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Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (U.S.A.)

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SUMMARY

1. Larvae of cased caddisflies (Limnephilidae and Phryganeidae) are among the most abundant and conspicuous invertebrates in northern wetlands. Although species replacements are often observed along permanence gradients, the underlying causal mechanisms are poorly understood. In this paper, we report on the distributional patterns of caddisflies in permanent and temporary high-altitude ponds, and how those patterns reflect differences in life history characteristics that affect desiccation tolerance (fundamental niches) versus constraints related to biotic interactions (realised niches).
2. Species (*Hesperophylax occidentalis* and *Agrypnia deflata*) that were encountered only in permanent ponds are probably restricted in distribution by life history (no ovarian diapause, aquatic oviposition, and/or inability to tolerate desiccation). Although the egg masses of *H. occidentalis* tolerate desiccation, the larvae leave the protective gelatinous matrix of the egg mass because adults oviposit in water.
3. Three species (*Asynarchus nigriculus*, *Limnephilus externus* and *L. picturatus*) have life history characteristics (rapid larval growth, ovarian diapause and terrestrial oviposition of desiccation-tolerant eggs) that should facilitate the use of both permanent and temporary habitats. However, *A. nigriculus* is rare or absent in most permanent ponds, and *L. externus* and *L. picturatus* are rare or absent in most temporary ponds. Experimental data from a previous study on the combined effects of salamander predation and interspecific interactions among caddisflies (e.g. intraguild predation) suggest that biotic interactions limit each species to a subset of potentially exploitable habitats.
4. Many wetland invertebrates exhibit species replacements along permanence gradients, but few studies have separated the relative importance of the effects of drying *per se* from the effects of biotic interactions. Our results emphasise the complementary roles of comparative data on life histories and experimental data on competition and predation for understanding invertebrate distributions along permanence gradients.

Keywords: caddisfly, life history, niche, permanence gradients, wetlands

Introduction

Ecologists have often observed shifts in community composition between permanent and temporary lentic habitats (Batzer & Wissinger, 1996; Schneider & Frost, 1996; Wellborn, Skelly & Werner, 1996; Williams, 1996; Schneider, 1999; Wissinger, 1999). Although there is an abundance of comparative evidence for species replacements along permanence gradients for a wide array of freshwater taxa, the underlying mechanisms are well studied only for amphibians. In amphibians, species replacements along permanence gradients reflect tradeoffs between traits that facilitate coexistence with different types of predators,

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or tradeoffs between vulnerability to permanent-habitat predators and rapid development in temporary habitats (Wellborn *et al.*, 1996). Although there are equally compelling comparative data for the importance of permanence for structuring lentic invertebrate assemblages, few studies have attempted to disentangle the underlying mechanisms (but see McPeek, 1990a,b; McPeek, Schrot, & Brown, 1996).

Different species of cased caddisflies (especially in the Family Limnephilidae) are often segregated in permanent and temporary habitats (Wiggins, 1973; Otto, 1976; Wiggins, Mackay & Smith, 1980; Berte & Pritchard, 1986; Wissinger *et al.*, 1996; Sangpredub, Giller & O'Connor, 1999; Meyer & Meyer, 2000). 'Permanent habitat' and 'temporary habitat' species are assumed to differ in the degree to which one or more stages tolerate desiccation; i.e. patterns of caddisfly distribution are assumed to reflect mainly differences in fundamental niches (in the Hutchinsonian sense of environmental requirements; Leibold, 1995). This historical emphasis on desiccation tolerance in caddisflies overlooks a central feature of niche ecology that the realised niche of most species reflects both environmental tolerances and the effects of biotic interactions (e.g. Connell, 1961a,b; see review and other examples in Colwell & Fuentes, 1975; Schoener, 1989; Leibold, 1995; Begon, Townsend & Harper, 1998).

Caddisfly species replacements along permanence gradients are particularly obvious in high altitude wetlands; species that dominate in permanent ponds differ from those in autumnal (dry only in autumn) and vernal (dry except in spring) habitats (Wissinger *et al.*, 1996, 1999a,b). Correlations with habitat permanence are confounded by shifts in the presence of tiger salamanders (*Amybstoma tigrinum nebulosum* Hallowell). Stages of the salamanders that prey on caddisflies occur only in permanent habitats at subalpine and alpine (>3000 m) altitudes, but mainly in autumnal habitats at montane (2000–3000 m) altitudes (Wissinger *et al.*, 1999a; Whiteman & Wissinger 2002). Previous research found that an understanding of how biotic interactions shift along permanence gradients only partially explains observed caddisfly distributions (Wissinger *et al.*, 1996; Wissinger *et al.*, 1999a). Thus, we suspected that a complete understanding of caddisfly distributions among different types of habitats required complementary data on life history and desiccation tolerance.

The purpose of this study was to describe the life histories of caddisflies in high altitude wetlands (Wissinger *et al.*, 1999a,b). We focused on those life history characteristics that could affect their ability to exploit temporary waters (e.g. timing of emergence and egg deposition, rates of larval growth and development, diapause, and/or desiccation tolerance in one or more life stages). We combine these life history data with the results of previous studies to present a synthesis of the types of factors that affect caddisfly distribution at our study sites. We also compare our findings to life histories in low altitude populations of limnephilid and phryganeid caddisflies (Novak & Sehnal, 1963; Gower, 1967; Winterbourn, 1971a,b; Wiggins, 1973; Wiggins *et al.*, 1980; Martinson & Ward, 1982; Parker & Wiggins, 1985; Berte & Pritchard, 1986; Mathis, 1990; Meyer & Meyer, 2000). Our results suggest that the combined effects of drying in summer and freezing in winter help explain several unique life history traits observed at high altitudes.

Methods

Study sites and natural history

We studied the life histories of one phryganeid, *Agrypnia deflata* Milne and four limnephilid caddisflies (*Asynarchus nigriculus* Banks, *Limnephilus externus* Hagen, *Limnephilus picturatus* McLachlan, *Hesperophylax occidentalis* Banks) from 1989 to 2000 in subalpine and alpine (>3000 m altitude) ponds located in or near the Mexican Cut Nature Reserve in Gunnison County, CO, U.S.A. (39°2′N–107°4′W) (Fig. 1). The region receives an average of 130 cm of rain-equivalent precipitation annually, about 100 cm of which falls as snow (USDA National Resource Conservation Service SNOTEL Station at Elko Park and NOAA weather station at RMBL). Snowfall ranges from 1000 to 1500 cm with an average maximum snow pack of 300–500 cm. Snowmelt is the main hydrological input to the ponds and wetlands at Mexican Cut and enters from intermittent streams and overland flow. The three main types of aquatic habitats at Mexican Cut are:

1. *Alpine (3600–3900 m) ponds and lakes* including two avalanche-impact ponds on the upper shelf of Mexican Cut (53 & 54 in Fig. 1), bedrock depressions along Galena ridge and the upper shelf (e.g. 57, 58 &

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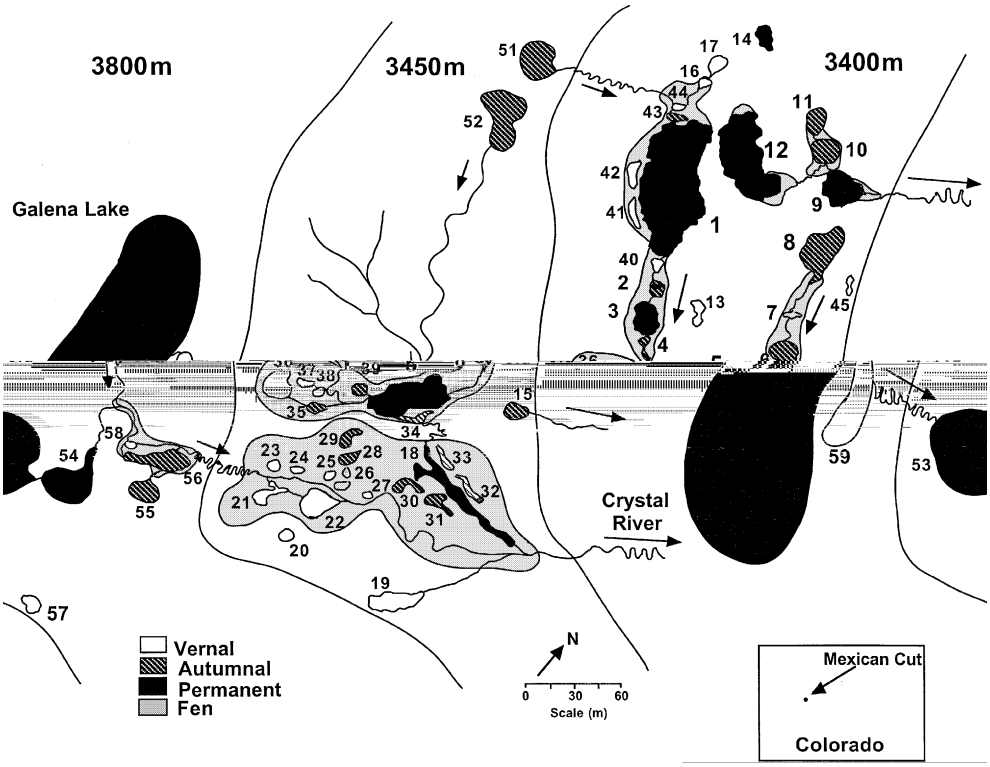

Fig. 1 Schematic map of aquatic habitats at the Mexican Cut Nature Reserve in west-central Colorado. Vernal ponds dry by mid-summer and do not fill until spring, autumnal ponds dry in some years in late summer and refill in autumn, and permanent ponds have not dried in at least the last 50 years. Contour lines mark the boundaries between the relatively flat shelves at different altitudes on the Reserve (modified from Wissinger *et al.*, 1999b). Arrows indicate direction of stream flow.

59), and Galena Lake situated at the head of the catchment. The substratum is predominately bedrock or rocky rubble with little or no organic matter. These habitats are the last to melt (late June to early August), and ice and avalanche debris occasionally persist throughout the summer. There is no submergent vegetation and emergent plants (*Carex aquatilis* Wahlenb.) are limited to small patches along the shorelines. These habitats are all above treeline and surrounded by alpine meadow (see Langenheim, 1962).

2. *Intermittent alpine and subalpine streams* that flow from the lake and between the wetlands on the upper and lower shelves. The streams typically dry in late summer, although permanent pools persist in bedrock depressions and 'flow-through' ponds (e.g. 18, 53, 54) on both shelves.

3. *Subalpine wetlands* on the upper and lower shelves (Fig. 1). There are over 50 shallow (0.2–1.5 m depth) ponds that vary in size (<4 to >4000 m^2), thickness of organic substrata (<10 cm to >1 m), hydroperiod and water chemistry (moderate to low alkalinity, oligotrophic to ultraoligotrophic, slightly basic to slightly acidic; details in Wissinger & Whiteman, 1992; Wissinger *et al.*, 1999b). Most of these ponds are embedded in fens dominated by *Carex aquatilis*, *Caltha leptosepala* DC. *Trollius laxus* Salisb., *Juncus confusus* Coville, *Deschampsia caespitosa* Beauv, *Salix planifolia* Pursh. and *Vaccinium caespitosum* Michaux (Buck, 1960). Many are covered by a short lawn of submergent vegetation (*Isoetes bolanderi* Engelmann) and bordered by stands of emergent sedges (*Carex aquatilis*). Additional details about the physical and biological characteristics of these wetland habitats are summarised in Wissinger *et al*. (1999b). The wetlands on the lower shelf are just below the treeline and surrounded by open spruce-fir woodland (*Picea engelmanni* Englemann – *Abies lasiocarpa* Hooker).

Following Wiggins (1973) and Wissinger (1999), we identified three hydroperiod types: permanent, autumnal (dry in late summer but typically refilled before winter, and vernal [filled after snowmelt and

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dry by early summer (Fig. 1)]. Previous work at Mexican Cut indicates that invertebrate community composition is strongly correlated with hydroperiod and covarying abundance of the aquatic stages of salamanders (Wissinger *et al*., 1999b). Salamanders take 2–5 years to develop at subalpine altitudes; thus the stages that prey on caddisflies (>1-year-old-larvae and paedomorphic adults) occur only in permanent ponds (Whiteman, Wissinger & Bohonak, 1994; Whiteman, Wissinger & Brown, 1996; Whiteman & Wissinger, 2003). At montane altitudes, salamanders can complete development in autumnal ponds before drying, and are therefore top predators on caddisflies in both permanent and autumnal habitats (Whiteman & Wissinger, unpublished data).

Species distributions and larval development at Mexican Cut

There were three phases to our study of the distribution and larval development of the five caddisfly species at Mexican Cut. From 1989 to 1991, four quantitative samples were taken at least biweekly (weekly during pupation) using a 0.25-m^2 drop box (after Wissinger, 1989) in four permanent (numbers 1, 5, 9, 12), four autumnal (6, 8, 10, 11) and four vernal (7, 13, 15, 19) ponds (see Fig. 1). Initially, larvae were sorted live from detritus and preserved in 90% ethanol to establish instar categories based on head width and body mass (Appendix 1). Subsequently, larvae collected during the censuses were identified to species and instar at pond side, and then returned live to minimise sampling effects on the populations. These data established the basic pattern of species distribution and larval growth that were necessary for studying biotic interactions among caddisflies (Wissinger *et al*., 1996). In the second phase of the study (1992-present) we expanded the coverage of annual quantitative censuses to include four habitats with *L. picturatus* (ponds 35 & 39) and *H. occidentalis* (pond 54 and Galena Creek). Four D-net sweep samples (0.33 m^2) were taken at least monthly along the shoreline of each of the 16 habitats. These data were collected as part of an ongoing monitoring programme to track long-term fluctuations in caddisfly populations (Wissinger, unpublished data). Finally, in a third phase of sampling (1995–98), the distribution of caddisfly species across >60 aquatic habitats at Mexican Cut was determined from monthly presence–absence surveys. These data were collected as part of a broad community survey of all invertebrates across all types of hydroperiods. Ordination of these data revealed that hydroperiod and the covarying abundance of salamanders are the two most important variables that are correlated with community composition at Mexican Cut (Wissinger *et al*., 1999b).

The developmental phenology of each species differed among ponds depending on when they melted in spring. Thus, a composite summary of development across ponds would misrepresent the degree of synchrony within each pond. In this paper, we present larval instar data for each species from one representative pond and describe how the phenology in that population compares with others at Mexican Cut. Although the actual dates of ice melt differed among years, there is a predictable sequence of pond melting each year; thus, the relative phenology of larval growth among ponds is preserved from year to year (Wissinger *et al*., 1999b).

Pupation and emergence

Two species affixed stony pupal cases to rocks and wood (*Hesperophylax occidentalis, Asynarchus nigriculus*); thus, we could easily observe the timing of pupation and emergence from visual censuses. For the species that pupated in soft sediments (*Limnephilus externus, Limnephilus picturatus, Agrypnia deflata*), pupae were collected as part of weekly larval censuses using the methods described above. In 1989–92, we also placed late final instar (metamorphotype) larvae of all species into 0.25 m^2 screen cages with overhead emergence traps (described in Wissinger *et al*., 1996) to monitor closely the timing of pupation and emergence, and to confirm larval–adult associations (see Wiggins, 1996).

Mating, egg deposition and resistance to desiccation

During and after emergence, we searched for adults in the vegetation along the shoreline and adjacent terrestrial habitats to observe flight and mating behaviour. We collected females and dissected eggs to infer their reproductive status at emergence and during the subsequent flight season. Morphological and egg stage terminology (stages A–D) followed Khalifa (1949), Unzicker (1968), Gower (1967) and

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Wiggins (1996). The timing and location of egg deposition was inferred from: (i) direct observation of ovipositing females, (ii) searches for egg masses attached to submerged aquatic substrata, if females oviposited in filled ponds (*Agrypnia* and *Hesperophylax*) and (iii) searches for egg masses under rocks and woody debris in dried ponds and in terrestrial habitats along the shores of both dried and wet basins (*Asynarchus* and *Limnephilus* spp.).

From 1996 to 1999, we conducted a series of short-term laboratory studies to understand the details of early development and infer desiccation tolerance. To observe embryological development, egg masses attached to aquatic (*Agrypnia* – vegetation; *Hesperophylax* – rocks) or terrestrial substrata (*Asynarchus and Limnephilus* spp. – under rocks or wood) were collected and held in small laboratory aquaria (4.5 L; 300 cm^2 bottom area). *Agrypnia* and *Hesperophylax* egg masses were held on 2 cm natural substrate with 5 cm of pond water, and the other species on moist soil. To determine the desiccation tolerance of these egg masses, we collected six egg masses of each species and transferred them to aquaria with only terrestrial habitats available (i.e. under rocks on moist sand). Larvae were transferred to water after 30 days to assess survival. To study the effects of inundation on the emergence of first instars from the egg matrix, six egg masses of each of the four limnephilid species were collected and submerged in 5 cm of water in aquaria. First instar larvae that left the egg mass matrix and built cases were transferred to small microcosms (100 cm^2 bottom area; 5 cm detritus from pond 8; 5 cm water), and slowly cooled to 3 °C, where they were held for 48 h. We then froze the microcosms until ice had formed to the bottom of the substratum, melted the ice and recorded survival. Finally, we determined the desiccation tolerance of final instar larvae by placing one individual in a microcosm ($n = 12$ for each species) fitted with an emergence chamber (100 cm^2 bottom area; 2 cm detritus and 5 cm water). We allowed the microcosms to dry over a 7–10-day period and then, to assess survival, rehydrated them after 48 h.

Caddisfly assemblages at other study sites

During summers 1995–98, planktonic and benthic invertebrates, salamanders, vegetation and a variety of abiotic data including drying times were surveyed in 80 habitats near Mexican Cut, as part of a regional study of montane and subalpine wetland communities (Wissinger *et al.*, 1999b; S.A. Wissinger & W.S. Brown, unpublished data). In this paper, we present previously unpublished data on the caddisfly populations in those habitats to corroborate the distributional patterns observed at Mexican Cut with respect to habitat duration (permanent, autumnal, vernal) and salamanders. In addition to *A. deflata, A. nigriculus, L. externus* and *L. picturatus*, we also regularly encountered *Limnephilus secludens* Banks, *Limnephilus tarsalis* Banks, and *Grammotaulius lorretae* Denning.

Results

Patterns of distribution and abundance

There was considerable habitat segregation among the caddisfly species at Mexican Cut (Fig. 2). *Hesperophylax occidentalis* occurred mainly in streams and 'flow-through' permanent ponds in the outflow drainage of Galena Lake (ponds 53 & 54) and the lower shelf wetlands (ponds 4 & 18). Elsewhere in the region, we mainly encountered *H. occidentalis* in alpine and subalpine streams, although it also occurred in deep alpine lakes (Table 1).

All other species at Mexican Cut were predominately lentic. *Agrypnia deflata* larvae occurred only in large permanent ponds in the wetlands on the lower shelf (1, 3, 5, 9 & 12; Fig. 1). Elsewhere in the region, *A. deflata* larvae were only found in shallow, permanent ponds at subalpine altitudes, and always with

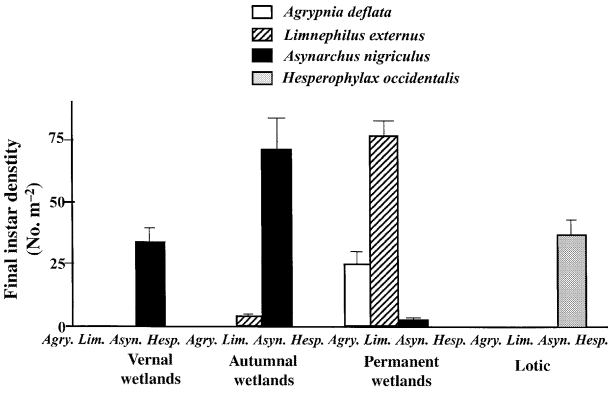

Fig. 2 Mean (±SE) densities of final instar caddisfly larvae during summer 1990 based on weekly drop box sample taken in vernal (13, 15, 19, 51, 52), autumnal (4, 6, 8, 10, 11), and permanent ponds (1, 3, 5, 9, 12), and in streams at the Mexican Cut Nature Reserve.

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Table 1 Distributions of high-altitude caddisflies along a predator-permanence gradient in subalpine (3100–3800 m) and montane (2500–3000 m) wetlands near the Rocky Mountain Biological Laboratory in central Colorado. Number of sites censused in each category is given in parentheses. Table values indicate number of sites at which larvae of each species were found. 'Salamanders' indicate one or more gilled stages of *Ambystoma tigrinum nebulosum*. Because of slow growth, salamanders occur only in permanent habitats at subalpine altitudes. At montane sites they can complete larval development in 1 year and hence can also exploit autumnal wetlands. *Hesperophylax* occurs mainly in lotic habitats, although occasionally encountered in deep alpine lakes

	Permanent (18) (14 with salamanders)	Autumnal (16)	Vernal (15)
(a) Alpine/subalpine wetlands			
Agrypnia deflata	5	0	0
Limnephilus externus	14	1	0
Limnephilus picturatus	3	0	0
Asynarchus nigriculus	3*	15	15
Hesperophylax occidentalis	2*	0	0
	Permanent (6) (all with salamanders)	Autumnal (18) (all with salamanders)	Vernal (7)
(b) Montane wetlands			
Limnephilus externus	6	18	0
Limnephilus picturatus	2	5	0
Limnephilus secludens	0	8	0
Grammotaulius lorettae	0	12	0
Asynarchus nigriculus	0	0	4
Limnephilus tarsalis	0	0	3

*indicates deep alpine lakes with introduced trout but no salamanders.

salamanders (Table 1). *Limnephilus externus* was the most abundant species in permanent ponds at Mexican Cut, but also occurred in lower abundances in many autumnal (e.g. ponds 6, 8, 10, 11, 39, 51, 52, 55 & 56), and occasionally in vernal habitats (ponds 7 & 13). In contrast, *Asynarchus nigriculus* was the most abundant species in autumnal habitats, and the only species regularly encountered in vernal ponds (Fig. 2). The reciprocal dominance of *L. externus* and *A. nigriculus* in permanent and temporary ponds, respectively, was also observed at other subalpine/alpine altitudes throughout the region; i.e. *L. externus* typically occurred in shallow permanent habitats with salamanders and *A. nigriculus* in temporary (autum-

Table 2 Larval and adult measurements for the five species of caddisflies at Mexican Cut

	Larval instars						
	I		II		III		IV
Species	HW	Mass	HW	Mass	HW	Mass	HW
Agrypnia deflata	0.45 (0.4–0.5)	0.24 (0.20–0.30)	0.76 (0.7–0.8)	0.62 (0.48–0.72)	1.01 (0.9–1.1)	3.04 (2.87–3.45)	1.32 (1.2–1.4)
Asynarchus nigriculus	0.27 (0.2–0.3)	0.11 (0.09–0.13)	0.44 (0.4–0.5)	0.33 (0.25–0.39)	0.72 (0.68–0.80)	0.59 (0.50–0.62)	1.04 (0.90–1.10)
Hesperophylax occidentalis	0.32 (0.3–0.4)	0.07 (0.06–0.08)	0.52 (0.42–0.5)	0.20 (0.18–0.26)	0.78 (0.72–0.83)	0.89 (0.82–0.94)	1.10 (0.95–1.20)
Limnephilus externus	0.28 (0.2–0.3)	0.08 (0.07–0.09)	0.46 (0.4–0.5)	0.21 (0.18–0.26)	0.75 (0.70–0.82)	0.83 (0.75–0.88)	1.15 (1.03–1.29)
Limnephilus picturatus	0.20 (0.15–0.25)	0.05 (0.03–0.06)	0.38 (0.35–0.45)	0.18 (0.12–0.20)	0.66 (0.62–0.70)	0.76 (0.70–082)	1.04 (0.91–1.12)

Mass = dry body mass (mg); HW = larval head width (mm), Wing = adult forewing length (mm). Values are mean with ranges from

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nal and vernal) habitats without salamanders (Table 1). The pattern shifted at montane altitudes, where *L. externus* was the dominant species in both permanent and autumnal ponds where it typically co-occurred with salamanders and several other less abundant limnephilids (*L. secludens*, *L. picturatus*, *G. lorretae*) (Table 1). *A. nigriculus* was rare at montane study sites (2000–3000 m), occurring only in a few vernal ponds above 2800 m (Table 1). *Limnephilus picturatus* were regularly encountered at Mexican Cut in four small autumnal ponds (34, 35, 39 & 43), although they were sporadically present in other ponds (1, 3, 5, 55 & 56; see Fig. 1). At other locations, *L. picturatus* was frequently encountered in permanent and autumnal habitats, but was typically less abundant than *L. externus* in those habitats.

Life histories of species at Mexican Cut

Agrypnia deflata. Adults emerged during mid- to late-July in most years, with male emergence beginning about a week earlier than that of females. Females were considerably larger than males (Table 2), and emerged with fully developed eggs. Females mated immediately after emergence and deposited globular egg masses (68–233 eggs clutch^{-1}) to vegetation by crawling into the water along the shoreline. Newly deposited egg masses were bright green, but became increasingly brown during embryological development. Larvae built cylindrical, spiralled cases composed of a colourful patchwork of live and dead aquatic plant material (mainly *Isoetes*). Neither eggs (0/912 survived) nor final instar larvae (0/12 survived) were desiccation tolerant.

Early larval development occurred during late summer so that most *Agrypnia* reached the third instar by the end of September (Fig. 3a). In early October, larvae moved to the middle of the ponds where they burrowed in organic sediments. There was little to no larval development during winter (Fig. 3a). Larvae reappeared on the surface of substrata 1–2 weeks after ice melt in spring, and growth resumed in late spring with pupation occurring from mid- to late-July, depending on the pond (Fig. 5). Final instars burrowed into soft substrata to pupate. Pupal cases differed from larval cases in that they had silk mesh and attached debris over the anterior opening of the case. Pupation times ranged from 10 to 14 days in experimental cages in the ponds.

Hesperophylax occidentalis. The main emergence period occurred between mid-July and mid-August, although the population was more asynchronous than other species. Adults were collected as early as late June and as late as early September. Males emerged before females and the sexes were easily distinguished in flight because males have much larger wings than females (Table 2). Females were reproductively mature (stage C eggs) and mated within a few days of emergence. The brown, globular egg

			Adult Male		Adult Female		
	V						
Mass	HW	Mass	Wing	Mass	Wing	Mass	Eggs
6.32 (5.88–6.95)	1.83 (1.7–2.0)	13.52 (11.45–14.22)	15.5 (14.3–15.9)	11.1 (9.5–13.8)	19.8 (17.7–20.4)	21.6 (17.4–23.4)	178 (68–233)
1.65 (1.58–1.70)	1.46 (1.20–1.52)	7.89 (5.55–9.32)	12.92 (9.5–13.1)	4.2 (2.9–5.2)	11.5 (10.2–12.4)	5.2 (2.4–7.6)	48 (26–64)
2.23 (2.00–2.35)	1.55 (1.42–1.70)	9.95 (8.66–10.12)	12.5 (11.3–13.2)	4.2 (3.1–4.9)	9.4 (8.9–9.8)	6.1 (5.4–7.9)	91 (55–134)
2.12 (1.93–2.24)	1.60 (1.51–1.78)	8.54 (7.75–10.33)	16.7 (16.2–17.2)	6.9 (5.8–7.6)	17.4 (16.3–18.0)	10.1 (6.08–14.4)	114 (34–145)
1.58 (1.37–1.65)	1.39 (1.30–1.49)	7.02 (6.55–7.44)	8.9 (8.0–9.5)	2.6 (2.0–3.1)	9.2 (8.7–9.4)	4.3 (2.8–5.6)	34 (21–43)

data combined from among years and ponds at Mexican Cut.

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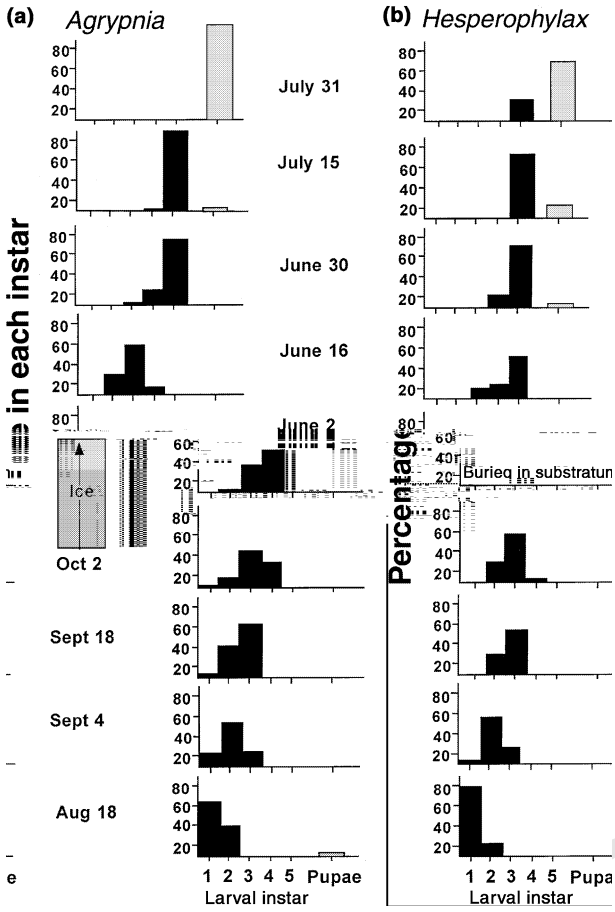

Fig. 3 Larval development of (a) *Agrypnia deflata* based on data from pond 5, and (b) *Hesperophylax occidentalis* based on data from Galena Creek. Bars represent the percentage of all individuals in each stage on each date. Grey bars are pupae.

masses (55–124 eggs clutch^{-1}) were deposited under submerged rocks along the edges of stream pools and ponds associated with Galena Creek. In the field, embryos developed rapidly in the gelatinous egg masses and larvae left the eggs mass matrix immediately after hatching. In the laboratory, early instar larvae remained in the gelatinous egg masses when held under terrestrial conditions and 93% (361/347) survived and emerged from the matrix when immersed in water.

Because of the relatively long period of egg deposition (6 weeks) in *Hesperophylax*, early larval development was relatively asynchronous, and four different instars were present in late September (Fig. 3b). The cylindrical larval cases were composed of small fragments of wood and light-coloured stones, giving them a speckled appearance. Early instar larvae remained in pools and ponds in dry years, but dispersed into streams if they began to flow before winter. By spring, larvae were distributed widely in erosional zones of Galena Creek and its tributaries, and most had reached the fourth instar, suggesting that larvae remained active during winter (Fig. 3b). Larvae completed development in late June to early July, and the onset of pupation was accompanied by a decrease in wood and an increase in stones on the cases. Final instar larvae aggregated in pools and ponds where the stony pupal cases were attached to rocks and to each other. Although a few *Hesperophylax* pupated in early July, most did so in mid- to late-July so that the main pulse of emergence was in early August. None (0/12) final instar larvae survived desiccation.

Limnephilus externus. Emergence occurred over a 2-week period in mid-August (Fig. 5). Males emerged slightly earlier and were smaller than females which contained immature (stage A) eggs (Table 2). Females mated soon after emergence and then dispersed into the surrounding terrestrial vegetation until early October. We collected females from willows and spruce trees in September and found that eggs were still immature, suggesting an extended ovarian diapause. In early October, females deposited amber, elliptical, gelatinous egg masses (85–156 eggs clutch^{-1}) under rocks and logs along the banks of dried and filled ponds. This is the last species to oviposit at Mexican Cut, and in October 1993 an extraordinarily early snowfall prevented *L. externus* from depositing eggs. Nearly the entire cohort perished at Mexican Cut, and cohorts failed completely at four other subalpine sites where we had been following the life history. Egg deposition in populations below 3000 m was not affected.

Embryonic development occurred immediately after egg deposition, but first instar larvae remained in the gelatinous matrix under terrestrial conditions in the laboratory. Under terrestrial conditions, 96% (567/590) of the eggs and first instar larvae survived. When immersed in water, larvae left the matrix and began to construct cases. None (0/567) survived freezing. First instar *L. externus* larvae appeared at Mexican Cut in mid-June and most of larval development occurred in July (Fig. 4a). Cases of early instar larvae were rectangular, bright green structures of live *Isoetes* fragments. Late instars increasingly incorporated larger fragments of live and dead *Carex* stems, so

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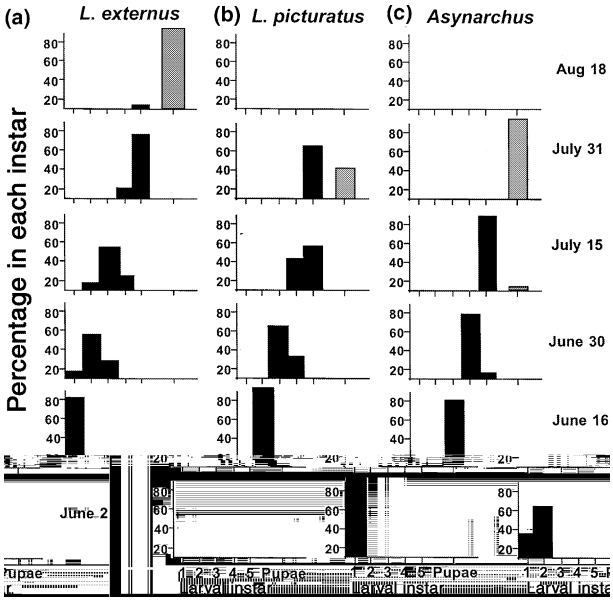

Fig. 4 Larval development of (a) *Limnephilus externus* based on data from pond 5 (b) *Limnephilus picturatus* based on data from pond 35, and (c) *Asynarchus nigriculus* based on data from pond 8. Bars represent the percentage of individuals in each stage on each date. Grey bars are pupae.

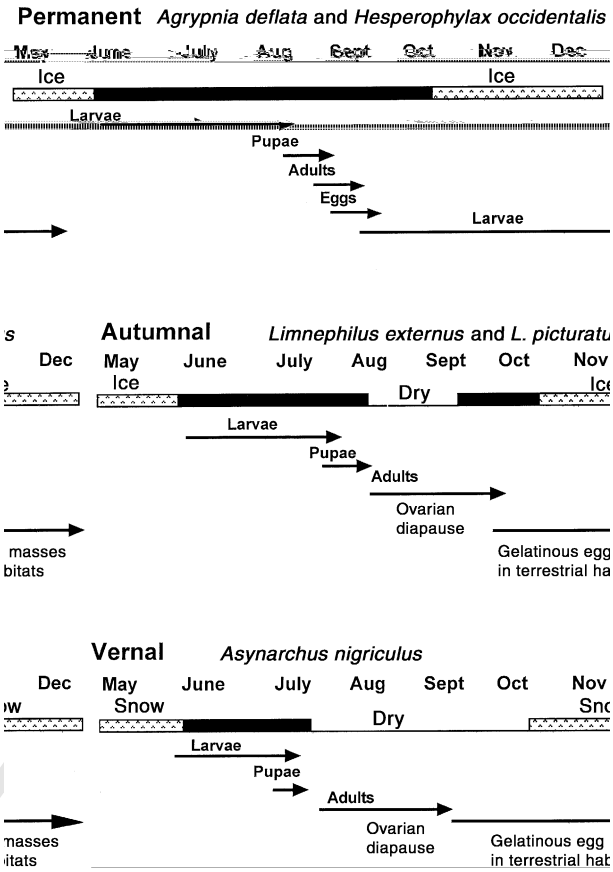

Fig. 5 Summary of life history patterns that allow caddisflies to exploit permanent, autumnal and vernal habitats. *Asynarchus nigriculus* is the only species that can complete its life cycle in all three wetland types. *Limnephilus* spp. can complete development in autumnal and permanent wetlands, whereas *A. deflata* and *H. occidentalis* are restricted to permanent habitats.

that cases were much larger relative to the size of the larvae than in other species. Cases at other sites were also composed predominately of aquatic vegetation, but varied in shape from loosely constructed rectangles to tightly woven cylinders. Larvae were most abundant on the stems of emergent vegetation and on overhanging terrestrial vegetation along the shorelines of the ponds. The duration of the final instar was longer than any of the other limnephilids. Most *L. externus* reached the final instar by late July but did not pupate until mid-August (Fig. 4a). Prior to pupation, final instars sealed the anterior end of the larval case with silk. We estimated pupation time to be 10–14 days based on known onset and emergence times of animals in cages in the ponds. No final instar larvae (0/12) survived desiccation in the laboratory.

Limnephilus picturatus. Adults of this small-bodied species emerged in late July. Females had immature eggs (stage A), mated soon after emergence, and then dispersed to the surrounding terrestrial habitat. Females still had immature eggs in September, suggesting an ovarian diapause similar to that observed in *L. externus* (Fig. 5; Table 3). Although we did not observe egg deposition directly, light brown, gelatinous egg masses (25–53 eggs clutch^{-1}) were found in late September on sedges adjacent to ponds where larvae were present (e.g. 35 & 39). Survival of eggs and first instar larvae in the egg masses was high (93%; 233/249) under terrestrial conditions in the laboratory, and immersion stimulated larvae to leave the egg mass matrix. None (0/233) of the larvae survived freezing.

First instar larvae appeared during the second week of June and larval development was rapid and synchronous in early summer with pupation in late July and early August (Fig. 4b). Larval cases were loosely constructed cylinders of the stems of dead sedges arranged in longitudinal whorls. There was little change in the structure of the larval case at the beginning of pupation, which was preceded by a decline in larval activity. Pupation was short (7–10 days) with adults emerging synchronously in

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late July. Final instar larvae were not desiccation tolerant (0/12 survived).

Asynarchus nigriculus. Adult emergence was extremely synchronous within populations, but varied considerably among years and among habitats. Emergence was earliest in vernal habitats on the lower shelf (early July) and latest in permanent alpine habitats such as Galena Lake (early August). Emerging females had immature eggs (stage A), mated immediately, and then dispersed into terrestrial habitats where they entered an ovarian diapause (Table 3). Females became active again in late August to early September and deposited brown, elliptical egg masses under wood and rocks in dried vernal ponds, and along the margins of filled ponds. Hundreds of gelatinous egg masses (26–64 eggs/clutch) were predictably clustered year after year under logs along the margins of several habitats in which larvae of this species were abundant (e.g. 6, 8, 10 & 11). Hatching occurred 2 weeks after egg deposition, but larvae remained in the egg masses. In the laboratory, 89% (214/242) of the larvae survived in egg masses that were held under terrestrial conditions. When placed in water in the laboratory, larvae left the egg mass matrix and began to build cases. These larvae were not freeze tolerant (0/214 survived).

First-instar *A. nigriculus* were among the earliest benthic invertebrates to become active in spring, and larval development was rapid and synchronous during June and early July (Fig. 4c). Larval cases were cylindrical and varied considerably among habitats in composition. In most temporary ponds, cases were composed of bark, spruce needles and pieces of wood, but in several large, permanent habitats (e.g. 1, 5 & 12), cases were composed predominately of fragments of *Isoetes*. Pupation was preceded by a dramatic increase in mineral fragments on the cases, and the stony pupal cases were affixed to rocks and other hard substrata. Pupation was synchronous and typically lasted only 1 week or less, depending on the pond (Fig. 4c). Final instar larvae faced with drying in vernal ponds pupated and emerged in <48 h. Despite this apparent ability to rush late instar and pupal development, we have often observed entire cohorts of dead final instar larvae and pupae in vernal ponds that had dried unusually early. Most final instars (9/12) did not survive desiccation, although three pupated and emerged under drying conditions in the laboratory.

Discussion

Caddisfly life histories in permanent habitats

Agrypnia deflata and *Hesperophylax occidentalis* were the only caddisflies at our study sites that occurred only in permanent waters. Eggs of both species are deposited under water and hatch immediately so that early larval development is completed before winter (Fig. 3; Table 3). In *A. deflata*, none of the aquatic stages (eggs, larvae, pupae) are desiccation tolerant, and there is no adult diapause to survive the dry phase of temporary habitats (Fig. 5). Although *H. occidentalis* is often associated with intermittent alpine streams (Martinson & Ward, 1982; Parker & Wiggins, 1985), the population at Mexican Cut is dependent on permanent water because females deposit eggs in the water, hence guaranteeing that larvae will leave the gelatinous egg masses. However, because the egg masses are desiccation tolerant, we suspect that this species could exploit temporary habitats if females laid eggs terrestrially (Table 3).

The association of *A. deflata* with permanent water is typical of many Phryganeidae, although a few species can exploit temporary waters [e.g. *Trichostegia minor* (Curtis) and perhaps *Ptilostomus ocellifera* (Walker) *and Fabria inornata* (Banks)] (Wiggins, 1996; Wissinger & Gallagher, 1999). At study sites with many ponds, phryganeids are typically found in the largest, permanent ponds, whereas different species of limnephilids span a gradient from permanent through different types of temporary hydroperiods (Wiggins *et al*., 1980; Larson & House, 1990; Wissinger & Gallagher, 1999; Schneider, 1999; this study).

An advantage for *Agrypnia* and *Hesperophylax* of ovipositing eggs in aquatic habitats in late summer is that much of the larval growth and development can be completed before winter, a strategy that could be important for attaining univoltinism in high altitude per latitude caddisflies (Gislason, 1977). One disadvantage is that larvae must be able to survive freezing, which is an important source of mortality for aquatic invertebrates in high altitude per latitude habitats (Irons, Miller & Oswood, 1993; Frisbee & Lee, 1997). Most wetlands at Mexican Cut freeze

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Table 3 Summary of life history characteristics of caddisflies at subalpine and alpine (>3000 m) altitudes in central Colorado. Phenologies varied considerably from pond to pond and year to year depending on when ponds melt in spring. Range shown is for the modal week of ice melt (first week of June) during 1989–2000 and modal habitat for each species (*A. deflata* – pond 5; *H. occidentalis* – Galena Creek; *L. picturatus*, pond 35; *A. nigriculus*, pond 8; *L. externus*, pond 5). Males emerged either distinctly or slightly earlier than females (protandry) in all species. Egg stage (A–C) designations follow Unzicker (1968). Three species over wintered as first instar larvae in the egg mass matrix

Species	Emergence		Egg stage at ovarian			Egg deposition		Stage in	Desiccation tolerance	
	Duration	Phenology	Protandry	Emergence	Diapause	When	Where	Winter	Eggs	Larvae
Agrypnia deflata	10–14 days	Mid-late July	Distinct	Mature (C)	No	July–August	Aquatic	Instar 2–4	No	No
Hesperophylax occidentalis	20–28 days	Mid-late July	Distinct	Mature	No	July–August	Aquatic	Instar 2–4	Yes	No
Asynarchus nigriculus	3–10 days	Mid-late July	Slight	Immature (A)	July–September	August–September	Terrestrial	Egg mass	Yes	No
Limnephilus picturatus	7–10 days	Late-July	Slight	Immature (A)	July–September	August–September	Terrestrial	Egg mass	Yes	No
Limnephilus externus	10–14 days	Early-mid August	Slight	Immature	September–August	September–August	Terrestrial	Egg mass	Yes	No

solid into the substratum, but a thin layer (5 cm) of slushy 'frazil ice' (*sensu* Oswood, Miller & Irons, 1991) is present above the substratum in the deepest areas of the largest ponds (Wissinger *et al*., 1999b). *Agrypnia* larvae appear to survive winter by burrowing in these deep organic sediments. The tendency to burrow in soft substrates, both in winter and during pupation, may explain why *Agrypnia* is absent from other permanent alpine habitats with hard substrata.

In contrast, winter survival of *Hesperophylax* appears to depend on the presence of running water. Eggs and early instars are aggregated in bedrock ponds and permanent pools associated with intermittent streams. By spring, larvae are widely distributed in both erosional and depositional areas, and we suspect that the dispersal of larvae from natal sites occurs as streams begin to flow under the snow pack in early winter. Migration away from zones of freezing and towards running water is probably a common strategy in stream invertebrates at high altitudes per latitudes (Irons *et al*., 1993). *Hesperophylax* larvae continue to develop (albeit slowly) during winter, suggesting that larvae remain active under the snow pack where they feed predominantly on lotic periphyton (S.A. Wissinger, unpublished data). Final instars migrate back to permanent pools to pupate, emerge and deposit eggs, a pattern also observed in populations of this species that inhabit headwater springs (Martinson & Ward, 1982). This seasonal migration of *Hesperophylax* between permanent ponds and temporary streams is similar to that observed for riverine limnephilids that move to temporarily flooded wetlands to feed on detritus before returning to rivers to pupate and emerge (Huryn & Gibbs, 1999). Although the lentic–lotic direction differs, both types of migration allow species in permanent habitats to exploit seasonal resources in adjacent temporary habitats. The ancestral habitat of limnephilids is assumed to be lotic and such movements might have played an evolutionary role in the invasion of lentic habitats (Wiggins, 1996). Such movements can also provide spatial subsidies of energy and nutrients for wetland and stream food webs (Polis, Anderson & Holt, 1997; Wissinger, 1999).

Caddisfly life histories in temporary habitats

Limnephilus externus, *L. picturatus* and *Asynarchus nigriculus* can complete their life cycles in both

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temporary and permanent wetlands. Adults emerge before ponds dry in summer, mate immediately, and then females enter an ovarian diapause in nearby terrestrial vegetation (Table 3; Fig. 5). Females become active again in autumn and deposit gelatinous egg masses under rocks and logs in vernal habitats, and adjacent to autumnal and permanent ponds. Embryonic development and hatching occur in autumn, but first instar larvae remain within the gelatinous matrix under the snow during winter. Larvae enter the ponds with melt water in spring, develop rapidly, pupate and emerge before ponds dry in early to mid-summer (Fig. 5). This suite of life history characteristics probably allows three other species (*Limnephilus secludens, L. tarsalis, Grammotaulius lorettae*) to exploit temporary habitats at our montane study sites (Table 1). All are univoltine, despite the absence of a prewinter period of larval growth (cf. Gislason, 1977).

Asynarchus differs from the other species in that it can complete its life cycle in vernal habitats that dry up after only 4–5 weeks of open water (Fig. 5). This is especially remarkable in light of the relatively cold and nutrient-poor conditions in these high-altitude habitats (Wissinger *et al*., 1999b). Some limnephilids that inhabit extremely ephemeral ponds have larvae and/or pupae that are tolerant of desiccation (Anderson, 1967; Williams & Williams, 1975; Zamora-Munoz & Svensson, 1996; Whiles, Goldowitz & Charlton, 1999). However, *Asynarchus* larvae and pupae are not desiccation tolerant and, in dry years, entire cohorts die from desiccation (S.A. Wissinger and J.A. Jannot, unpublished). The ability of this species to exploit vernal habitats is facilitated mainly by extremely rapid larval development and short pupation time. Elsewhere we have argued that the strong selection on development time in this species explains the extremely high activity rates of larvae and their extremely aggressive behaviour towards other caddisflies including intraguild predation and cannibalism (Wissinger *et al*., 1996; Wissinger *et al*., 1999a). Although *Asynarchus* gut contents are dominated by detritus, we have experimentally shown that individuals that eat only detritus during larval development pupate later and have lower adult fitness (small size and low fecundity) than those that eat invertebrate prey (S.A. Wissinger, Alexander & Steinmetz, unpublished).

The strikingly synchronous nature of *Asynarchus* development could be related to at least two types of selective pressures. First, synchrony is often a life history trait associated with time-constrained development (Lytle, 2001), especially in extremely ephemeral habitats like those that *Asynarchus* often inhabit. Interestingly, *A. nigriculus* development in late drying ponds is more asynchronous than in early drying ponds (S.A. Wissinger, unpublished data). Synchrony should also be favoured in cannibalistic species because slow-growing (small) individuals are the most likely victims of intracohort cannibalism (Hopper, Crowley & Kielman, 1996). Although there is some cannibalism among same-sized *Asynarchus*, it increases dramatically among larvae that differ in size by one or more instars (S.A. Wissinger, unpublished data).

Drying, freezing and life histories at high altitudes

The three key life history traits of the temporary-habitat species at our study sites: (i) rapid larval development, (ii) adult ovarian diapause and (iii) desiccation-tolerant eggs, have been described in other temporary-habitat limnephilids. However, there is considerable variation between species in the timing of adult diapause, and when and where they deposit egg masses (e.g. Novak & Sehnal, 1963; Winterbourn, 1971a; Wiggins, 1973; Wiggins *et al*., 1980; Berte & Pritchard, 1986; Mathis, 1990; Meyer & Meyer, 2000). One of the puzzling differences between our results and those of previous studies is related to the timing and spatial position of egg deposition at Mexican Cut. Most species with gelatinous egg masses deposit them in locations that will be inundated as ponds fill in the autumn (Novak & Sehnal, 1963; Gower, 1967; Wiggins, 1973; Wiggins *et al*., 1980; Berte & Pritchard, 1986; Sangpredub *et al*., 1999; Meyer & Meyer, 2000). Inundation stimulates larvae to leave the egg mass and early larval development often coincides with a flush of food resources in the newly filled basins (Wiggins *et al*., 1980). At our study sites, eggs are deposited above the basin-full waterline, even at autumnal and permanent sites, and consequently early instars remain in the egg masses until the following spring. One hypothesis for the terrestrial location of egg masses is that pond inundation in autumn is often a 'false alarm', i.e. late summer rains fill autumnal ponds only for a few days

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or weeks after which they dry up again. However, this 'false-alarm' hypothesis does not explain why these species deposit eggs adjacent to (rather than in) permanent wetlands and, hence, do not take advantage of the autumn growing season (as in *Hesperophylax* and *Agrypnia*; Fig. 5).

An alternative hypothesis is that first instar larvae that remain in gelatinous egg masses deposited under protected terrestrial habitats (under rocks and logs) are less vulnerable to freezing than free-living larvae would be in the pond basins. Unlike *Agrypnia* (large, permanent ponds with deep organic substrates) and *Hesperophylax* (running water habitats), *Asynarchus* and *Limnephilus* spp. occur mainly in shallow standing waters that freeze solid into the substratum (see above). We know that once larvae leave the egg mass matrix, they are vulnerable to freezing and suspect that the relatively humid and insulated conditions under a 3-m snow pack are more benign than those that that would be faced in shallow high-altitude wetlands (also see Irons *et al*., 1993). Ovarian diapause in limnephilids typically provides a timing mechanism that allows females to deposit eggs just before temporary wetlands refill (Novak & Sehnal, 1963; Wiggins *et al*., 1980; Berte & Pritchard, 1986; Wiggins, 1996). However, in high-altitude populations, ovarian diapause could function mainly to reduce the time that terrestrial egg masses are vulnerable to predators (e.g. spiders, rodents), desiccation, and/or freezing before the snow pack provides insulation. This might explain why *L. externus* adults deposit eggs just before snow begins to accumulate in late autumn.

Compared with other species (Novak & Sehnal, 1963; Gower, 1965, 1967; Wiggins, 1973; Berte & Pritchard, 1986; Gullefors, 1994), and populations of the same species (*L. externus* and *H. occidentalis* in Parker & Wiggins, 1985; Berte & Pritchard, 1986), adults at our study sites are smaller and/or have fewer eggs (Table 2). This could reflect the relatively short, cold, alpine growing season, especially in temporary habitats, and/or the nutrient-poor status (oligotrophic to ultraoligotrophic) of these wetlands (Wissinger *et al*., 1999b). Preliminary data indicate that *A. nigriculus* females emerging from early drying ponds have smaller clutches than those from late drying ponds, suggesting that development time constrains fecundity (S.A. Wissinger unpublished data).

Life history and tradeoffs along predator–permanence gradients

There is considerable comparative evidence for species replacements along lentic permanence gradients, but cause and effect relationships are better understood for amphibians than freshwater invertebrates (Batzer & Wissinger, 1996; Schneider & Frost, 1996; Wellborn *et al*.,1996; Williams, 1996). Our results suggest that caddisfly species replacements along permanence gradients at high altitude reflect both fundamental niche constraints associated with desiccation tolerance, and shifts in the importance of biotic interactions. An understanding of the life history constraints is sufficient to predict the distributions of *Agrypnia* and *Hesperophylax*, but insufficient for *Asynarchus* and *Limnephilus* spp. (Fig. 1, Table 1). *Asynarchus* can complete its life cycle in both permanent and temporary ponds, and in experimental cages actually develops slightly faster in permanent than in temporary habitats (Wissinger *et al*., 1996). The absence of *Asynarchus* from most permanent wetlands is probably a result of this species' vulnerability to salamander predation. The high activity and aggressive interactions of larvae that allow *Asynarchus* to exploit even the most vernal habitats make them highly visible to salamanders (Wissinger *et al*., 1999a). In contrast, larvae of *L. externus* are rather inactive and coexist with salamanders, but cannot complete development in time to escape vernal habitats (Wissinger *et al*., 1999a). They can complete development in autumnal habitats but, in the absence of salamanders, *Asynarchus* probably reduces or eliminates *L. externus* through intraguild predation (Fig. 6; Wissinger *et al*., 1996). In previous studies at other geographic locations, *L. externus* has been found in temporary habitats (Berte & Pritchard, 1986), but at our subalpine study sites is almost always in permanent wetlands. One caveat is that *L. externus* quickly invades autumnal and vernal habitats when *Asynarchus* populations decline (S.A. Wissinger unpublished data). The role of salamanders in creating enemy-free habitat (by eliminating *Asynarchus*) for *L. externus* is emphasised by the altitude shift in salamanders from permanent to autumnal wetlands. At montane study sites, where salamanders can complete larval development before autumnal ponds dry, *Asynarchus* is absent, but *L. externus* and other limnephilids are present (Table 1).

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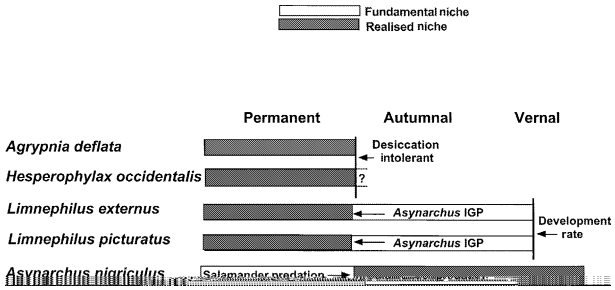

Fig. 6 A summary of fundamental and realised niches of caddisflies along a permanence gradient in subalpine wetlands. Fundamental niches are based on life history and desiccation tolerance data presented in this paper and realised niches on experimental studies on biotic interactions (Wissinger *et al.*, 1996; Wissinger *et al.*, 1999a). IGP = intraguild predation.

The particular behavioural mechanism that underlies the tradeoff between predator vulnerability and desiccation tolerance in *Asynarchus* and *Limnephilus* (i.e. high versus low rates of larval foraging activity) appears to be a common feature of many anuran species replacements along permanence gradients (Werner & Anholt, 1993; Skelly, 1997). However, the general importance of this mechanism as an underlying cause of species replacements in invertebrates other than caddisflies (e.g. odonates, beetles, water bugs, crustaceans) is not known (Batzer & Wissinger, 1996; Wissinger, 1999). Other behavioural and morphological traits can affect both desiccation tolerance and biotic interactions (Wellborn *et al.*, 1996), and differences in vulnerability to different types of predators can underlie species replacements along permanence gradients, independent of desiccation tolerance (e.g. McPeek, 1990a,b; McPeek *et al.*, 1996). Our results emphasise that understanding the causes of such species replacements for other wetland invertebrates will require a detailed understanding of the life history and desiccation tolerance of each species, and experimental evidence for habitat-specific differences in the importance of biotic interactions.

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