## 4 Nymph Ecology and Behavior

The estimated 1,800 world and 575 North American Plecoptera species (Arnett 1983) are important, integral components in stream ecosystems. The various species within given stream biotopes have temporally segregated their life histories and partitioned their food and space resources, and they play vital roles in the energy economy and production of these systems. Despite this importance, the precise life histories, trophic interactions, growth and development, spatial distribution, and behavior of nymphs are well known for less than 5% of the species.

Hynes (1976) reviewed the biological knowledge of stoneflies through 1974; it is our intent in this chapter to update the rapidly expanding knowledge of stonefly nymph biology, particularly in reference to North American fauna, through the 1985 and to some extent 1987 literature. The references used to illustrate biological aspects or patterns related to nymphs are not to be considered exhaustive, and a more complete referencing of nymph biology can be found for respective species in the generic sections of each family (Chapters 7-15). A brief overview of North American Plecoptera biology and tabular summaries of life cycle patterns and ecological and distributional data, as well as keys to the genera, were presented by Harper & Stewart (1984).

## LIFE CYCLES AND VOLTINISM

The known life cycles of North American stoneflies are either univoltine (1 yr) or semivoltine (2 or more yr) (Hynes 1961 classification, 1976). Both types may be: (1) heterodynamic (Wigglesworth 1974, Butler 1984), having an egg or nymph diapause, or (2) homodynamic, having no regular period of dormancy. Development of species with heterodynamic cycles is referred to as fast (short-term development and cohort production interval), and that of species with homodynamic cycles indicated as slow (development over most of the required generation time). Only a few species such as *Zapada columbiana* (Mutch & Pritchard 1982), *Paragnetina media* (Harper 1973b), and *Calineuria californica*, all from northern latitudes, have been shown to possibly require 3 yr for development. The term "merovoltine" was introduced by Pritchard (1983) to describe these longer cycles.

Determinate Voltinism. Voltinism seems to be determinate for species with restricted ranges and for some widespread species, although few studies have been designed to examine any differences in populations of endemic species or northern and southern populations of ubiquitous species. Ernst & Stewart (1985a) showed that three univoltine, fast species, *Amphinemura delosa*, *Prostoia completa*, and *Haploperla brevis* (Fig. 4.1A,B;4.2B) from an Oklahoma Ozark stream had cycles generally similar to their northern counterparts in, or adjacent to, Canada (Harper & Magnin 1969; Coleman &