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LARVAL SPECIALIZATION AND PHENOTYPIC VARIATION IN *ARCTOPSYCHE GRANDIS* (TRICHOPTERA: HYDROPSYCHIDAE)¹

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Abstract. Life history, trophic dynamics, abundance, and microdistribution of *Arctopsyche grandis* (Banks) were investigated in the Flathead River Basin, Montana. Two morphologically and ecologically distinct larvae (Type I, with a head stripe; and Type II, without a head stripe) were found throughout the drainage except in lower order streams. Type II larvae grew more rapidly and attained a larger size in final instar than Type I larvae. In areas where *A. grandis* biomass was greatest, Type I larvae were >10 times as abundant as Type II larvae. Type II larvae selected microhabitats characterized by larger interstitial spaces; Type I larvae were more common in tightly compacted substrata. Food items consumed by both larval phenotypes varied between sites, indicating a natural variability in the environment. Significant differences in foods ingested were also observed between larval types within particular riverine locations, suggesting phenotypic differentiation in food habits. Larvae of both phenotypes were reared in laboratory streams. Type I were both male and female, but all Type II were female. We concluded that the presence of Type II larvae increased resource utilization and species fitness.

Key words: *Arctopsyche*; caddisflies; Flathead River; habitat selection; life histories; Montana; phenotypic variation; species fitness; trophic dynamics.

INTRODUCTION

Net-spinning larvae often contribute significantly to zoobenthic biomass and energy processing in running water ecosystems (Cummins 1974, Wallace et al. 1977, Ward and Short 1978). Although stream size preference (Gordon and Wallace 1975, Wiggins and Mackay 1978) and the importance of various environmental factors such as current velocity (Wallace 1975, Haddock 1977) have been documented for certain species of hydropsychid larvae, the biology of caddisflies is not well known, especially in western Montana.

As part of an ongoing study of the limnology of the Flathead River-Lake Ecosystem, we investigated ecological relationships of *Arctopsyche grandis* (Banks). We found this large hydropsychid widely distributed throughout the Flathead Basin in third- and fourth-order high mountain streams, as well as in the riffles of the mainstream rivers above Flathead Lake. *A. grandis* larvae were very abundant (maximum 600 larvae/m²) in fifth- and sixth-order segments of the Flathead River and were frequently one of the numerically dominant caddisfly species in riffle areas.

Soon after the initiation of our research, it became apparent that two morphologically distinct larvae of *A. grandis* were commonly found in close association. The two morphs had different color patterns and after close examination, we observed that they selected

slightly different microhabitats (i.e., built retreats in different areas) and responded differentially (e.g., frequency ratios, abundance) along specific resource gradients within the river system. Although *A. grandis* is widespread in western North America and has been the subject of numerous taxonomic (Smith 1968, Givens 1976) and ecological (Furnish 1979, Alstad 1980, Cuffney 1980) studies, such morphological differentiation has not been investigated. To delineate fully the means of apparent morphological heterogeneity within the species, we examined growth and emergence, habitat selection, and possible sexual differences between the two larval phenotypes.

STUDY AREA

The Flathead River Basin is located along the west slope in heavily glaciated areas of the Continental Divide in northwestern Montana and the southeastern corner of British Columbia. There are three major tributaries of the Flathead River: the North Fork, with a mean annual flow of 85 m³/s; the Middle Fork, with a mean annual flow of 84 m³/s; and the South Fork, which is regulated by Hungry Horse Dam, with a mean annual flow of 101 m³/s (Fig. 1). These fifth-order rivers are characterized by cobble and small-boulder substrata. Gravel deposits are extensive in the floodplains, creating large areas of hyporheic habitat (Stanford and Gaufin 1974).

Most physicochemical parameters, such as temperature, alkalinity, pH, and flow are similar in the North and Middle Forks. The North Fork valley is open, broad, and rounded, but the Middle Fork courses

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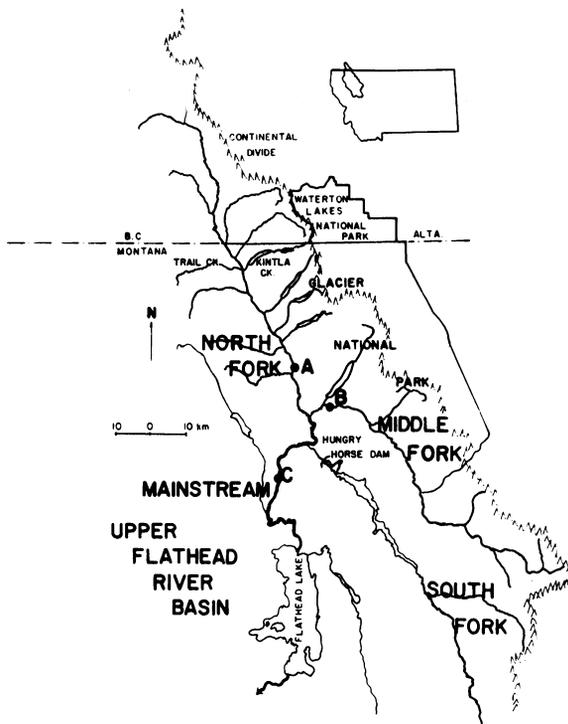


FIG. 1. Map of Flathead River Basin indicating sampling locations.

through narrow canyon sections. Although both rivers erode extensive deposits of glacial clays, the Middle Fork carries a larger sediment load during spring runoff (R. Hauer and J. Stanford, *personal observation*). It does not clear as rapidly as the North Fork after runoff and becomes turbid following occasional summer rainstorms in the drainage basin. Fine particulate organic matter (FPOM), composed of both allochthonous and autochthonous materials, is closely associated with the clay sediments in a colloidal matrix. The organically rich sediments are transported downstream and are deposited on and within the substrata of both rivers. Because the Middle Fork carries a higher sediment load than the North Fork, more interstitial space in the rubble has been partially filled with fine sediments, coarse sands, and gravel.

The South Fork below Hungry Horse Reservoir has been significantly altered due to hypolimnial discharges; flow may fluctuate between 7.5 and 300 m³/s diurnally. *A. grandis* no longer occurs in this river segment, apparently due to frequent alteration of discharge, thermal regime, and trophic dynamics (see Stanford and Ward 1979).

The Mainstream River below the confluence of the regulated South Fork is also characterized by a rubble substrate and abundant riffles. However, this reach of the river is influenced in late summer, fall, and winter by diurnal variations in discharge from the South Fork. Summer and fall temperatures are suppressed

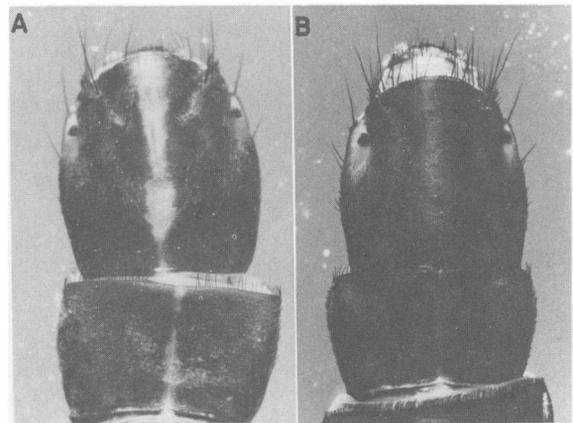


FIG. 2. Two morphological variations of *Arctopsyche grandis* larvae from the Flathead Rivers, Montana: Phenotype I (A) has a distinct stripe on head and thorax, Phenotype II (B) does not.

2°–3°C in comparison to the North and Middle Forks; winter waters are warmed 1°–2°C by hypolimnion discharges from Hungry Horse Reservoir. This river section differs significantly from the unregulated tributaries in that algae are sloughed by the sluicing effect of the regulated discharges. Algal filaments were frequently observed heavily packed into and trailing from *A. grandis* filter nets. Green and diatomaceous algae contributed significantly to the trophic dynamics of *A. grandis* in this river segment.

METHODS

Three stations were established for collection of quantitative, time-series data (Fig. 1): Station A was located on the North Fork ≈20 km above confluence with the Middle Fork, Station B on the Middle Fork ≈15 km above confluence with the North Fork; and Station C on the Mainstream River ≈15 km downstream from the South Fork confluence. In addition, qualitative samples were obtained in a variety of smaller tributary streams throughout the drainage, particularly the North Fork tributary streams, Trail Creek and Kintla Creek.

Immature and adult stages of *A. grandis* were collected in 1977–1979 using both quantitative and qualitative techniques to establish microdistributional relationships, levels of abundance, and to provide sufficient numbers of individuals to document life history events. Larvae were collected with a 225- μ m mesh, 1.2 m \times 1 m, modified kick net. Quantitative larval collections were made monthly from August through April. Seasonal abundance data sets were established as fall, August through 15 November; winter, 16 November through 15 February; and spring, 16 February through April. High water prevented quantitative sampling during spring runoff in late April, May, June, and early July. Qualitative collections of

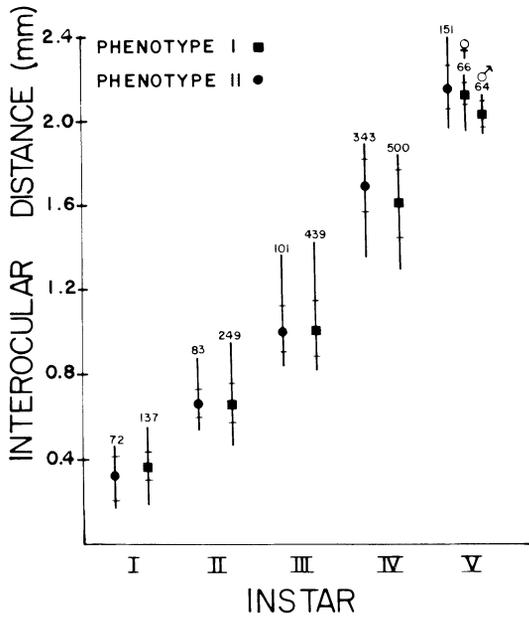


FIG. 3. Instar discrimination of *Arctopsyche grandis* by phenotype. Bar length equals range, short cross bars equal 1 SD, center mark equals mean, and sample size is denoted by number over bar.

larvae and pupae were made during the runoff period by entering the river with diving gear. Instar determinations were established using the technique described by Mackay (1978) for 2136 specimens.

Several hundred larvae were collected and returned to the laboratory for rearing. Larvae were reared in spring water in circular Plexiglas chambers containing gravel and rock substrate. Temperature was controlled near mean river temperature and light banks provided a natural photoperiod. Larvae were fed commercial, frozen brine shrimp by placing thawed food particles in individual capture nets. Morphological variations of

the larvae were associated with the adults by rearing field-collected larvae to the pharate adult in the laboratory streams. Late-development pharate adults were also collected from the river. Larva-adult association was accomplished by dissection of the cocoon which contained larval sclerites and a pharate adult with completely formed, hardened, and colored genitalia (see Vorhies 1909, Milne 1938, Ross 1944).

Adults were collected with insect aerial nets and ultraviolet night-light traps using a direct current electrical source and an alcohol entrapment reservoir.

We followed the procedure of Mecom and Cummins (1964) for food analysis. The alimentary canal was dissected from the crop to the mesenteron in last-instar larvae. Contents of the proventriculus were suspended in 15 mL of 2% formalin solution and filtered onto 0.45- μ m acetate filters. The filters were placed on microscope slides, dried, and cleared with immersion oil before microscopic analysis. Gut contents were calculated by estimating the percentage volume of the proventriculus displaced by each food category. Proventriculi from 10 larvae of each morph were examined in seasonal samples from each field site. The proventriculus containing the largest food volume in each data set was established as the "full-gut" reference from which percentages in each category were calculated.

RESULTS AND DISCUSSION

Larval morphology and life cycles

A. grandis is the largest of the net-spinning caddisflies in the Flathead Rivers. The two distinct morphological types, designated Phenotype I and Phenotype II, were determined by differences in head and thorax color pattern. The head of Phenotype I larvae is dark brown with a pale yellow mid-dorsal stripe running from the anterior edge of the frontoclypeal apotome posteriorly through the coronal suture and mid-dorsal

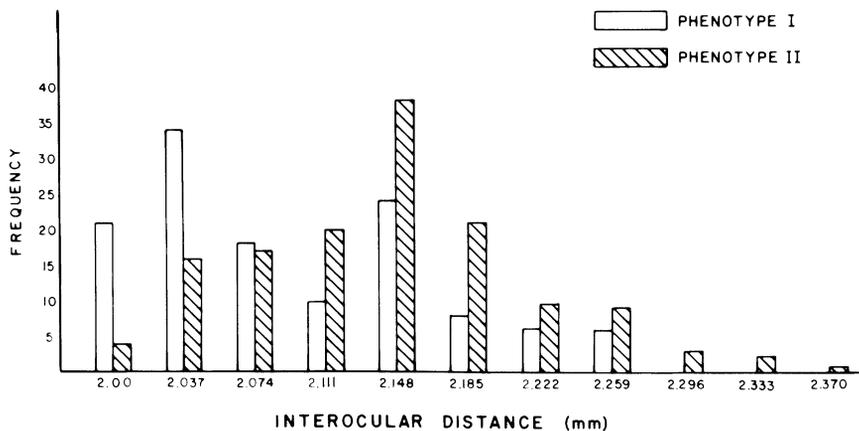


FIG. 4. Size-frequency distribution of final-instar *Arctopsyche grandis* larvae showing differences between the two phenotypes.

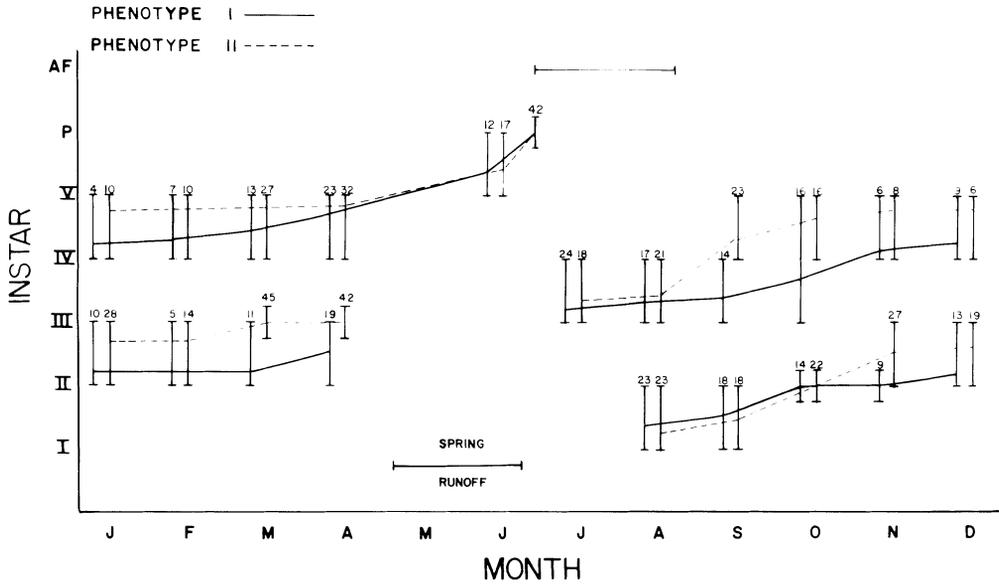


FIG. 5. Life cycles of the two phenotypes of *Arctopsyche grandis* in the North Fork. Monthly distribution of instars (I-V) and pupae (P) for Phenotype I are shown to the left of those for Phenotype II, along with adult flight period (AF). Modes have been joined to indicate growth, bar length shows range of instars found each month, and sample size is denoted by number over bar.

ecdysical line of the pronotum and mesonotum (Fig. 2A). The head and thorax of Phenotype II larvae are dark brown with no stripe (Fig. 2B). Individuals reared in the laboratory maintained their distinct markings through successive instars. Larvae were rarely collected in which the mid-dorsal line on the head was slightly broken at the constriction of the lateral sutures at the frontoclypeal apotome.

Distribution of larval instars over the annual cycle

revealed that *A. grandis* had five instars (Fig. 3). A size-frequency distribution of final-instar larvae yielded a bimodal distribution of Phenotype I larvae. Phenotype II larvae, however, were normally distributed (Fig. 4). Adult female *A. grandis* were significantly larger than adult males, and thus may account for the bimodal distribution. An analysis of variance of these data indicated that second-mode Type I and Type II larvae were significantly larger than first-mode Type

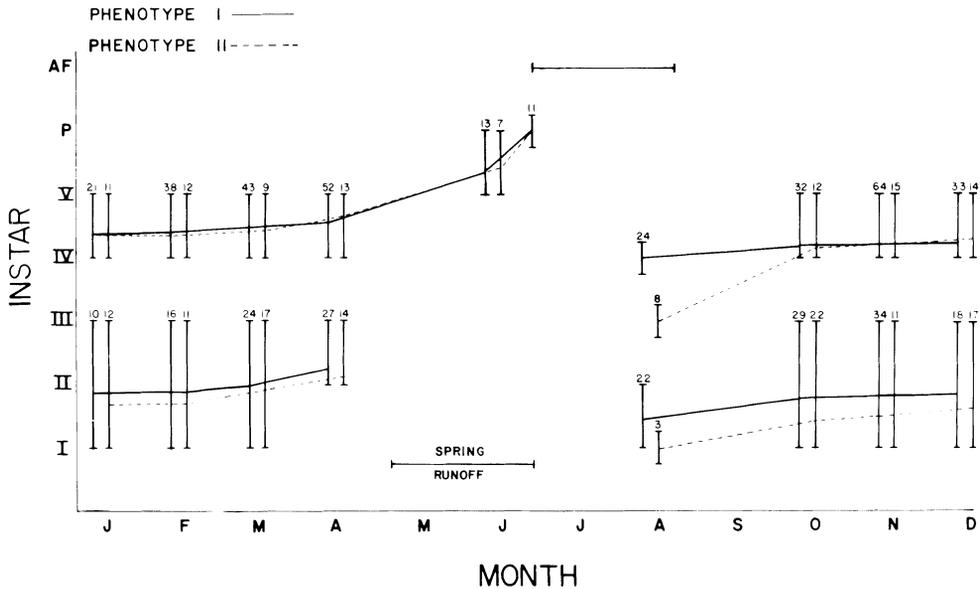


FIG. 6. Life cycles of the two phenotypes of *Arctopsyche grandis* in the Middle Fork. Presentation as in Fig. 5.

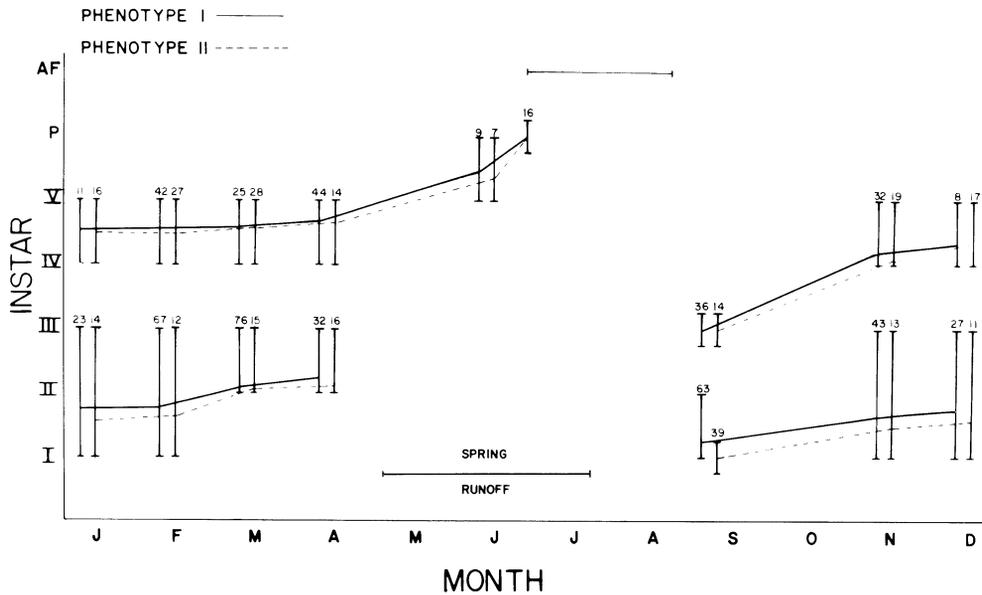


FIG. 7. Life cycles of the two phenotypes of *Arctopsyche grandis* in the Mainstream below the regulated South Fork. Presentation as in Fig. 5.

I larvae ($P < .05$). Type II larvae were not significantly larger ($P < .10$) than second-mode Type I larvae, although this general trend was suggested by the larger upper range of Type II larvae (Figs. 3 and 4).

Larval growth of both phenotypes was monitored

over a 2-yr cycle. In the North Fork, where Phenotype II larvae were consistently more abundant than those of Phenotype I, Phenotype II larvae grew rapidly in the autumn. This was especially evident among 2nd yr class larvae. Type II larvae generally reached fifth instar before winter (Fig. 5). Phenotype I larvae, in contrast, did not grow as rapidly in fall, overwintering primarily in fourth instar. In the Middle Fork and Mainstream, where Type I appeared to be the favored phenotype, larval growth of the two phenotypes was very similar (Figs. 6 and 7).

The adult flight period for *A. grandis* throughout the Flathead Rivers occurred from late June to mid-August (see Figs. 5, 6, and 7). Emergence took place primarily just prior to and at dusk. Teneral adults swam to the surface, then horizontally to the river edge, whereupon they crawled out of the river via shoreline rubble and riparian vegetation. During the day, adults were found resting exclusively among the boughs of large Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) scattered along the riverbank. Individuals disturbed from a particular tree would fly over the river, but frequently would return to the same tree. Flight activity was greatest immediately after dusk and adults were readily attracted to ultraviolet lights.

Relative abundance and distribution

Phenotype I and Phenotype II larvae of *Arctopsyche grandis* have responded differentially to the environment parameters in the different river segments. Phenotype II larvae were dominant in the North Fork: total numbers of individuals per square metre were approximately twice that of Phenotype I larvae (Fig.

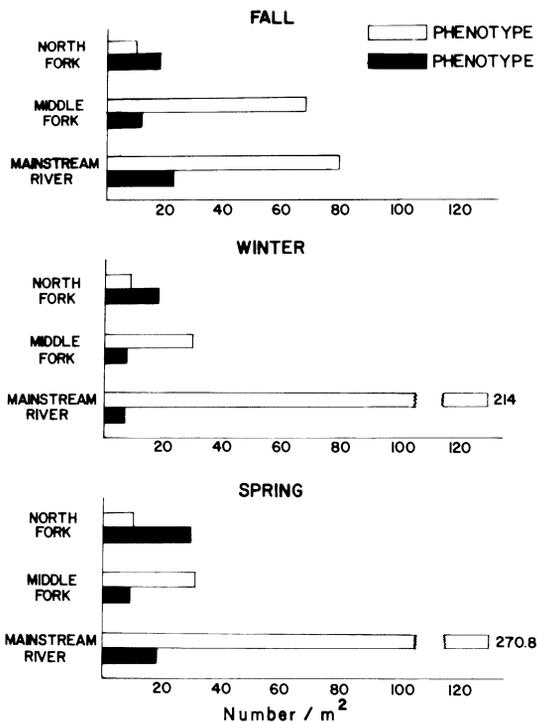


FIG. 8. Seasonal abundance (as numbers per square metre) of the phenotypes of *Arctopsyche grandis* at the three major sampling sites.

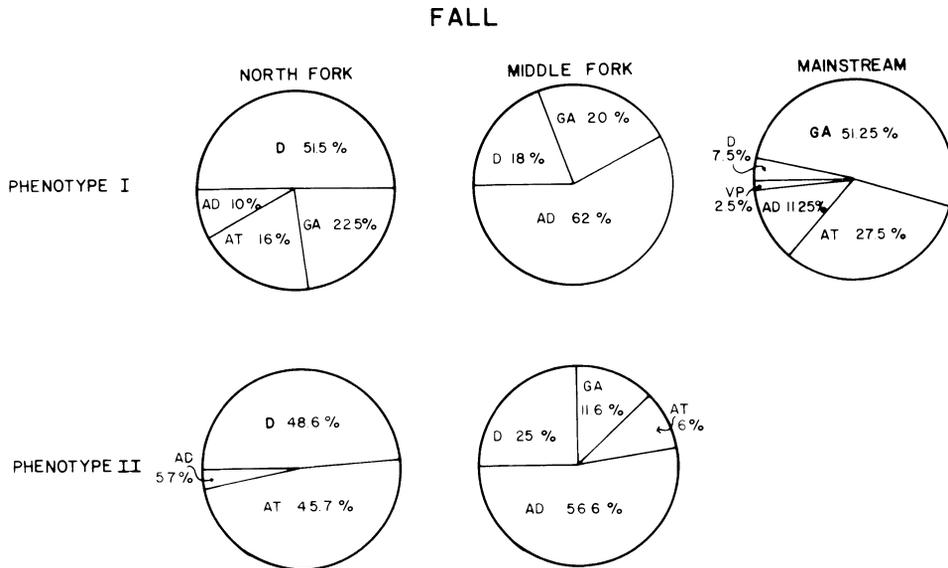


FIG. 9. Trophic relationships of *Arctopsyche grandis* by phenotype at the riverine sites during fall. Percent of total food ingested by 10 larvae is given with each food category (i.e., diatoms, D; green algae, GA; vascular plant tissue, VP; animal tissue, AT; amorphous detritus, AD) in each pie chart. (Numbers of late-instar Phenotype II larvae collected in the Mainstream were insufficient to allow comparison.)

8). In the Middle Fork and Mainstream, Phenotype I larvae were significantly ($P < .05$) more abundant than Phenotype II larvae. The total number per square metre of both phenotypes combined was greatest in the Mainstream, followed by the Middle Fork.

A. grandis larval retreats were restricted, at all stations throughout the Flathead Rivers, to the undersides of rocks and within the interstitial space of the rubble on riffles. The only locations in the drainage where *A. grandis* larvae were observed building retreats and filter nets on the surface of the substrate were below lake outlet streams draining the large, glacial lakes on the east side of the North Fork in Glacier National Park. Presumably, this adaptation occurred in response to the less rigorous winter environment at these locations; lake outlet streams rarely developed anchor or surface ice, which heavily scoured the substrate in the major tributary and Mainstream rivers.

Phenotype II larvae were observed only in very large rubble where the space between the rocks was not filled with coarse sands and gravel. Such habitat was found throughout the course of the North Fork, but was less frequently observed in the Middle Fork and Mainstream. Phenotype I larvae were also observed in large rubble. However, they were found primarily in areas of small interstitial space along seams where rocks rested together and in areas where interstitial spaces were limited by gravel, sand, and fine sediments, or tightly compacted rocks.

Trophic relationships

The gut contents of *A. grandis* were comprised primarily of five food types: (1) diatoms, largely *Synedra*,

Navicula, and *Gomphonema*; (2) green algae, primarily *Ulothrix* and some *Hydrurus*; (3) vascular plant tissue, entirely of terrestrial derivation; (4) animal tissue, from a wide variety of sources (e.g., Plecoptera nymphs, *Ephemerella* nymphs, chironomid larvae, and *Glossosoma* and *Hydropsyche* larvae); and (5) amorphous detritus.

During the fall, diatoms comprised $\approx 50\%$ of the food items for both larval types in the North Fork (Fig. 9). However, Phenotype II larvae consumed 45% animal tissue, while Phenotype I larval guts contained roughly equal amounts of animal tissue and green algae. Larvae from the Middle Fork consumed large quantities of amorphous detritus (accounting for $>50\%$ of gut contents). Larvae from the Mainstream River contained $>50\%$ green algae, largely *Ulothrix*.

We observed a distinct shift in the trophic relationships of Phenotype II larvae in the North Fork (Fig. 10) during the winter. Diatoms comprised 80% of the gut contents and animal tissue decreased as a food item. Winter food habits of larvae from the Middle Fork were similar to those exhibited in the fall. Larvae from the Mainstream changed from consumers of green algae to consumers of diatoms. Animal tissue remained an important food item.

During the spring, dominance of animal tissue was observed among all groups with the notable exception of Phenotype I larvae in the Mainstream (Fig. 11). We have no explanation for this observed phenomenon other than that the appearance of green algae in the gut contents of the Type I larvae coincided with observed increased *Ulothrix* production at that site. The large amount of animal tissue consumed may be ex-

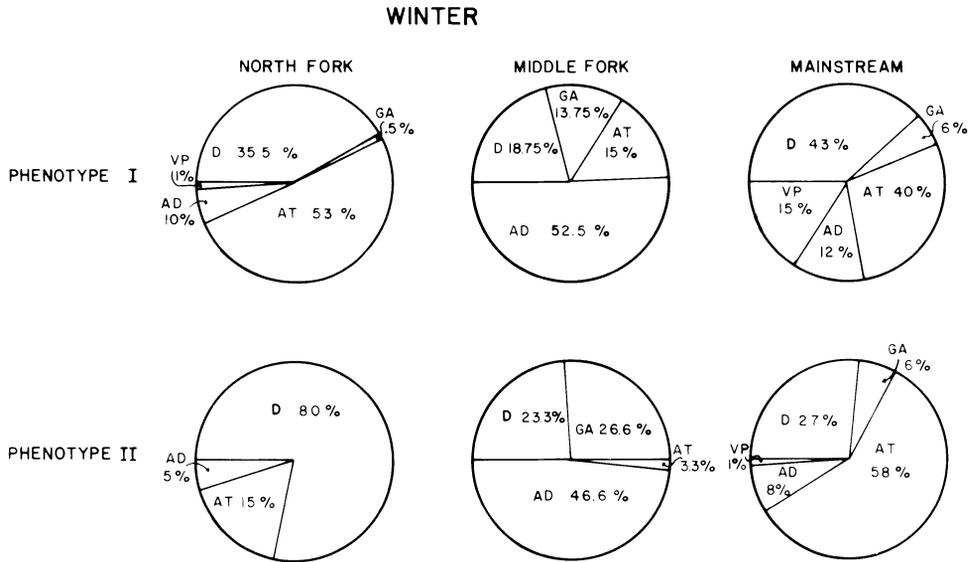


FIG. 10. Trophic relationships of *Arctopsyche grandis* by phenotype at the riverine sites during winter. Presentation as in Fig. 9.

plained by a possible increase in feeding activity and movement of prey species after ice-out, thus making them more susceptible to drift, and/or the more aggressive feeding of last-instar larvae due to an effort to maximize energy input into gonadal tissue in preparation for pupation and emergence. Frequently other aquatic insects, primarily early-instar Plecoptera, Ephemeroptera, chironomids and *Hydropsyche oslari*, were found in close association with *A. grandis* retreats. These taxa were the most prevalent in the gut, and thus, increasingly aggressive *A. grandis* larvae apparently exploited this source of animal tissue. Capture nets were maintained through the winter season at all sampling sites. Therefore, observed seasonal differences in gut contents were not a function of net maintenance.

Variance among stations for each season was high and reflects natural differences in the trophic structures of the sites. But, within-site differences between phenotypes indicate significant differentiation in food habits. An analysis of mesh size of the filter nets indicated no significant differences between phenotypes and a wide variation in mesh widths of both phenotypes. Consequently, the within-site differences in food ingested must have been a function of food selection by the larvae. This selection could have been accomplished by positioning nets in different areas or by differential selection of foods collected on the nets. We believe the former is more plausible, because retreats of the two phenotypes were consistently found in different microhabitats.

Larva-adult associations

The investigation of growth rates, microhabitat selection, relative site-specific abundance, and trophic

dynamics of the *A. grandis* larval phenotypes indicated a divergence of functional relationships. To resolve the specific consequences of the apparently different ecological roles played by the two larval phenotypes, it was necessary to determine firmly whether different species were involved or if a sexual dimorphism was occurring.

Twenty-three field-collected larvae were successfully reared to late-development pupae in the laboratory microcosms. An additional 35 late-development pupae were collected from the North Fork. Thirty-seven of the 58 pupae were from Phenotype I larvae, 21 from Phenotype II larvae. In all 58 specimens, adult taxonomic characteristics, determined from pharate adults, were typical of *A. grandis*. Twenty-one of the 37 Phenotype I pupae were male and 16 female, while all 21 of the Phenotype II larvae were females. This apparent interspecific distribution of sexes explains the frequency distribution of last-instar larvae shown in Fig. 4 and discussed above in relation to life histories: first-mode Type I larvae were all or predominantly males, second-mode Type I larvae were all or predominantly female, and all Type II larvae were female.

Speculation on adaptive significance

The competitive exclusion principle is one of the mainstays of ecological theory (Pianka 1974, Huston 1979), and although complete exclusion has been achieved in simple laboratory systems (Gause 1934), it is unlikely to occur readily in complex and diverse systems with multiple feedback mechanisms (Hutchinson 1961). Discrete phenotypic differentiation within a species may result in interactions which encourage ecological divergence. The tendency for a population

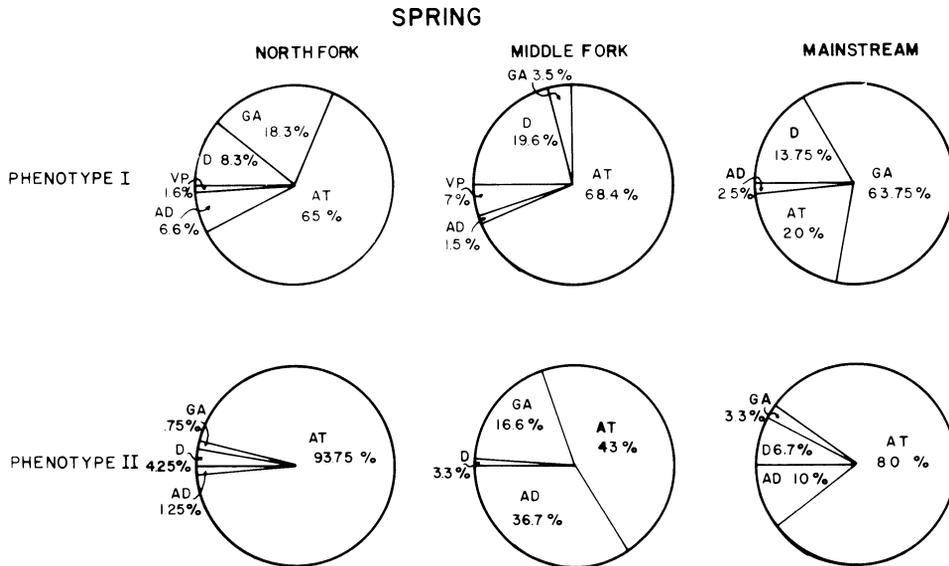


FIG. 11. Trophic relationships of *Arctopsyche grandis* by phenotype at the riverine sites during spring. Presentation as in Fig. 9.

experiencing intense intraspecific competition to increase utility along a resource gradient may lead to a phenotypic deviant, which then may exploit an overlapping, yet different, segment of the resource. This should result in a shift in optimal resource use by the deviant. Greater utilization of resources is insured for the species, thereby enhancing its fitness.

A. grandis may have developed the Type II phenotype in response to an abundance of large interstitial space in the river segments, which was insufficiently exploited by the "typical" phenotype. However, the second phenotype is more restricted in habitat utilization. We found it abundant in fifth- and sixth-order river segments where large interstitial spaces and diatomaceous periphyton characterized the substrate and the annual thermal regime yielded a temperature summation of 2300 to 2400 degree days. It was not collected from tributary creeks, such as Trail Creek, which had an annual temperature summation of 1900 degree days. Therefore, the Type II morph may require the specific thermal criteria associated with the large, open-canopied river and, thus, is excluded from lower order streams, even though the microhabitat spatial requirements may be suitable. Regardless of this, we believe that the development of the Type II phenotype was in direct response to a niche expansion phenomenon in river segments, which has extended the scope of resource utilization. Also, this adaptation has apparently increased the production of females, which probably increases species fecundity. Dimorphism among females is known to occur in the aquatic order Odonata. In the damselfly genus *Ischnura*, several species exhibit a female which is phenotypically similar to the male and a female phenotypically dissimilar to the male (Johnson 1966 and 1969). However,

unlike *A. grandis*, the dimorphism among females in the Odonata occurs in the adult stage, not in the larval stage. These findings do not preclude the possibility that Type II males may exist, but were not found, or that Type II males may exist in other portions of the species' range. Also, it is possible that Type II females are parthenogenic. This interpretation is consistent with the hypothesis suggested by Powell and Taylor (1979) that environmental diversity and intraspecific habitat choice establish genotype variability. The apparent phenotypic variability of this species may well explain its wide distribution among and between drainage basins in western North America. If the two phenotypes can be reared from eggs of known origin (e.g., from mated and unmated females of each phenotype) to adult, it should be possible to determine if Type II females are parthenogenic or possess other genetic advantages. We have been unable to hatch sufficient numbers of preselected eggs and late-instar larvae are difficult to rear, due to cannibalism. Study of genetic variability across geographic ranges, possibly by use of electrophoresis, should also help firmly explain the apparent adaptive plasticity in *A. grandis* reported here.

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