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FEEDING HABITS OF THE PREDACEOUS NYMPHS OF DOLANIA AMERICANA IN NORTHWESTERN FLORIDA (EPHEMEROPTERA : BEHNINGIIDAE)

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Abstract

Feeding habits of nymphs of the predatory mayfly *Dolania americana* Edmunds & Traver in northwestern Florida were examined during 1971 and 1972. Larvae of Chironomidae (Diptera) formed the bulk of prey items. The size of the predaceous *D. americana* nymphs was correlated with the size of chironomid prey taken. Differential microhabit utilization allows partition of prey resources with the other major predator species present. The relationship between predator and prey biomass throughout the year is discussed.

Introduction

During a long-term study of the sand burrowing mayfly, *Dolania americana* Edmunds & Traver, in the Blackwater River, northwestern Florida, we discovered that its nymphs are carnivorous. Predatory feeding is relatively uncommon among the predominately detritivorous-herbivorous order Ephemeroptera and we felt that the feeding habits of *D. americana* merited further investigation. The objectives of the present study were: to determine the nature of the food (prey) consumed by the nymphs of *D. americana;* to determine whether food consumption showed seasonal variations; to determine the size relationship between the nymphs of *D. americana* and their prey, if any; and to examine resource partitioning among macroinvertebrate predators in the Blackwater River.

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Dolania is a monotypic genus of the family Behningiidae which also contains the Palaearctic genera *Behningia* Lestage, with three species, and *Protobehningia* Tshernova, with one species. *Dolania americana* is known from northwestern Florida, southwestern Louisiana, and the Savannah River drainage in Georgia and South Carolina. Further general biological and zoogeographic data on *D. americana* can be found in Peters & Peters (1977). Nymphs examined in this study were collected from two sampling stations on the Blackwater River. Both sites were located in the vicinity of the Florida A & M University Biological Field Station near Holt, Okaloosa County, Florida. The physical and chemical characteristics of the Blackwater River were described by Beck (1973), and the flora and fauna were discussed by Peters & Jones (1973).

Methods

Nine collections of *D. americana* nymphs were made between June, 1971, and May, 1972, in which a total of 208 nymphs were dissected for gut analyses. Each nymph examined for gut contents was split meso-ventrally and the entire gut was removed and spread in a drop of CMC-10 (Turtox) mounting medium on a standard microscope slide. The entire gut was examined and the contents enumerated. Size of the prey organisms was determined (in the case of dipteran larvae, the length of the head capsule was measured), and the size of the *D. americana* nymphs was measured by the interorbital distance (shortest distance between the eyes).

Estimates of chironomid (Diptera) population densi-

ties at the study areas were made in the months of February, March, and April, 1974. Five one-litre sand samples were taken at hazard each month from the river bottom, preserved in ethanol, and stained with Rose Bengal (100 mg l^{-1} preservative). The entire sample was examined and the total number of dipteran larvae in each litre of sand was determined.

Sand particle size distribution was examined by running a transect perpendicular to the shore and taking periodic bottom samples. The samples were then processed through standard soil sieves, separated into size-classes, air-dried, and weighed, and percentage composition was calculated.

Horizontal and vertical distribution of macroinvertebrate predators was examined by taking periodic samples along a transect perpendicular to the shore. The samples were examined and the density and kind of predators present were determined.

Results and discussion

In the Blackwater River nymphs of *D. americana* are found burrowing in about the top five centimetres of clean, shifting sand. The shifting sand biotope is one of the major habitats found in the river and occupies a great majority of the river bottom. The sand is loose and continuously shifting with grain sizes mostly in the range of 0.25-1.0 mm. Morphologically, the nymph is well adapted for burrowing in this substrate and has evolved various protective structures to counteract the molar action of the shifting sand grains (Edmunds & Traver, 1959). Preliminary studies indicated that *D. americana* has primarily a univoltine life cycle in the Blackwater River, and nymphs are present in the river throughout the year (Fig. 1). Emergence occurs in late April to May (Peters & Peters, 1977). A smaller cohort of *D. americana* nymphs in the Blackwater River apparently does not emerge the first year but remains in the river until the following spring. The reasons for this dichotomy remain unknown.

Other predators coexist with *D. americana* in lesser densities in the shifting sand biotope of the Blackwater River. The two major competitors of *D. americana* are the dragonfly *Progomphus obscurus* (Rambur) (Odonata : Gomphidae) and the mayfly *Pseudiron meridionalis* Traver (Ephemeroptera : Heptageniidae). Preliminary study indicated that although a dietary overlap occurs among these three carnivores, partitioning of resources and a lessening of potential competition is

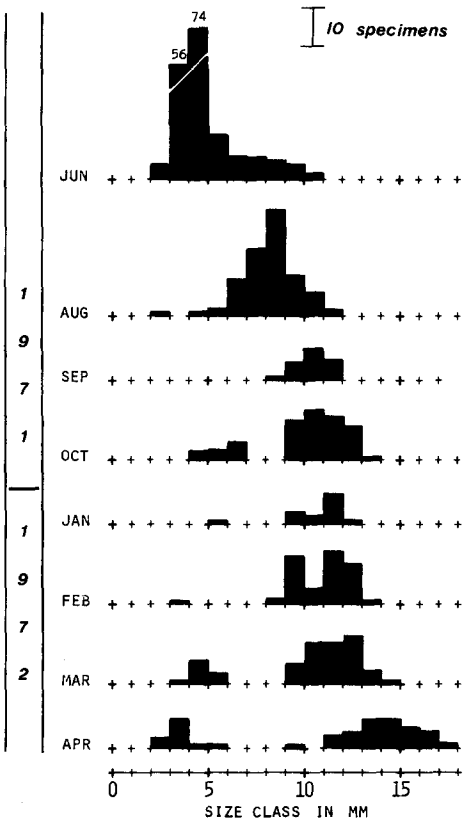

Fig. 1. Seasonal size (body length) distribution of *Dolania americana* nymphs in the Blackwater River.

acheived through differential microhabitat utilization. In contrast to the burrowing habit of *D. americana* and *P. obscurus*, the nymphs of *P. meridionalis* occupy the surface of the sand, not burrowing beneath the substrate. In addition to this vertical partitioning, horizontal partitioning also occurs. Nymphs of *P. obscurus* burrow mostly at the peripheral areas of the stream, whereas *D. americana* nymphs burrow in more submarginal to midstream areas. Samples along transects from the shore reveal that the density of *P. obscurus* lessens with increasing water depth (i.e., distance from shore) and that the density of *D. americana* increases concurrently until almost no *P. obscurus* occur (Fig. 2). Shore transects also indicate that the sand particle size of the substrate likewise increases with increasing water depth, with the percentage of sand particles 0.5 mm or greater in diameter increasing from about 30% at 50 mm depth to 65% at 350-500 mm depth.

Based on gut analyses of *D. americana* nymphs during

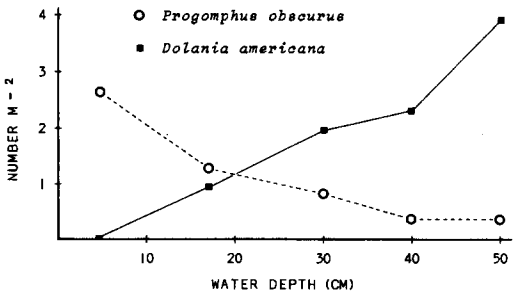

Fig. 2. Density of nymphs of *Dolania americana* and *Progomphus obscurus* along a transect perpendicular to the shore in the Blackwater River (Kennedy Bridge, 16-II-1974).

the study period we discovered that 95% or more of the prey organisms were Chironomidae larvae (Diptera). The overwhelming majority of these chironomid larvae belong to an undescribed species in the subfamily Chironominae. Other prey organisms found in much lesser numbers in gut contents of *D. americana* included microcrustacea, ceratopogonid larvae, nematodes, and occasionally tardigrades. These food organisms are all elements of the interstitial fauna of the sandy river bottom. Keffermüller (1959), in a brief investigation of gut contents of the related species *Behningia lestagei* Motas & Bacesco in the Warta River, Poland, was unable to determine the type of food utilized except that the digestive canal contained traces of 'small grains of sand, diatoms, small pieces of sponge spicules, and an indeterminable organic matter'.

Because chironomid larvae formed the main bulk of the prey items consumed by *Dolania* nymphs we therefore focused our attention on this prey category. Mean numbers of chironomid larvae per litre of sand were 65, 76, and 90 for the months of February, March, and April, 1974, respectively.

For a species to establish and maintain itself in any environment where there is competition, for food or for other resources, certain adaptive mechanisms must have evolved to allow increased utilization of those resources. Macan (1958), Hynes (1961), and Sheldon (1969) have suggested that size variation between individuals of a species can effectively reduce intraspecific competition for food within a population if feeding habits of the individuals are size-dependent. We examined the size range of nymphs of *D. americana* for eight months between June, 1971, and April, 1972 (Fig. 1). Growth rate of the nymphs seemed to be greatest during the first three months after hatching from the egg stage. Obvious variation in size range of the nymphs occurred throughout the study period. Such size variability within the predator population might be an important adaptive feature if the feeding habits of the predator are size-dependent since this would allow better partition of the available food resources.

Fig. 3 is a graphic presentation of the size relationship between the nymphs of *D. americana* and their chironomid prey. Small larvae were consumed by nymphs of all sizes, as illustrated by the essentially unchanging lower size limits of the prey, while the upper, mean, and median size limits increased with increasing predator size, indicating a size dependent relationship on the upper end of the prey size distribution. The product moment correlation coefficients for predator size and the largest, mean, and median prey sizes were .732, .707, and .817 respectively. All of these values are statistically significant ($p < .01$). Thus, as nymphs of *D. americana* grow larger, they consume an increasingly wider range of chironomid prey size. This fact, coupled with the extensive variation in size range of the *Dolania* nymphs at any one time, results in a greatly lessened prey size overlap. This feeding pattern is similar to that of another aquatic insect predator, *Doroneuria californica* (Banks) (Plecoptera : Perlidae), reported (as *Acroneuria*) by Sheldon (1969).

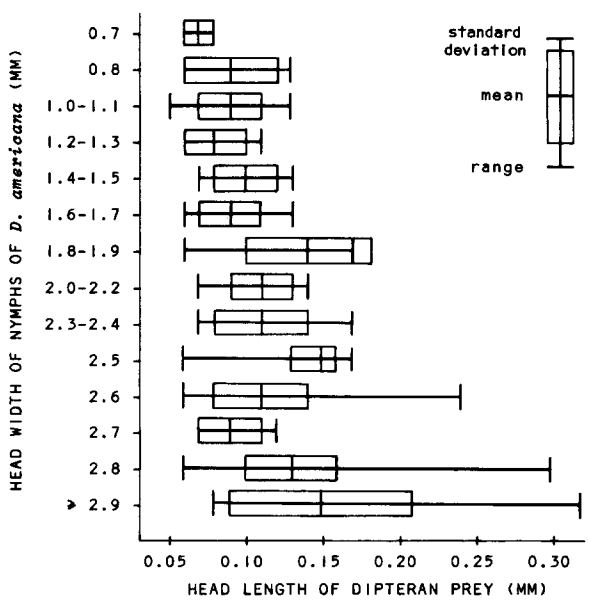

Fig. 3. Distribution of Chironomidae prey size (head capsule length) in relation to *Dolania americana* predator size (interorbital distance) in the Blackwater River.

To obtain an estimate of relative amounts of feeding throughout the year, we felt that the use of biomass as an indicator parameter would be most appropriate. Lacking a direct measure of biomass (because our data were taken in a different form), we have used relative volume (which varies positively with biomass) for this parameter. The relative volume of the prey chironomids was approximated by taking the cube of the head capsule length. That of *D. americana* nymphs was approximated by taking the cube of the total length. Because these approximations of volume are based on two different linear measurements direct relation of them is inappropriate. However, taking the ratio to form a unitless index number (which we call 'prey-predator volume ratio index') is possible. This index number will allow indirect comparison of biomass between sampling periods.

Fig. 4 shows the ratio of the total prey biomass/volume to the total predator biomass/volume for each sampling period. Especially notable is the sharp increase in biomass intake (i.e., prey consumption) during March and the equally sharp decline in April, just prior to emergence of *D. americana* adults. The mean number of prey chironomids per *D. americana* nymph for each sampling period (Fig. 5) again demonstrates the sharp rise in feeding in March and the decline in April prior to emergence. The increase in mean number of prey per predator throughout the life cycle as the size of *D. americana* nymphs increase should also be noted.

The volume ratio index for the median prey individual volume and median predator individual volume for each sampling period is shown in Fig. 6. The ratio holds relatively constant throughout the life cycle except for a high peak in late spring and early summer. This early high prey-predator volume ratio may be explained by the constant lower threshold on prey size (Fig. 3; i.e., size of prey chironomids present). This lower threshold size is relatively large compared to the size of early instar *D. americana* nymphs (ca. 3 mm at hatching).

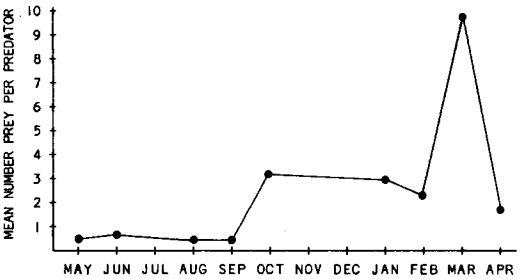

Fig. 5. Mean number of Chironomidae prey per *Dolania americana* from the Blackwater River.

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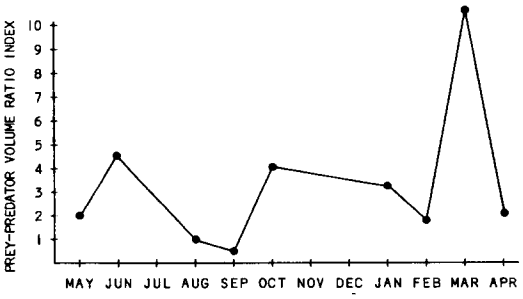

Fig. 4. Ratio index of total Chironomid prey volume per total *Dolania americana* predator volume in the Blackwater River.

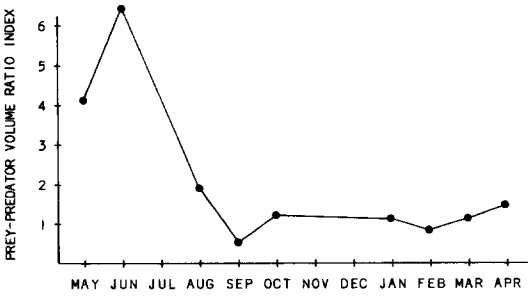

Fig. 6. Ratio index of median Chironomidae prey volume per median *Dolania americana* predator volume in the Blackwater River.

Summary

1. Prey of *Dolania americana* consisted primarily of larval Chironomidae (Diptera). Microcrustacea, other dipteran larvae, nematodes, and occasionally tardigrades were also found among prey items.

2. The size of the predaceous *D. americana* nymphs was positively correlated with the mean, median, and upper sizes of chironomid prey larvae resulting in a lessened competition for food items of any one size (and thus generally) with the *D. americana* population.

3. A method is developed to allow indirect comparison of biomass between predator and prey.

4. There is a sharp increase in both biomass and number of prey ingested in March and an equally sharp decline in April just prior to emergence of *D. americana.*

5. Differential microhabitat utilization within the Blackwater River allows partition of prey resources with the other major predators present viz., the odonate *Progomphus obscurus* (Rambur) and the mayfly *Pseudiron meridionalis* Traver.

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