Zoosymposia 5: 413–419 (2011)
www.mapress.com/zoosymposia/

ISSN 1178-9905 (print edition)
ZOOSYMPOSIA
ISSN 1178-9913 (online edition)

The biology of the limnephilid caddisfly *Dicosmoecus gilvipes* (Hagen) in Northern California and Oregon (USA) Streams

Vincent H. Resh, Morgan Hannaford, John K. Jackson, Gary A. Lamberti & Patina K. Mendez*
Department of Environmental Science, Policy & Management, University of California, Berkeley CA 94720-3114 USA
**Corresponding author: resh@berkeley.edu*

Abstract

The limnephilid caddisfly *Dicosmoecus gilvipies* (Hagen) occurs in many streams of northwestern United States and British Columbia. Because of the large size of the fully grown larva, its synchronous emergence pattern, and its frequent imitation by fly-fishing anglers, *D. gilvipes* is one of the best known North American aquatic insects. Egg masses are found at the bases of *Carex* sedges. Cases of early larval instars are made of organic material and detritus; 3rd and 4th instars incorporate pebbles into cases. The 5th-instar case is made entirely of mineral material. Larvae can travel up to 25 m per day, and are predominantly scraper-grazers. Fifth instars attach their cases to the underside of boulders in mid-summer and remain dormant until pupation in autumn. All northern California populations known are univoltine. Adult females use sex pheromones to attract males; most males come to trapped females in the 1st hour after sunset. In laboratory studies, males and females fly during the mate attraction period but generally not at other times. Males but not females exhibit circadian rhythms that govern flight periodicity. In enclosures to study biotic interactions, the density of *D. gilvipes* larvae has a negative effect on the densities of sessile grazers. This species has been widely used in trophic and behavioral studies conducted in the laboratory and field, and may be a model organism for ecological studies of caddisflies and other benthic macroinvertebrates.

Key words: Trichoptera, life history, sessile grasers, Northwest USA

Introduction

The limnephilid caddisfly *Dicosmoecus gilvipes* (Hagen, 1875) occurs in streams from northern California and Colorado, north to British Columbia, and east to Alberta, Montana, Idaho, and Nevada (Anderson 1976; Nimmo 1977; Morse 2009). Because of the large size of the fully grown larva (25−30 mm), its high population densities, and its synchronous emergence pattern, *D. gilvipes* is one of the best known aquatic insects in California and the Pacific Northwest. Fly-fishing anglers refer to it as the "October caddis" or "Autumn caddis" because of its fall emergence period. This species is also called the “giant orange sedge” by these anglers, perhaps for its large adult size and ruddy color.

A variety of studies have been conducted on this species over the past 3 decades at the University of California, Berkeley, and at Oregon State University. For example, in the McCloud River (Siskiyou Co., CA), substrate relationships, movement patterns, foraging ecology, and larval behavior were examined (e.g., Resh 1978, 1979; Lamberti & Resh 1979; Hart & Resh 1980). In Big Sulphur Creek (Sonoma Co., CA), detailed studies on adult behavior such as flight activity, pheromone production, mating, and larval behavior were conducted (e.g., Hart 1981; Resh & Wood

Accepted by K. Majecka, J. Majecki & J. Morse: 1 Nov. 2010; published: 10 Jun. 2011

1985; Jackson & Resh 1989, 1991), and in the Eel River (Mendocino Co., CA) a variety of *D. gilvipes* experimental-biotic-interaction studies (Power *et al*. 2008 and references therein) were conducted in addition to studies elucidating its phenology (Hannaford 1998). Oregon researchers have studied *D. gilvipes* in natural habitats (e.g., Li & Gregory 1989, Wright & Li 1998) and in a series of grazing studies in artificial streams (e.g., Lamberti *et al*. 1987, 1992, 1995). A life history of the closely related species *Dicosmoecus atripes* (Hagen) has been described in an Alberta stream (Gotceitas & Clifford 1983). In this paper, we synthesize the outcomes of these many studies to describe the life history and ecology of *D. gilvipes* in northern California and Oregon streams.

Life cycle

Egg masses of species in this genus are reported to occur on tree leaves over-hanging streams (e.g., Wiggins & Richardson 1982, Wiggins 1996). However, we have not found egg masses in these reported locations despite extensive search for these potential oviposition sites. Instead, we have found egg masses of *D. gilvipes* among the bases of stems of *Carex* sedges located along stream margins and in isolated islands in 3rd and 4th order streams. Anecdotal observations from anglers suggest females may oviposit directly on the water surface.

Larvae have 5 distinct instars, and 5th instars attach their cases to the underside of boulders in mid-summer and remain dormant until pupation in autumn. Larvae grow to be quite large and 5th instars commonly grow > 30 mm in length. This size contrasts with the 40 mm maximum length of populations found in Montana (Hauer & Stanford 1982). The prepupal diapause for *D. gilvipes* lasts from 4−6 weeks. Pharate adults emerge in late afternoon and then swim and crawl to shore.

All populations observed in northern California are univoltine (e.g., Fig. 1), which also appears to be the case in Oregon. Although eggs are oviposited in autumn, first instars are not typically found until spring when floods subside in these mediterranean-climate streams. During late spring, we find that *D. gilvipes* larvae are among the first to colonize flood-scoured mid-channel areas of streams. The majority of the year is spent in the larval stage, followed by a late summer prepupal diapause. Adults exhibit a synchronous emergence period. The univoltine life cycle of *D. gilvipes* in northern California and Oregon contrasts with that reported in the studies of Hauer and Stanford (1982), who found a 2-year life cycle in the higher-elevation and -latitude sites in the Flathead River, Montana. There, 1st instars appear in spring, grow throughout the summer, but then overwinter as 5th instars, attaching their cases to the undersides of rocks in an apparent diapause. Larvae are again active when temperatures are greater than 1°C. After a 4−6 week prepupal diapause, adults in Montana emerge from August to October.

In the Eel River, CA, temperature also influences development. In terms of the average accumulated degree days (>0° C, Snyder 1985), *D. gilvipes* reached the 5th instar 2 weeks earlier at a downstream site (2 585 degree days) than at a site located 4 km upstream (2 485 degree days). Below the downstream site *D. gilvipes* were rare, perhaps reflecting temperature limits or related intolerances (Hannaford 1998).

Ecology and behavior

Larvae are predominantly scraper-grazers with gut contents containing diatoms, filamentous algae, some mineral particles, and occasional animal parts (e.g., other caddisfly larvae). However, animal prey items have not been reported in Oregon studies of this species (e.g., Li and Gregory 1989).

Densities in northern California streams may be as high as 80-100 larvae/m^2 (M. S. Parker, Southern Oregon University, Personal Communication). In some unshaded desert streams in Oregon, *D. gilvipes* may account for 55-96% of the benthic macroinvertebrate biomass (Tait *et al*. 1994).

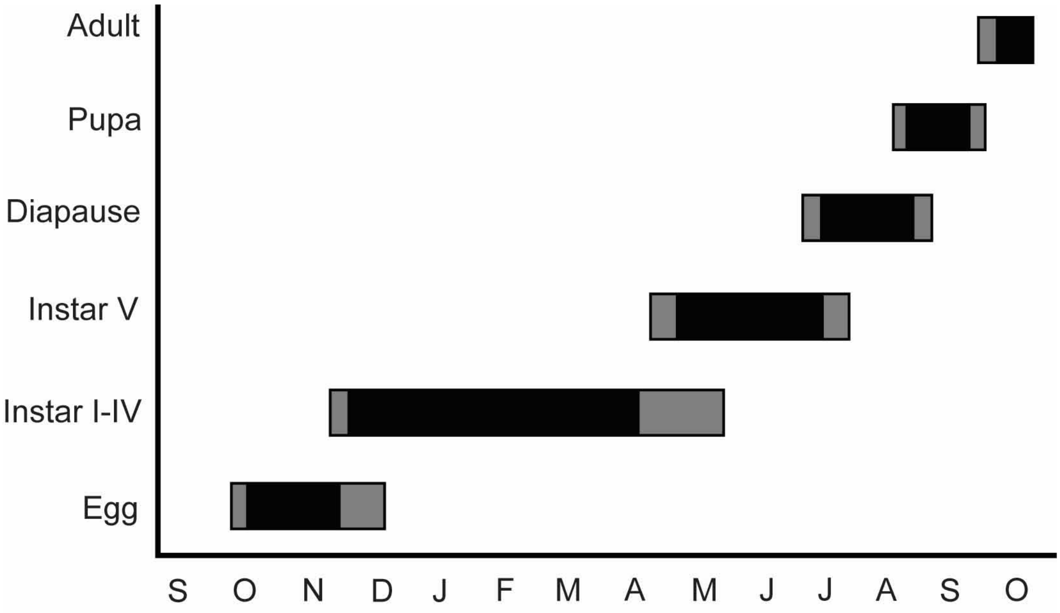

FIGURE 1. Phenology of *D. gilvipes* in the McCloud River, California (from Hannaford 1998). Darker areas represent the time when the majority of the population is in a particular stage; lighter areas represent the full temporal range observed.

Larvae of *D. gilvipes* are exceptionally mobile, capable of traveling up to 25 m per day in the McCloud River of California (Hart & Resh 1980). Movement patterns follow a random-walk model, with larger larvae moving farther than smaller ones and there is a pronounced diel rhythm to movement in which more travel occurs during the day (Hart & Resh 1980). In Big Sulphur Creek, larvae feed in areas with more food and minimize their “turn angle” (e.g., they tend to travel in straight lines when searching for food patches), possibly reducing their probability of returning to a recently grazed patch (Hart 1981).

Larvae in the McCloud River spend the majority (approximately 2/3) of their time feeding (Hart & Resh 1980) and in some streams larvae may compete exploitatively for food. In Oregon streams, Li and Gregory (1989) found that different instars spend different amounts of time feeding compared to casemaking, and feeding on diatoms compared to feeding on filamentous algae. When grazing, impact on their food resources can be so high that, when they begin to pupate, there is a noticeable periphyton increase with their absence.

Cases of early instars are made of organic material and detritus, with 3rd instars incorporating some mineral materials into their cases. Fourth instars add more mineral particles and the 5th-instar case is made entirely of mineral material, often with an ornate arrangement of rocks. This case-structure transition occurs in late spring in northern California rivers when discharge recedes to summer low flows.

The mating system of *D. gilvipes* involves sex pheromones produced by paired exocrine glands located on the 5th abdominal sternite (Resh & Wood 1985). This is the location reported for several other species (but not all) of Trichoptera that have been found to use a pheromone mating system (Resh *et al*. 1987). Studies in northern California indicate that adult females use sex pheromones to attract males during the night, with 58% of males flying to trapped females in the 1st hour after sunset (Jackson & Resh 1991). In laboratory studies, males and females flew during the mate attraction period but generally not at other times. Males but not females exhibit circadian rhythms that govern flight periodicity, with females rarely flying during periods of pheromone release presumably to make the pheromone trail most effective. These brief but coordinated activities may contribute both to reproductive success and to reproductive isolation. Copulation lasts up to 16 hours, and mating pairs remain *in copula* throughout the mate attraction period, ensuring that a female mates with 1 male per day (Jackson & Resh 1991).

The importance of *D. gilvipes* as prey for birds has been noted in a variety of studies throughout their range, such as harlequin ducks (Wright *et al*. 2000) in Oregon and dippers (Teague *et al*. 1985) in California. In studies in Utah, Harvey and Marti (1993) suggested that *D. gilvipes* inhabits deeper water in response to dipper predation.

Dicosmoecus gilvipes may also be involved in disease transmission. For example, in California, horses ingesting *D. gilvipes* may become infected with trematodes that cause Potomac Horse Fever (Madigan *et al*. 2000).

Laboratory and field studies of biotic interactions

Dicosmoecus gilvipes has emerged as a prime model for a variety of ecological studies of caddisflies and other benthic macroinvertebrates. For example, because of their large size and the ease of keeping them in the laboratory, several laboratory studies of grazer influences on algal composition (e.g., Steinman *et al*. 1987a,b; DeNicola *et al*. 1990; Walton *et al*. 1995) and comparisons of grazer effects (e.g., Lamberti *et al*. 1987, 1992, 1995) have been conducted using them. Most of these studies reveal strong effects of these caddisflies on algal assemblages and in sequestering energy, thereby confirming observations from field studies. Other studies in stream channels have examined relationships with sediment size and found different survival rates correlated with instar (e.g., Parker *et al*. 2002). Wright and Li (1998) found similar differential survival from areas in an Oregon stream with human recreational activity.

In a field study in the Eel River, Hannaford (1998) examined the influences of *D. gilvipes* on algae and other benthic macroinvertebrates in a series of experiments that locally excluded *D. gilvipes*. He used cylindrical cages, each 0.8 m^2 in area, at 6 sites. Cages were constructed from 6-mm mesh hardware cloth to create the 3 treatments: (1) enclosures (with 40 4th and 5th instar *D. gilvipes*/m^2), (2) exclosures (where access by *D. gilvipes* was denied), and (3) ambient-density controls (which were open-access cages with large 10x20 cm holes cut into the base to allow entrance). He found that fewer sessile invertebrates colonized enclosures than colonized either exclosures or controls (ANOVA $F_{[2,5]=}$12.77, $p<0.0018$) and that algal biomass was significantly lower in enclosures than in exclosures or controls (ANOVA, $F_{[2,5]}=4.84$, $p<0.0375$). A significant negative correlation existed between the observed densities of active *D. gilvipes* larvae and the densities of sessile macroinvertebrates in the control cages ($r=-0.91$, $p<0.013$, Fig. 2).

In a second study, Hannaford (1998) examined interference effects of *D. gilvipes* on the numerically dominant, sessile, algal feeder in the stream, *Tinodes* (Psychomyiidae) caddisfly larvae. In boxes stocked with cobbles colonized by *Tinodes* larvae in their tube cases, *D. gilvipes* were added to half of the boxes and the percent occupancy of the tubes was recorded before and 24 hours after the addition. Hannaford found evidence of direct interference in a series of enclosures containing *Tinodes* caddisfly larvae in that 37% of the epilithic *Tinodes* tubes (n=38) were damaged in the presence of *D. gilvipes* larvae after 24 hours of exposure. Significantly more *Tinodes* larvae abandoned their tubes in treatment boxes compared to control boxes (t-test, $p<0.0065$, n=10).

Furthermore, 20% of the *D. gilvipes* guts contained *Tinodes* body parts, which suggests that *D. gilvipes*, normally classified as a grazer, may also be a predator.

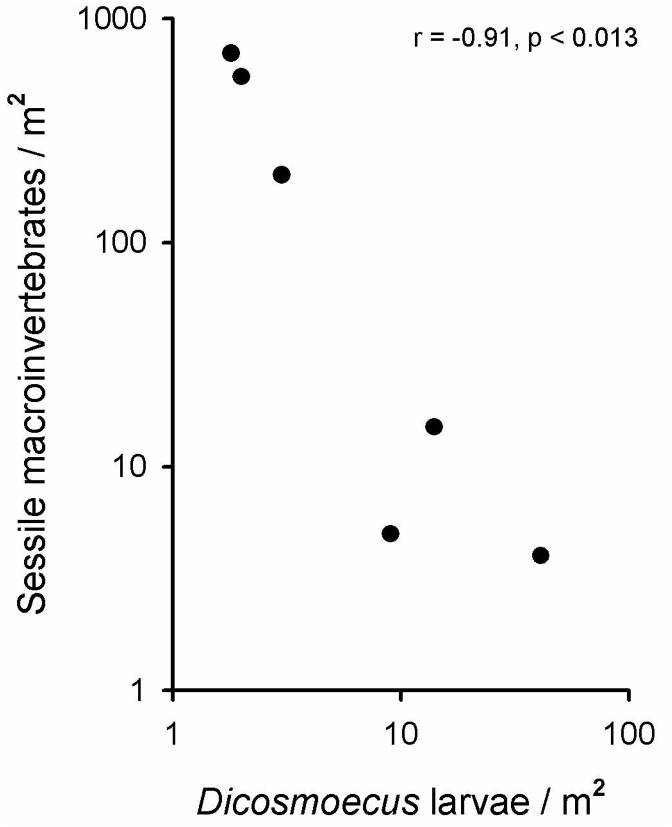

FIGURE 2. Number of sessile macroinvertebates in relation to number of *D. gilvipes* in enclosure experiments in the Eel River, California (from Hannaford 1998).

Conclusions

Perhaps because of its simple life cycle, its tolerance to being maintained in laboratory streams, its ability to be observed directly because of its large size, and its high densities, *D. gilvipes* has provided important insights into stream community dynamics. For example, in addition to the studies described above, *D. gilvipes* has been a key component in the experimental studies on food webs and trophic dynamics conducted by Mary Power over 18 years in the Eel River (Power *et al.* 2008). It also has been used to demonstrate how benthic sampling can be made more efficient (Resh 1978, 1979; Lamberti & Resh 1979). Perhaps most noteworthy, *D. gilvipes* has been shown to serve as a model organism for the variety of studies to elucidate the natural history and ecological role of stream-dwelling caddisflies.

Acknowledgements

We thank our collaborators and the scores of undergraduate and graduate students at the University of California, Berkeley, and Oregon State University that have assisted in field and laboratory studies of this species.

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