Vertical Distribution in the Water Column of Drifting Stream Macroinvertebrates

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ABSTRACT

We examined the macroinvertebrate composition and drift density in a Mediterranean lotic system, the Erro River (northwestern Italy). Drift density and composition were sampled for one year at three levels of the water column; temperature and flow velocity were also measured. We found that drift density was generally highest near the bottom. We also noticed that various taxa tended to drift at preferential levels of the water column, with 41.4 % of taxa mainly at the bottom level and 31.0 % mainly at the top. Drift density decreased with increasing water temperature. Both taxa richness and macroinvertebrate abundance in the drift were positively associated with natural riverbed richness and abundance.

INTRODUCTION

Since the early works of Müller (1954) and Waters (1961), the "downstream transport of aquatic organisms in the current" has become a central topic in freshwater science. It is well known that benthic macroinvertebrates are in a state of continuous redistribution (Townsend and Hildrew 1976) and drift is a main component of this process, which also involves upstream movements, aerial ovideposition by adult insects, and vertical movements through the substrate (Müller 1982).

Drift is not simply passive transport caused by the drag force of flow but a complex mechanism involving behavioral, hydrological, seasonal, and taxonomical aspects (Mackay 1992). It is an important element in lotic system ecology, constituting a prime mechanism of dispersion of benthic macroinvertebrates responding to competition for space (Hildrew 1996) and food (Hinterleitner-Anderson et al. 1992) or escaping from predators (Peckarsky 1980) or unfavorable environmental conditions (Wallace et al., 1989, Wiederhohn 1984). Four categories of drift are commonly considered (Brittain and Eikeland 1988) – catastrophic, associated with hydrological or chemical disturbances; behavioral, due to the general activity of stream invertebrates; distributional, due to dispersal exigencies; and constant, due to accidental dislodgement from the substrate. Stream macroinvertebrates have great dispersal capabilities, and drift is a key element in the colonization cycle of freshwater insects (Müller 1982).

An increasing amount of data on drift has accumulated in recent decades (Brittain and Eikeland 1988). We now have detailed information about it in northern European (Huhta et al. 2000), Nearctic (Koetsier 1989), and tropical (Ramirez and Pringle 2001) lotic systems, but there are few data concerning Mediterranean streams. Studies of drift have greatly benefited from new techniques such as stable isotope (Hershey et al. 1993) and genetic analyses (Schmidt et al. 1995, Bunn and Hughes 1997). Many studies have shown the importance of current velocity (Bird and Hynes 1981), water chemistry (Wiley and Kohler 1980), season (Brittain and Eikeland 1988), diel periodicity (Hutha et al. 2000), behavior, and life cycles (Benke et al. 1991), but only a few studies have focused on the vertical distribution of animals in the water column. Waters (1965) conducted an early study of drift dispersal in two species of macroinvertebrates, the mayfly *Baetis vagans* and the scud *Gammarus limnaeus*. He found that both species were almost uniformly distributed in the first 15-25 cm of the water column and realized that organisms did not enter the drift nets only as a result of activity along the stream bottom. Brittain and Eikeland (1988) also reported that *Baetis* sp. tended to drift near the surface.

The aims of our study were (a) to provide data about drift composition and density in a northwestern Italian stream, analyzing the importance of the considerable seasonal temperature variation in the Mediterranean area, and (b) to assess if macroinvertebrate abundance and taxonomic composition in drift varies among different levels of the water column.

METHODS AND MATERIALS

Experiments were carried out in the Erro River, northwestern Italy (44°38' N, 8°25' E). To assess the density and vertical distribution of drift, we used a custom-made drift net. Following Brittain and Eikeland (1988) and Koetsier and Bryan (1995), we used a single device at the station. This apparatus had three distinct openings, each 37 cm wide and 16 cm high. The bottom mouth collected invertebrates drifting from 0 to 16 cm, the middle mouth from 16 to 32 cm, and the top mouth from 32 to 48 cm. Mesh size was 250 µm.

We sampled on 51 days from March 2002 to March 2003; each time, the net was left in place in the same position for two hours, and we conducted our experiments at the same time, starting at 0900-0930 hours. Water column depth was quite constant during the study (50-55 cm). We measured the current velocity with an Eijkelkamp 13.14 current-meter and water temperature with an Eijkelkamp 18.28 portable instrument. Drift density was expressed as the mean number of drifting individuals/m^3.

To quantify the macroinvertebrate community structure on the natural river bottom, we collected Surber samples on the same days that we placed the drift nets. Surber samples were collected in a riffle 10 m upstream from the nets, using a 0.25 m^2 sampler with a 250 µm mesh, when the nets were not in the water.

In the laboratory, the macroinvertebrates collected in each drift or Surber sample were classified, counted, and preserved in ethyl alcohol (70°). All organisms were identified to the genus level, except for Trichoptera and Diptera, which were sorted to the family level, and Hydracarina, which were sorted as a single taxonomic group. Each taxon was also assigned to a functional movement group (swimmers, crawlers, truly benthic), according to Merritt and Cummins (1996).

For the statistical analysis, we considered taxa richness (S), total drift density (ind./m^3), and density of each taxon (ind./m^3). The mean values for the different vertical strata were compared by ANOVA of log-transformed data. The vertical stratum preferences of individual taxa were evaluated using indicator species analysis computed with INDVAL 2.0 software (Dufrêne 1998). Indicator species analysis is a randomization-based test that compares the relative abundance and relative frequency of occurrence of taxa to find indicator assemblages characterizing groups of samples. A taxon's affinity for a sampling group is expressed as a percentage (Dufrêne and Legendre 1997).

RESULTS

Total drift composition and relationships between abiotic factors and density

All total we classified 3,394 drifting organisms belonging to 28 taxa, and 15,351 organisms collected in the riverbed belonging to 45 taxa (Table 1). Five taxa (Chironomidae, Hydracarina, Elmidae, *Baetis* sp. and Simuliidae) constituted 90% of the total invertebrate number in the drift. Chironomids were the dominant drifting invertebrates at all three levels (bottom = 78.7%, middle = 68.6%, top = 67.6%) and were also the most abundant in the riverbed (31.5% of sampled invertebrates).

Table 1. Taxonomic list of invertebrates found in the riverbed and invertebrates collected in the drift, with relative abundances at different depths.

Taxon	Natural riverbed	Water column Bottom	Water column Middle	Water column Top	Indicator analysis [a]
Plecoptera					
Chloroperla sp.	0.30	0.15	-	-	2.00 B
Protonemura sp.	1.20	-	0.15	-	2.04 M
Leuctra sp.	5.20	0.45	0.21	-	4.98 B
Capnia sp.	0.90	-	0.57	0.68	2.13 T
Brachyptera sp.	1.20	1.04	1.05	1.07	5.87 T
Ephemeroptera					
Ecdyonurus sp.	4.30	-	0.15	-	2.04 M
Habroleptoides sp.	0.80	0.15	0.15	-	1.03 M
Serratella ignita	3.20	0.45	-	-	6.00 B
Habrophlebia sp.	0.70	0.30	0.33	0.20	1.59 M
Potamanthus luteus	0.15	0.59	0.19	0.10	1.18 B
Electrogena sp.	0.60	0.15	0.19	-	3.98 M
Caenis sp.	1.50	0.15	1.53	1.27	10.43 M
Baetis sp.	5.90	2.23	4.80	6.50	16.48 T
Trichoptera					
Rhyacophilidae	0.80	-	-	0.10	2.00 T
Philopotamidae	0.70	0.10	-	-	11.25 B
Limnephilidae	2.50	0.10	-	-	11.25 B
Hydropsychidae	2.90	0.15	0.19	0.98	5.54 T
Diptera					
Limoniidae	0.60	-	-	0.10	2.00 T
Ceratopogonidae	0.90	0.30	0.19	0.10	10.46 B
Simuliidae	3.50	2.38	3.15	4.10	13.79 T
Chironomidae	31.5	78.75	68.61	67.58	24.98 B
Hemiptera					
Micronecta sp.	0.30	0.89	0.86	1.46	7.17 B
Coleoptera					
Helodidae	0.7	0.15	0.33	-	2.98 M
Dytiscidae	0.3	0.45	0.75	0.88	4.30 T
Elminthidae	1.4	2.37	7.44	4.49	17.53 M
Odonata					
Onychogomphus sp.	0.5	0.15	-	-	4.00 B
Oligochaeta					
Lumbricidae	1.1	0.15	0.10	0.10	1.99 B
Naididae	0.9	1.04	2.67	2.73	10.32 T
Arachnida					
Hydracarina	8.8	7.28	6.39	7.22	43.05 B
Other taxa [b]	16.2	-	-	-	
Total N	15351	1313	1056	1025	

[a] The column shows the indicator value and the water level preferred by each taxon; T = top, M = middle, B = bottom.

[b] Taxa found only in natural riverbed: *Amphinemura* sp., *Ancylus fluviatilis*, Athericidae, *Boyeria irene*, *Calopteryx* sp., Driopidae, *Dugesia* sp., *Ephemera* sp., Hydraenidae, *Isoperla* sp., Limnephilidae, Lumbriculidae, *Lymnaea* sp., *Nemoura* sp., Polycentropodidae, Stratiomydae, Tipulidae.

At our study site, drift density was significantly associated with water temperature ($r = -0.46$, $P < 0.001$); the density was minimal in high summer temperatures (Fig. 1).

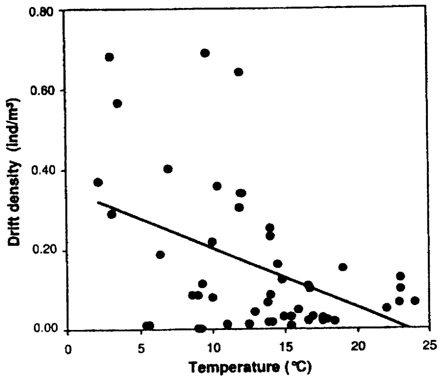

Figure 1. Relationship between total drift density and temperature.

Total drift density was significantly related to natural riverbed density ($r = 0.574$, $P < 0.001$); a higher presence on the river bottom was associated with a larger number of drifting organisms (Fig. 2). Furthermore, the taxa richness of drift was positively correlated with the richness of macroinvertebrates in the riverbed ($r = 0.477$, $P = 0.008$).

Interestingly, the faunal composition of drift differed from that of the riverbed assemblages. Seventeen taxa were not found in the drift, even though they represented 16.2% of total individuals in the substratum (Table 1).

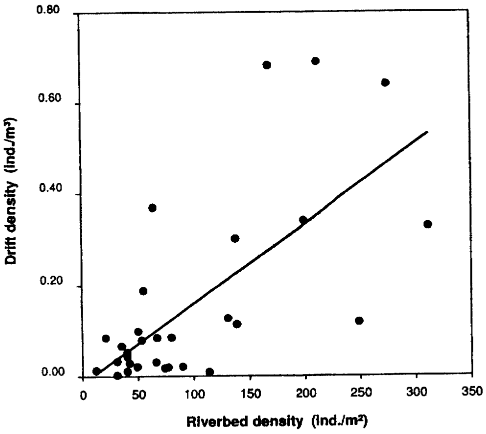

Figure 2. Relationship between total drift density and riverbed density of macroinvertebrates.

Drift stratification

When we considered daily taxa richness and invertebrate densities of drift in the different strata for all sampling dates, we noticed a bottom-top decrease. On a daily basis, taxonomic richness was significantly higher (ANOVA $F_{2,50,100} = 4.37$, $P < 0.015$) in the bottom samples (mean: 4.21 taxa ± 0.35 s.e.) than in the middle (3.41 ± 0.32) and top samples (3.51 ± 0.32).

The density of invertebrates in the drift also significantly (ANOVA $F_{2,50,100}$ = 13.5, P < 0.001) decreased from the bottom level to the surface (bottom mean = 0.177 ± 0.029 ind./m3, middle = 0.145 ± 0.025, and top = 0.139 ± 0.024) (Fig. 3).

The indicator species analysis used to assess vertical stratum preferences of taxa revealed interesting differences (Table 1). Most taxa (41.4%) drifted preferentially near the stream bed, while others showed a tendency to drift in the top (31.0%) and middle strata (27.6% of taxa).

There were behavioral differences in the taxonomic composition of invertebrates found at the three water levels. Swimmers were significantly (X^2_4 = 35.9, P < 0.001) more abundant in the top level of the water column, while benthic and crawler invertebrates were more abundant in the middle and bottom strata (Fig. 4).

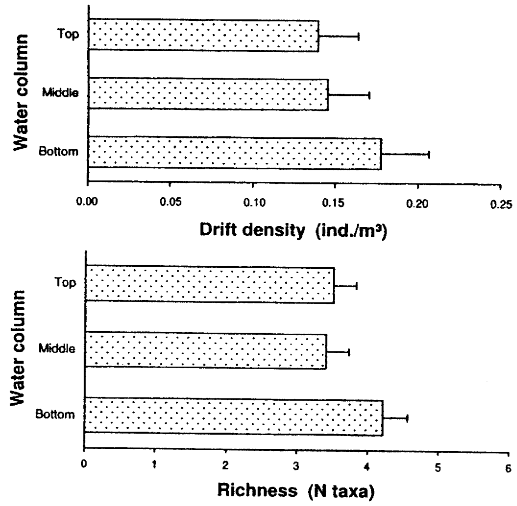

Figure 3. Vertical distribution of mean individual abundance and mean taxa richness in the water column, on a sample day basis.

DISCUSSION

Since Waters (1961), many studies have interpreted drift as a density-dependent process, even though recent studies have shown that movements of highly mobile animals are independent of natural riverbed abundance (Humphries 2002). Our results confirm previous findings that drift could be a constant proportion of benthic density (Hildebrand 1974) and that the abundance and taxonomic richness of drift are density-dependent. Furthermore, although it is well known that drifting invertebrates derive from the benthos, we found that some of the natural riverbed taxa had a greater propensity to drift than others, while several taxa rarely drifted.

Chironomids were the most abundant organisms in the drift, as found in other temperate fresh waters (Allan 1995, Lencioni et al. 2001). Baetidae and Caenidae were also very abundant in drift, while Heptageniidae, some Diptera, Tricladida, Mollusca and others were rare or absent.

Some studies reported that drift was usually minimal during winter in temperate regions (Clifford 1972, Brittain and Eikeland 1988). In contrast, we found less drift in summer. It is conceivable that the invertebrates inhabiting Mediterranean rivers and streams have adapted to life cycles that minimize the costs and risks of the hottest season. In our study area, summer is the most unfavorable period, with high water temperatures and droughts (Acquarone et al. 2003). Therefore, because of its behavioral and auto-ecological aspects, summer drift is an ineffective strategy for freshwater organisms. It would be better to stay still in favorable environments or to use other strategies to overcome the critical period (diapause, hyporrheic refuge, etc.; Lake 2003).

We recorded highest drift densities near the bottom. It is conceivable that drifting taxa have evolved behavioral mechanisms and strategies to stay near the riverbed. Stratification in the water column was linked to behavioral differences among taxa. Active swimmers, such as Baetidae and Dityscidae, were mostly found near the surface; crawlers, such as Hydracarina and Ceratopogonidae, tended to drift near the stream bottom; permanently attached or truly benthic taxa, such as Tipulidae and Tricladida, were not found in the drift. Our results confirm that drift patterns of stream macroinvertebrates can be specifically conditioned by behavior or feeding mechanisms; therefore, in drift studies, organisms could be grouped according to their behavioral characteristics (Corkum 1978, Brittain and Eikeland 1988).

Many studies have reported that drift is the primary means of redistribution of benthic organisms in streams (Minshall and Petersen 1985, Mackay 1992), and recolonization studies in running water habitats have shown that animals promptly reappear in affected areas (Williams 1980). In particular, a recent study in northwestern Italy showed that downstream displacement is the main direction of colonization (Fenoglio et al. 2002). Rapid colonization and displacement of animals between habitat patches on many scales appear to be key components of the dynamics of lotic systems (Speirs and Gurney 2001). Understanding the mechanisms and patterns of macroinvertebrate movements is important in explaining the structure and resilience of benthic communities.

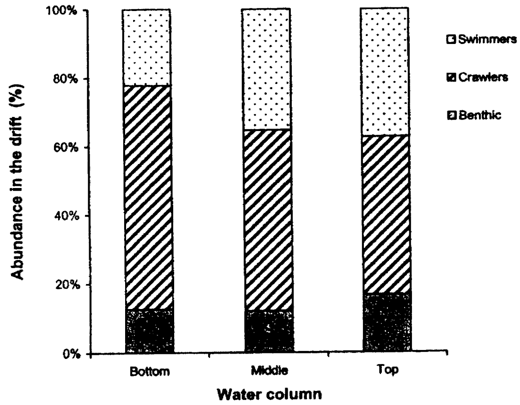

Figure 4. Distribution of swimmers, crawlers, and benthic invertebrates at different levels of the water column.

ACKNOWLEDGEMENTS

We thank P. Agosta for help in the field work, F. Bo for the drift net construction, and G. Malacarne for comments on the manuscript. Suggestions of the editor and two referees greatly improved our manuscript. This study was supported by Italian MURST grants.

LITERATURE CITED

Acquarone, C., M. Cucco, and G. Malacarne. 2003. Reproduction of the Crag Martin in relation to weather and colony size. Ornis Fennica 80: 79-85.

Allan, J.D. 1995. Stream ecology. Structure and function of running waters. Chapman & Hall, London: 388 pp.

Benke, A.C., K.A. Parsons, and S.M. Dhars. 1991. Population and community patterns of

invertebrate drift in an unregulated coastal plain river. Canadian Journal of Fisheries and Aquatic Sciences 48:811-823.
Bird, G.A. and H.B.N. Hynes. 1981. Movement of immature aquatic insects in a lotic habitat. Hydrobiologia 77:103–112.
Brittain, J.E. and T.J. Eikeland. 1988. Invertebrate drift - A review. Hydrobiologia 166: 77-93.
Bunn, S.E. and J.M. Hughes. 1997. Dispersal and recruitment in streams: evidence from genetic studies. Journal of the North American Benthological Society 16:338-346.
Clifford, H.F. 1972. Drift of invertebrates in an intermittent stream draining marshy terrain of west-central Alberta. Canadian Journal of Fisheries and Aquatic Sciences 50:985 - 991.
Corkum, L.D. 1978. The influence of density and behavioural type on the active entry of two mayfly species (Ephemeroptera) into the water column. Canadian Journal of Fisheries and Aquatic Sciences 56:1201-1206.
Dufrêne, M. 1998. IndVal or how to identify indicator species of a sample typology? Version 2.0. User's guide and application published at: http://mrw.wallonie.be/dgrne/sibw/outils/indval/home.html.
Dufrêne, M., and P. Legendre 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecology and Monography 67:345-366.
Fenoglio, S., P. Agosta, T. Bo, and M. Cucco. 2002. Field experiments on colonization and movements of stream invertebrates in an Apennine river (Visone, NW Italy). Hydrobiologia 474:125-130.
Hershey, A.E., J. Pastor, B.J. Petersen, and G.W. King. 1993. Stable isotopes resolve the drift paradox for *Baetis* mayflies in an arctic river. Ecology 74:2315-2325.
Hildebrand, S.G. 1974. The relation of drift to benthos density and food level in an artificial stream. Limnology and Oceanography 19:951-957.
Hildrew, A.G. 1996. Whole river ecology: spatial scale and heterogeneity in the ecology of running waters. Archiv für Hydrobiologie 10 324-343.
Hinterleitner-Anderson, D., A. E. Hershey, and J.A. Schuldt. 1992. The effects of river fertilization on mayfly (*Baetis* sp.) drift patterns and population density in an arctic river. Hydrobiologia 240:247-258.
Humphries, S. 2002. Dispersal in drift-prone macroinvertebrates: a case for density-independence. Freshwater Biology 47:921-929.
Hutha, A., T. Muotka, and P. Tikkanen. 2000. Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. Freshwater Biology 45:33-42.
Koetsier, P. 1989. The effects of fish predation and algal biomass on insect community structure in an Idaho stream. Journal of Freshwater Ecology 5:187-196.
Koetsier, P. and C.F. Bryan. 1995. Effects of abiotic factors on macroinvertebrate drift in the lower Mississippi River, Louisiana (USA). American Midland Naturalist 134:63-74.
Lake, P.S. 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48:1161-1172.
Lencioni, V., B. Maiolini, S. Zuccati, and F. Corradini. 2002. Zoobenthos drift in two high mountain streams in the de la Mare glacial system (Stelvio National Park, Trentino, Italy). Acta Biologica 78:49-57.
Mackay, R.J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 49:617-628.
Merritt, R.W. and K.W. Cummins. 1996. An introduction to the aquatic insects of North America, Kendall Hunt, Dubuque, IO.
Minshall, G.W. and R.C. Petersen. 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. Archiv für Hydrobiologie 104:49-76.
Müller, K. 1954. Investigations on the organic drift in north Swedish stream. Rep. Inst. Freshwater Res. Drottiningholm 35:133–148.
Müller, K. 1982. The colonization cycle of freshwater insects. Oecologia 52: 202-207.

Peckarsky, B.L. 1980. Predator – prey interactions between stoneflies and mayflies: behavioural observations. Ecology 61:932-943.

Ramírez, A. and C.M. Pringle. 2001. Spatial and temporal patterns of invertebrate drift in streams draining a Neotropical landscape. Freshwater Biology 46:47-62.

Schmidt, S.K., J.M. Hughes, and S.E. Bunn. 1995. Gene flow among conspecific populations of *Baetis* sp. (Ephemeroptera) - adult flight and larval drift. Journal of the North American Benthological Society 14:147-157.

Speirs, D.C. and W.S. Gurney. 2001. Population persistence in rivers and estuaries. Ecology 82:1219-1237.

Townsend, C.R. and A.G. Hildrew. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. Journal of Animal Ecology 45:759-772.

Wallace, J.B., G.J. Lughtarth, T.F. Cuffney and G.A. Schurr. 1989. The impact of repeated insecticidal treatments on drift and benthos of a headwater stream. Hydrobiologia 179:13-147.

Waters, T.F. 1961. Standing crop and drift of stream bottom organisms. Ecology 42:352-357.

Waters, T.F. 1965. Interpretation of invertebrate drift in streams. Ecology 46:327-334.

Wiederhohn, T. 1984. Responses of aquatic insects to environmental pollution. Pages 508-557 in: The Ecology of Aquatic Insects. (V.S. Resh and D.M. Rosenberg, eds.). Praeger Publisher, New York.

Wiley, M.J. and S.L. Kohler. 1980. Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. Canadian Journal of Zoology 58:618-622.

Williams, D.D. 1980. Temporal patterns in recolonization of stream benthos. Archiv für Hydrobiologie 90:56-74.

Received: 3 November 2003

Accepted: 5 March 2004