Relationships between size of stream insects and current velocity

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Size frequency distributions and dry weight – head width relationships for six insect species from two habitats with differing current velocities in the Pigeon River, Michigan, were compared. Early in their growth cycles, *Ephemerella subvaria, Ephemerella lata, Rhithrogena jejuna*, and *Glossosoma nigrior* generally were larger at the slow station, but near the end of the growth cycles they generally were larger at the fast station. For *Paraleptophlebia mollis*, early in the growth cycle size differences between stations were small but near the end of the growth cycles nymphs were larger at the fast station, whereas nymphs of *Ephemerella deficiens* were slightly larger at the slow station throughout the growth cycle. Larger size at the slow station probably was due to differential growth whereas larger size at the fast station probably was due to differential habitat selection controlled by oxygen requirements.

There were no significant differences in dry weight – head width relationships between habitats or between sexes. Sex ratios generally were similar at the two stations and did not deviate appreciably from 50:50.

The life history of each species is briefly described.

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Une étude sur six espèces d'insects provenant de deux habitats à vitesses de courant différentes de la rivière Pigeon au Michigan a permis d'établir des comparaisons entre les distributions de fréquence des tailles et les relations poids sec – largeur de la tête. Au début de la croissance, *Ephemerella subvaria, Ephemerella lata, Rhithrogena jejuna* et *Glossosoma nigrior* sont de taille plus importante à la station où l'écoulement est le plus lent, mais vers la fin de la croissance, ces espèces ont une taille plus élevée en eau rapide. Chez *Paraleptophlebia mollis*, les différences de taille entre les larves de deux stations sont minimes au début de la croissance, mais vers la fin, les larves sont plus grosses en eau rapide; les larves d'*E. deficiens* sont légèrement plus grosses en eau calme, en tous temps. La taille plus élevée en eau à écoulement lent vient probablement d'une croissance différentielle, alors qu'en eau rapide, elle est due sans doute à la sélection différentielle d'habitat, elle-même régie par les besoins en oxygène.

Il n'y a pas de différence significative dans les relations poids sec – largeur de la tête entre les habitats ou les sexes. Les rapports des sexes se comparent généralement aux deux stations et sont toujours autour de 50:50.

On trouvera en outre, dans cet article, une brève description du cycle biologique de chacune des espèces étudiées.

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Introduction

Little is known about the relationship between the size of stream organisms and current velocity in habitats where they are found. Allen (1951) reported that *Helicopsyche* from faster current regimes were larger than those from slower current regimes. Starmühlner (1953) reported that *Limnaea pereger* was smaller and *Ancylus fluviatilis* was taller in faster current regimes. Hynes (1970) suggested these differences may be due to current-related differences in growth rate or to size-related current preferences.

Size-related current preferences in insects may result from decreases in the surface area to volume ratio with increases in body size. Most aquatic insects depend on passive diffusion of oxygen through the body surface or gills to satisfy oxygen requirements (Hynes 1970). Consequently, larger individuals which have a lower surface area to volume ratio have greater difficulty satisfying oxygen requirements (see reference to Istenic by Hynes (1970)). Large nymphs and larvae may actively select fast current regimes because current renews water at respiratory surfaces, thereby increasing the rate of oxygen uptake (Hynes 1970).

If insects use current to facilitate oxygen uptake, one would predict current-related differences in weight–size relationships and sexual differences in current selection. There is considerable variation in weight of stream insects relative to body size. Individuals of a given size which weigh more have a lower surface area to volume ratio and, therefore, should select faster currents. Sexual differences in

current selection would be predicted from sexual differences in oxygen consumption rate (reviewed by Knight and Gaufin (1966)) and (or) size (Harper and Magnin 1969; Harper and Hynes 1972; Harper 1973a, 1973b).

This study was undertaken to determine the occurrence of current-related size differences in *Ephemerella subvaria*, *Ephemerella deficiens*, *Ephemerella lata*, *Paraleptophlebia mollis*, *Rhithrogena jejuna*, and *Glossosoma nigrior*, insects common to north temperate streams. The specific objectives were to compare: (1) size frequency distribution (SFD) of nymphs and larvae from two habitats with differing current velocities, (2) SFD of males and females in each habitat, (3) dry weight – head width relationships for each species from the two habitats, (4) dry weight – head width relationships for males and females, and (5) sex ratios in the two habitats. The life history of each species is also described.

Description of Study Area

This study was conducted in the Pigeon River, Otsego County, Michigan, in the vicinity of the Pigeon River Trout Research Station. For a general description of the Pigeon River, see Kovalak (1976). During this study, water temperatures ranged between a winter low of 0°C and a summer high of 23°C (Fig. 1). Frazil ice occurred periodically between December and March.

Two sampling stations were selected for differences in mean current velocity (Fig. 1). Station 1 (fast) was a riffle where mean current velocity was never less than 70 cm/s. Stream width was about 10.2 m and mean water depth varied between 10 and 35 cm depending on discharge. The stream bottom was primarily large pebble and cobble with very small amounts of coarse gravel. Station 2 (slow) was a run, about 50 m downstream of station 1, where mean current velocity rarely exceeded 50 cm/s. Stream width was 13.6 m and mean water depth ranged between 60 and 85 cm depending on discharge. The stream bottom was composed of pebble and cobble mixed with a larger amount of gravel and sand.

Methods

Kick samples were collected at the two stations at 4-week intervals between June 1972 and June 1973. A triangular dip net (471 μm mesh) was held perpendicular to direction of stream flow while an area approximately 0.10 m² was thoroughly disturbed with the foot. On each date, at each station, five kick samples were collected in transect across the stream. The five samples were combined and preserved in the field with 10% formalin. At each sampling point, current velocity was measured 5 cm above the bottom with a Gurley pygmy current meter.

Mayflies were separated from inorganic sediments by sugar flotation (Anderson 1959) and larvae of *G. nigrior* were sorted from the remaining sediments. Mayflies were sorted from organic debris under 10 × magnification, and all specimens were stored in 70% ethanol until analyzed.

Head capsule width across the eyes was measured to the nearest 0.05 mm for mayflies and to the nearest 0.025 mm for *G. nigrior*. Head width was used to discriminate instars of *G. nigrior* but no attempt was made to recognize instars of mayflies. The SFD of nymphs and larvae at the fast and slow stations and of males and females were compared using the Kolmogorov–Smirnov *t* (Conover 1972).

After measuring, individuals with all appendages intact were dried at 60°C for 24 h, cooled to room temperature, and weighed to the nearest 0.01 mg. For small individuals, groups of up to five individuals were weighed together and the mean weight recorded. Least squares regressions were computed for the relationship between dry weight and head width for all species and for the relationship between case weight and head width of *G. nigrior*.

The sex of small male mayflies was determined from medial eye development whereas the sex of large males was determined from the morphology of the ninth sternite.

Results

Life Histories

The earliest instars of all species were underrepresented in samples collected for this study because of the coarse mesh (471 μm) net used. Therefore, earliest stages of life histories were deduced from samples of epilithic fauna collected in 1973–1974 with a finer mesh (156 μm) net.

Eclosion of *E. subvaria* McDunnough (Fig. 2) extended from early July to late August. This period of delayed hatching may be an artifact attributable to inclusion of early instar *Ephemerella invaria* (Walker) which are indistinguishable from early instar *E. subvaria*. In the Pigeon River the life cycle of *E. invaria* lags 2–4 weeks behind that of *E. subvaria*.

Ephemerella subvaria grew rapidly between August and December. Growth ceased between December and March but resumed for a short period in late March and early April. Waters and Crawford (1973) reported exponential growth between September and May for *E. subvaria* in a Minnesota stream. Emergence from the Pigeon River probably began in late April and continued through
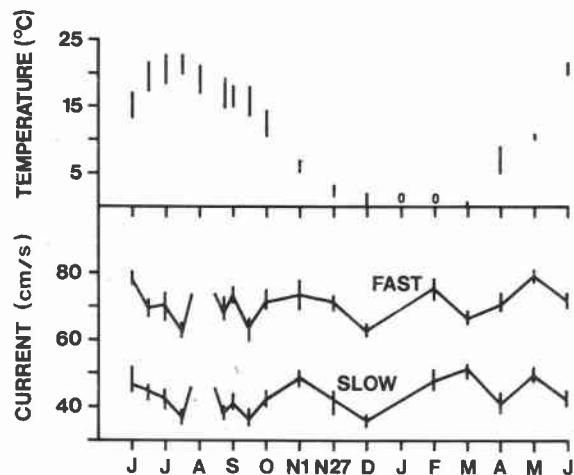

FIG. 1. Daily range of water temperatures and mean current velocities (vertical lines indicate range of values) at the two study sites.
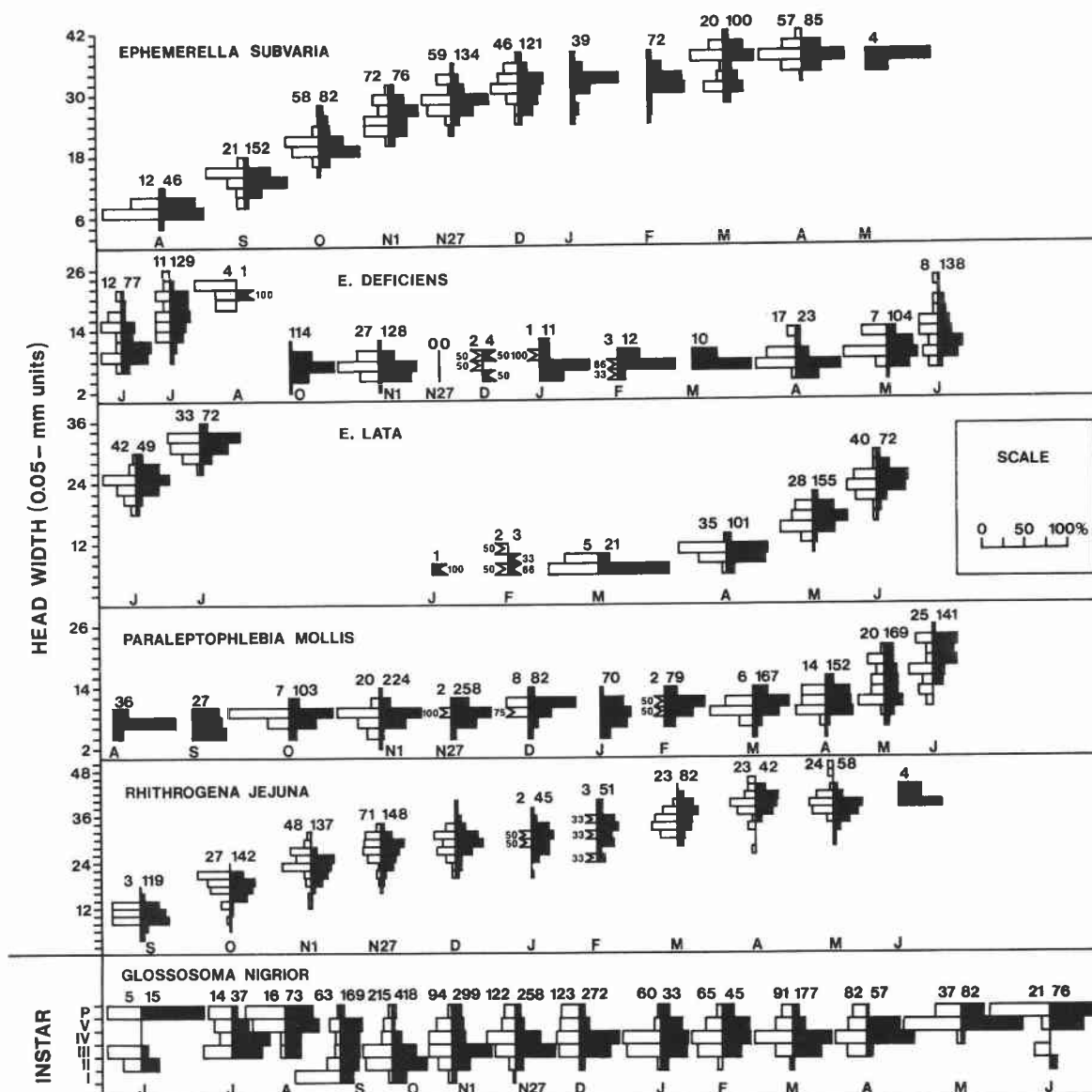
FIG. 2. Comparison of the SFD of six insect species at the fast (solid blocks) and slow (open blocks) stations. Numerals above histograms indicate sample size.

mid-May (D. Ottey, personal communication; Leonard and Leonard 1962).

Ephemerella deficiens Morgan (Fig. 2) began hatching in mid-October and large populations were present at the fast station in October and early November. Population densities at the fast station were markedly lower between late November and April but returned to high levels in May and June. Coleman and Hynes (1970) also reported that *E. deficiens* generally was absent at midstream in an Ontario river between December and February. The decrease in population density in November

reported here may have been attributable to movement to the stream margin as Leonard and Leonard (1962) and Vannote (1969) reported this species was common in leaf packets.

The nymphs grew little between October and April but grew rapidly between May and late July. If nymphs collected at midstream in April and May spent the winter in leaf packets, then little growth occurred in the leaf packets as the SFD in April was not significantly different from that recorded in November. Vannote (1969), however, reported *E. deficiens* exhibited exponential growth in leaf pack-

TABLE 1. Kolmogorov–Smirnov t values from comparison of the size frequency distribution of nymphs and larvae at the fast and slow stations

Date	E. subvaria	E. deficiens	E. lata	P. mollis	R. jejuna	G. nigrior
June 1972		0.292	0.164			0.333
July 1972		0.131	0.133			0.283
Aug. 1972	0.124					0.202
Sept. 1972	0.276					0.404*
Oct. 1972	0.113			0.107	0.208	0.191*
Nov. 1, 1972	0.165	0.160		0.083	0.210	0.204*
Nov. 27, 1972	0.104			0.341	0.133	0.194*
Dec. 1972	0.134			0.359	0.135	0.324*
Jan. 1973						0.250
Feb. 1973				0.127		0.168
Mar. 1973	0.040			0.248	0.319	0.114
Apr. 1973	0.040	0.253	0.105	0.083	0.087	0.179
May 1973		0.180	0.220	0.104	0.218	0.028
June 1973		0.147	0.189	0.427*		0.176

*$P < 0.05$.

ets. The overall growth pattern reported here was similar to that observed by Coleman and Hynes (1970). Emergence from the Pigeon River probably· occurred between mid-July and late August (Leonard and Leonard 1962).

Eclosion of *E. lata* Morgan (Fig. 2) began in late December and, following a period of delayed hatching and little growth between January and April, the nymphs grew rapidly and matured in mid-July. Emergence probably occurred between mid-July and mid-August (Leonard and Leonard 1962).

Paraleptophlebia mollis (Eaton) (Fig. 2) began to hatch in late July at the fast station. The nymphs grew slowly between August and March but grew rapidly between April and July. Coleman and Hynes (1970) reported *P. mollis* grew slowly between August and October, then not at all until April when the nymphs started rapid growth to maturity in mid-May. Emergence from the Pigeon River probably occurred between June and late July although Leonard and Leonard (1962) and Coleman and Hynes (1970) reported a much longer emergence period for this species.

Identification of *Rhithrogena jejuna* Eaton (Fig. 2) nymphs is tentative as it is likely that nymphs of *Rhithrogena impersonata* (McDunnough) were included in collections. *Rhithrogena jejuna* began to hatch in late August and grew rapidly until late November when growth ceased for the winter. Growth resumed between late February and early March and nymphs matured in May. Emergence probably occurred in late May and early June (J. Leonard, personal communication).

Glossosoma nigrior Banks was bivoltine (Fig. 2). The summer generation which lasted from June to late August – early September was characterized by rapid growth and low population densities. De-layed hatching of the winter generation extended from September to November. Larval growth was rapid during the fall and decreased sharply but did not stop during the winter. There was a second period of rapid growth in April and May. Pupae were present throughout the year and emergence probably was continuous from May to late September with peaks in June and late August coincident with the end of the winter and summer generations, respectively.

Size Frequency Distributions

The SFD of nymphs and larvae at the two stations are summarized in Fig. 2 and values for Kolmogorov–Smirnov t from comparisons of SFD are given in Table 1. The small number of individuals collected at the slow station rendered many of the differences in SFD statistically insignificant because the significance probabilities of the Kolmogorov–Smirnov t depend on sample size. Had the numbers collected at the slow station equalled those at the fast, many of the differences would have been significant. The small numbers of all species collected on 21 January and 17 February, particularly at the slow station, were attributable to large amounts of frazil ice on those dates.

The SFD of *E. subvaria* generally was similar at the two stations, but in September, October, and December nymphs were notably larger at the slow station. Nymphs of *E. deficiens* generally were slightly larger at the slow station. In March and April *E. lata* was slightly larger at the slow station, but between May and July nymphs were larger at the fast station. The SFD of *P. mollis* was similar at the two stations in October and early November but between March and June nymphs generally were larger at the fast station, the difference in June
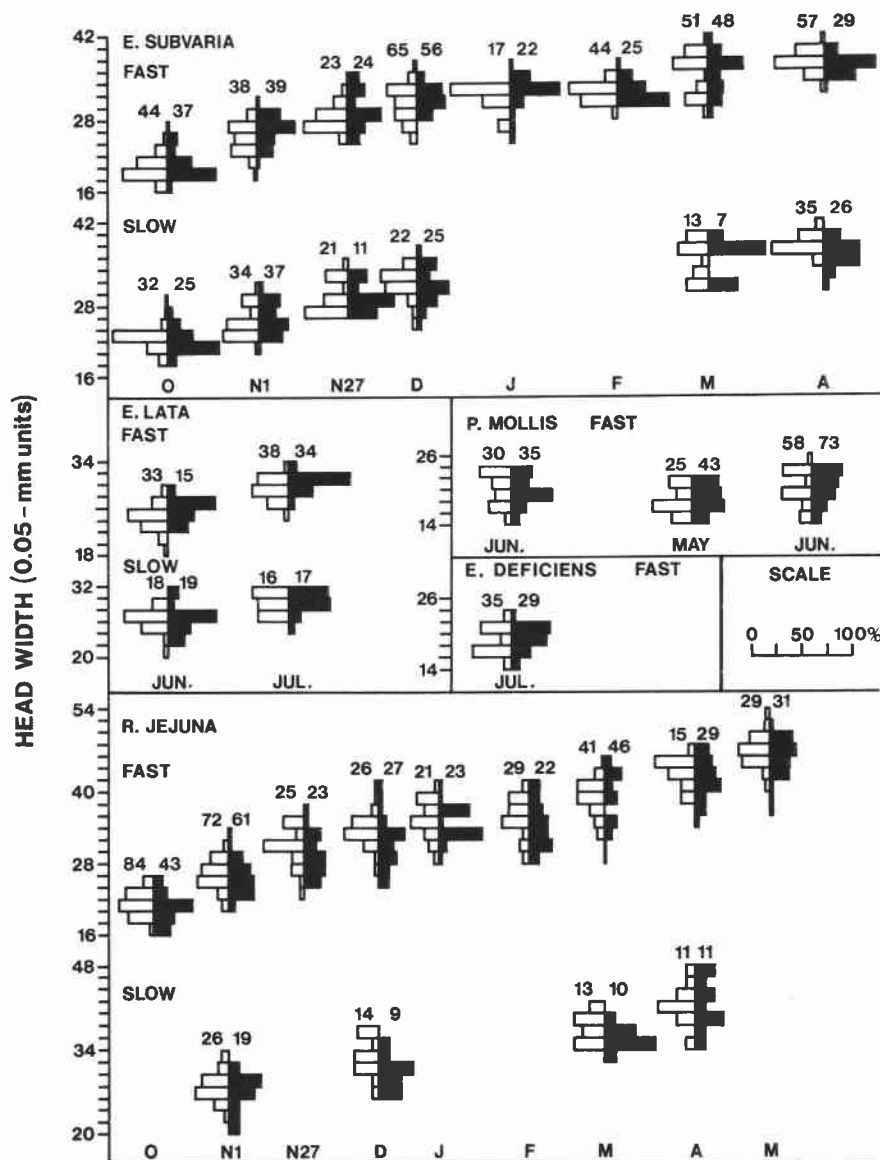
FIG. 3. Comparison of the SFD of male (open blocks) and female (solid blocks) mayflies at the fast and slow stations. Numerals above histograms indicate sample size.

was significant ($P < 0.05$). Between September and late November *R. jejuna* was larger at the slow station and in early November the difference was significant ($P < 0.05$). In December the SFD of *R. jejuna* was comparable at the two stations. In March and April *R. jejuna* was larger at the fast station but in May nymphs again were larger at the slow station. During the summer generation, *G. nigrior* generally was larger at the slow station. For the winter generation in September larvae were significantly ($P < 0.01$) larger at the fast station but between October and December larvae were significantly ($P < 0.01$) larger at the slow station.

From January to June, with the exception of March, larvae were larger at the fast station.

Comparisons of the SFD of male and female mayfly nymphs at the two stations are summarized in Fig. 3. For *E. subvaria*, at the fast station the SFD of males and females generally was similar, but in late November and in January females were notably larger. At the slow station the SFD of males and females also were similar but in April the males were notably larger. For *E. deficiens*, females were slightly larger than males in July 1972 at the fast station. For *E. lata*, in June and July 1972 at the fast station females were significantly ($P < 0.05$) larger
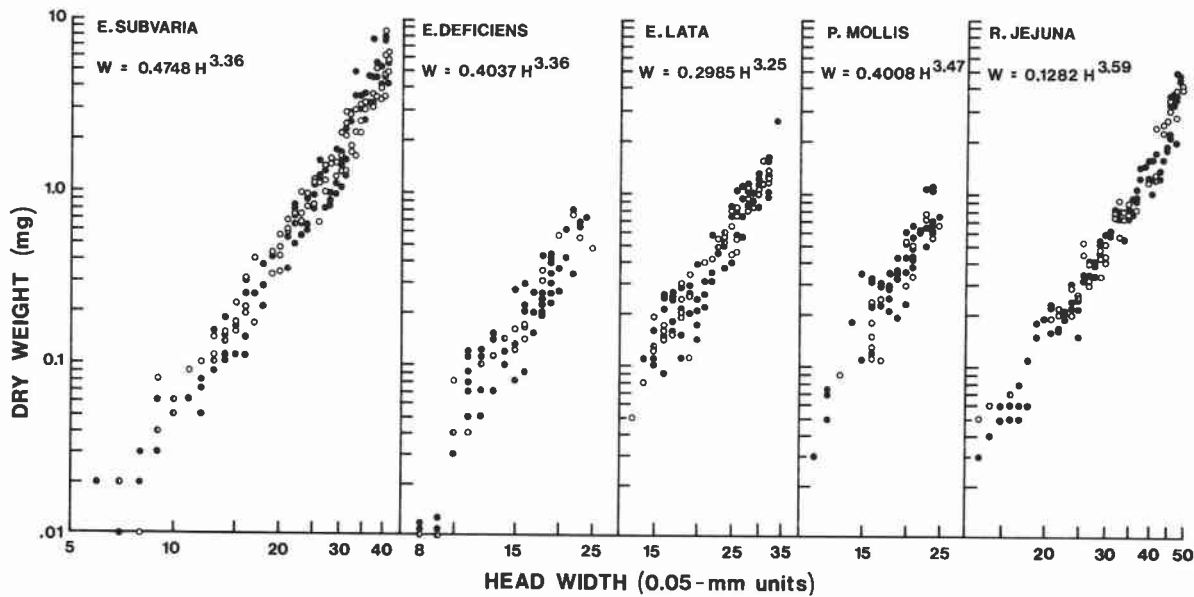
FIG. 4. Relationship between dry weight and head width of mayflies at the fast (solid circles) and slow (open circles) stations. Equations for the relationship between dry weight (W) in milligrams and head width (H) in millimetres for combined data are included.
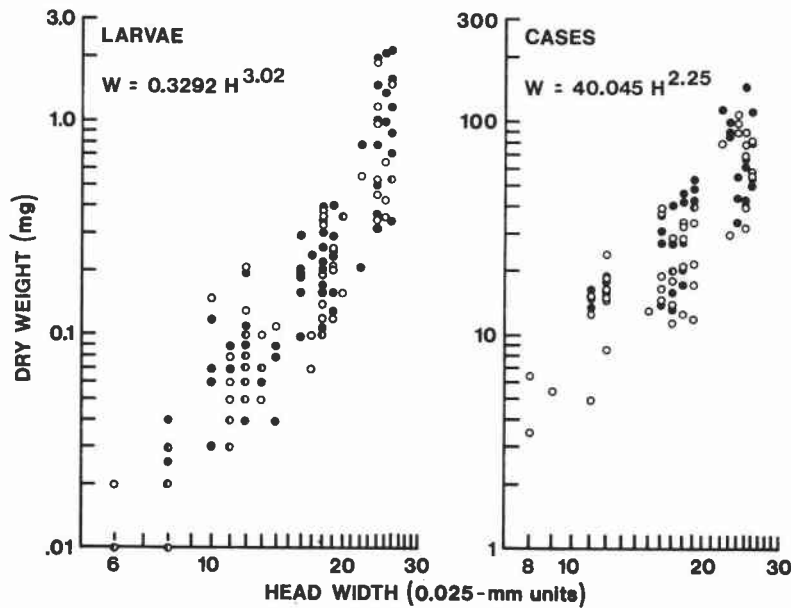

FIG. 5. Relationship between dry weight of *G. nigrior* larvae and cases and head width at the fast (solid circles) and slow (open circles) stations. Equations for the relationship between dry weight (W) in milligrams and head width (H) in millimetres for combined data are included.

than males, but at the slow station there were no differences. For *P. mollis*, at the fast station males were slightly larger than females in June 1972, but in May and June 1973 there were no differences. For *R. jejuna*, at the fast station between October and April males generally were larger than females but in May the difference was small. At the slow station in November, December, and March males

were larger than females, but in April the difference was small.

Dry Weight – Head Width Relationships

For all species, there were no significant differences in the dry weight – head width relationships between habitats when males and females from all dates were pooled and treated together (Figs. 4 and

TABLE 2. Seasonal changes in the proportion of male nymphs at the fast (F) and slow (S) stations

Date	E. subvaria F	E. subvaria S	E. deficiens, F	E. lata F	E. lata S	P. mollis F	P. mollis S	R. jejuna F	R. jejuna S
June 1972			0.48	0.68	0.49	0.46			
July 1972			0.55	0.53	0.48				
Oct. 1972	0.54	0.56						0.66	0.73
Nov. 1, 1972	0.49	0.48						0.54	0.58
Nov. 27, 1972	0.49	0.66						0.52	0.55
Dec. 1972	0.54	0.47						0.49	0.61
Jan. 1973	0.44							0.48	
Feb. 1973	0.64							0.57	
Mar. 1973	0.52	0.65						0.47	0.57
Apr. 1973	0.66	0.57						0.34	0.50
May 1973						0.37		0.48	0.33
June 1973			0.45	0.58	0.48	0.44	0.39		

5), nor was there a difference in the case weight – head width relationship for *G. nigrior* from the two habitats (Fig. 5). There were no significant differences in dry weight – head width relationships between males and females at a station nor for males or females between stations.

Sex Ratios

The proportion of male mayfly nymphs at the two stations is summarized in Table 2. For *Ephemerella* species the proportion of males generally was within the range of 0.45–0.55. Deviations from this pattern generally occurred near the end of the growth cycles, e.g. *E. subvaria* and *E. lata*, and for *E. subvaria* in association with frazil ice in January and February. For. *P. mollis*, the proportion of males was always less than 0.50 at both stations. For *R. jejuna*, at the fast station the proportion of males generally was near 0.50, and the proportion of males at the slow station generally was greater than at the fast.

Discussion

Although the relationships between SFD at the two stations varied among species and among dates, three general patterns emerged. Early in growth cycles, *E. subvaria*, *E. lata*, *R. jejuna*, and *G. nigrior* generally were larger at the slow station but near the end of the growth cycles they generally were larger at the fast station. For *P. mollis*, early in the growth cycle size differences between stations were small, but near the end of the growth cycle nymphs were larger at the fast station, whereas for *E. deficiens*, nymphs were slightly larger at the slow station throughout the growth cycle.

These patterns were more variable than one might predict, but were not inconsistent with the idea that selection of specific current velocities was used to help satisfy oxygen requirements. Early in growth cycles when individuals are small, the surface area to volume ratio is maximal. This was temporally coincident with autumnal decreases in water temperature which increased the oxygen content of water and decreased the metabolic rates of the insects. Consequently, in the fall there was little pressure for larger individuals to select faster currents. Larger size at the slow station during the early part of growth cycles may be attributable to higher growth rates at slower current speeds. Following Cummins' (1972) arguments, insects in slower current regimes, which spend less energy maintaining position in the stream, can channel more energy into growth.

Later in growth cycles when individuals are large, the surface area to volume ratio is minimal. Large size coupled with vernal increases in water temperature increased the probability of respiratory stress and, therefore, pressure to select faster current regimes. Specific differences in selection of current regimes by large individuals were not unexpected because not all species reach the same maximum size or the same surface area to volume ratio, nor do all species have the same metabolic rate at a given temperature. Some species (e.g. *E. subvaria*) emerge before water temperature gets too high.

That mature nymphs have difficulty meeting respiratory needs at higher temperatures had been used by Pleskot (1953) to account for the short emergence period of *Habroleptoides*. She suggested emergence was restricted to the early part of the summer by rising temperatures which were not directly lethal but which decreased oxygen supply at the time of transformation when oxygen uptake was particularly critical. Ide (1935) reported that for some species of mayflies,

emergence from warmer downstream areas was shorter and occurred earlier in the year than in cooler upstream areas. Ide suggested these differences were due to a direct temperature effect on eggs, but the oxygen limitation described by Pleskot (1953) explains these results equally well.

Respiratory stress may also account for decreases in the mean size of some nymphs and adults during vernal emergence periods (Macan 1957; Khoo 1964; Coleman and Hynes 1970). In the spring when temperatures are rising rapidly, individuals emerging near the end of the period experience higher temperatures than those emerging early. Temperature differences as small as 1°C may be critical at higher temperatures because of the logarithmic relationship between metabolic rate and temperature. Consequently, individuals which develop late may not be able to achieve maximum size before oxygen limitation induces emergence. This hypothesis is consistent with Macan's (1957) observation that *Rhithrogena semicolorata* achieved greater size in a colder stream, and Steffan's (1963, 1964) observation that Elmidae larvae from cooler headwaters are larger and weigh more than their counterparts from warmer downstream areas. It may also explain why for many bivoltine species, the maximum size achieved by individuals in the winter generation generally is greater than in the summer generation (Harker 1952; Macan 1957; Pleskot 1958; Waters 1966).

Alternatively, interhabitat differences in SFD may have been related to differences in substrate composition which also are controlled by current velocity. At the slow station the larger amounts of gravel and sand reduced the availability of interstitial space so that large mayfly nymphs may have been restricted to the coarser substrates at the fast station. This hypothesis, however, does not account for larger nymphs at the slow station early in the growth cycle unless substrate selection is important only in the latter stages of the growth cycle, nor does it explain why *G. nigrior*, which normally lives on current-exposed faces of stones (Kovalak 1976), showed the same pattern of interhabitat differences in SFD as mayflies. Clearly, elucidation of the relative importance of oxygen and substrate in controlling interhabitat differences in SFD depends on controlled experimentation. Perhaps the best direct method of determining the importance of oxygen in controlling size would be to measure oxygen delivery rates to sites occupied by nymphs and larvae using an oxygen meter of the type described by Madsen (1968). This could be done most readily for a relatively sedentary species like *G. nigrior* which lives on exposed faces of stones.

The idea that substrate composition controls interhabitat differences in SFD by determining the availability of interstitial space assumes that most species are cryptic. I, however, have observed large numbers of mayflies on tops of stones during the day (Kovalak 1978) and many diurnally cryptic species are known to move to tops of stones at night (Waters 1972). Differential erosion of variously sized nymphs or larvae from the current-exposed upper surfaces of stones may be a more important factor accounting for interhabitat differences in SFD. For some species large individuals are more liable to erosion and drifting presumably because they project above the boundary layer, whereas for other species small individuals are more liable to drift presumably because they are not strong enough to withstand exposure to current (reviewed by Waters (1972)). Differential erosion does not seem to be a plausible explanation for patterns of interhabitat differences in SFD reported here because most of the species showed the same general pattern although these species were very different morphologically. Dittmar (1955) and Dorier and Vaillant (1955) reported large interspecific differences in the ability of insects to withstand current even for systematically related taxa (e.g. *Epeorus*, *Rhithrogena*, and *Ecdyonurus*).

Conversely, it is hypothesized that drift acted to minimize interhabitat differences in SFD as well as interhabitat and sexual differences in dry weight – head width relationships. As in most rivers, mayflies were the predominant component of drift in the Pigeon River (Hildebrand 1973). High drift rates coupled with the close proximity of the sampling sites probably contributed to small interhabitat differences in SFD of mayflies. In contrast, *G. nigrior* generally showed larger, often significant, interhabitat differences in SFD. These differences may be attributable to the lower drift rates of *G. nigrior* (Hildebrand 1973) and (or) the larger number of *G. nigrior* collected. In the latter case it should be noted that the significance probabilities for the Kolmogorov–Smirnov t depend on sample size. As sample size increases, the Kolmogorov–Smirnov t becomes sensitive to smaller differences in SFD.

With few exceptions, differences in the SFD of males and females were small. Because sex ratios at both stations did not deviate appreciably from 1:1, what sex-related size differences were observed probably were not due to differential habitat selection but to differential growth. One possible exception was *R. jejuna* for which males generally were more common at the slow station.

Sexual dimorphism in mayflies was small com-

pared with that reported for stoneflies (Harper and Magnin 1969; Harper and Hynes 1972; Harper 1973*a*; 1973*b*). For some stoneflies, females occupy portions of the total size range of the species to the exclusion of males. The magnitude of these differences strongly suggests size segregation is the result of character displacement. Displacement may result from competition for food where particle size selection is a function of body size (reviewed by Wilson (1975)), but this seems unlikely for stoneflies which complete their growth when detritus on which they feed is seasonally most abundant. G. Finni (personal communication) suggested displacement may result from competition for interstitial space. Size segregation would optimize use of limited space where the dimensions of interstitial spaces are highly variable. Consequently, one might predict greater sexual dimorphism in species that make extensive use of interstitial space than in species which occur over a broader range of microhabitats. Capniidae and Taeniopterygidae, which make extensive use of interstitial space, show greater sexual dimorphism than setipalpian stoneflies which occur in other microhabitats as well (Harper and Magnin 1969; Harper and Hynes 1972; Harper 1973*b*). None of the mayfly species studied here made extensive use of interstitial spaces particularly when they were large enough to be sexed. This, coupled with the coarseness of size units used to measure head width, may account for the small differences in SFD between sexes.

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