Allan, 1978).

However, size-differential drift may be a consequence of diel migration and current velocity. Many aquatic insects display a nocturnal migration from the bottom to the top of stream substrate (Waters, 1972). This could be a response to nocturnal decreases of dissolved oxygen in the substratum (Wiley & Kohler, 1980) or to invertebrate predator avoidance (Malmqvist & Sjöström, 1987; Soluk & Collins, 1988). Larger-bodied invertebrates, migrating to the top substrate at night, would have a higher probability of being dislodged by the current than small-bodied ones (Kovalak, 1979), hence size-differential drift.

In summary, invertebrate drift in the lower Mississippi River displays a size-differential pattern: larger individuals drift at night while small ones drift both night and day. This correlates with Allan's hypothesis of predator avoidance (Alan, 1978). However, due to the high turbidity of the system, visually-dependent predators should be handicapped. Alternative explanations include: i) genetic fixation of 'drift' traits in immigrants coming into the river from surrounding bayous and/or ii) the effect of diel microhabitat migration coupled with the erosional force of the water current.

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