16 Riparian Sedge Meadows in Maine

A Macroinvertebrate Community Structured by River-Floodplain Interaction

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Small rivers with extensive tracts of riparian sedge meadows as floodplains are a conspicuous part of the Maine landscape. During spring increasing river discharge because of melting snow inundates these floodplains. Although the period of flooding is short (April–May), a rich macroinvertebrate community develops. Members of the community come from two general sources: floodplain and river. Floodplain fauna complete their entire life cycle on the floodplain, whereas river-floodplain fauna have life cycles with both river and floodplain phases. Conspicuous floodplain fauna includes mosquitoes (Aedes), *caddisflies* (Anabolia *and* Limnephilus), *and fingernail clams* (Pisidium). *River-floodplain fauna includes the mayflies* Leptophlebia, Siphlonisca, *and* Siphlonurus. *These mayflies are able to use the stream as a refuge during the dry period of the summer and the freezing temperatures of winter, and the floodplain during a short but critical period of rapid growth and development during spring. Approximately 75 percent of macroinvertebrate biomass on the floodplain during inundation is composed of the mayflies* Leptophlebia, Siphlonisca, *and* Siphlonurus. *Compared to this assemblage, contributions by other fauna to community biomass are minor. Both proximity and physical interconnection of the river and floodplain are required for development of the characteristic floodplain community structure during the short period of inundation.*

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FLOODPLAIN SEDGE MEADOWS

Once generally ignored by aquatic ecologists, the importance of floodplain wetlands to the ecology of rivers now seems almost self-evident. Much of what has been discovered about links between these systems, however, is based upon studies conducted in the tropics (Junk et al. 1989, Hamilton et al. 1992, Power et al. 1995, Goulding et al. 1996), where the physical structure of large rivers and their floodplains tends to be less altered by human activities compared to systems of similar scale in temperate regions (Ward 1989, Bayley 1995, Sparks 1995). These studies have provided a conceptual base for examining relationships between rivers and their floodplains in the form of energy and material flow, habitat formation and maintenance, and system biodiversity (primarily fishes, e.g., Goulding et al. 1996). It is now clear that this "lateral dimension" to river ecosystems must be seriously considered in designing studies of river ecosystem structure and function (Junk et al. 1989, Ward 1989).

Probably because of logistical difficulties in working in large rivers and the paucity of intact river-floodplain complexes outside of the tropics, quantitative data describing the ecology of these systems are generally lacking (Ward 1989, Power et al. 1995). There are few good examples of relatively unaltered large river-floodplain systems remaining for study in temperate North America (Ward 1989, Sparks 1995). There are, however, many examples of small systems that remain relatively unaltered (e.g., floodplains that receive floodwater from rivers with discharges $<<50\ m^{-3}\ s^{-1}$). Small river-floodplain complexes should be of particular interest to stream ecologists because they may provide small-scale analogues of larger systems that are both more abundant and more tractable for study. Almost all small river-floodplain complexes that have received comprehensive study, however, are forested systems of the southeastern United States (see review by Gladden and Smock 1990). In this chapter we introduce the macroinvertebrate community of a floodplain meadow in the extreme northeastern United States and attempt to show how the strong physical link between river and floodplain results in its characteristic structure.

Alluvial sedge meadows that border small low-gradient and meandering streams are a conspicuous part of the landscape of eastern and northern Maine (~24,000 ha in Maine, Gibbs et al. 1991). The invertebrates of these sedge meadows have received continuous attention since 1980, when the unusual carnivorous mayfly *Siphlonisca aerodromia* (Siphlonuridae) was discovered at Tomah Stream in eastern Maine (Gibbs 1980). Interest in the conservation biology of *S. aerodromia* has resulted in numerous studies of the invertebrate communities of sedge meadows throughout Maine (e.g., Gibbs and Mingo 1986, Gibbs and Siebenmann 1996). This species is now known from a number of locations in Maine, but appears to be most abundant in the river-floodplain complex at Tomah Stream.

THE RIVER-FLOODPLAIN COMPLEX AT TOMAH STREAM

Tomah Stream is a 4th-order tributary of the St. Croix River in Washington County, Maine. Along a 10-km reach of the stream south of Route 6 are extensive alluvial sedge meadows that function as floodplains. These floodplains gently slope toward the active river channel, or toward oxbow swales that drain into the active channel. The width of the floodplain varies depending on the geomorphology of the channel. Along freely meandering reaches, the floodplain may be >1 km wide, although widths of ~100 m are more common. Along reaches that are constrained by topography, the floodplain is often <30 m wide, or may be entirely absent.

Sediments of the Tomah Stream catchment are glacial till, aqueo-glacial outwash, and materials of marine origin (International Joint Commission Report 1957). The extensive floodplains of lower Tomah Stream are formed from aqueo-glacial outwash, e.g., sediments deposited by streams associated with melting glaciers at the end of the Pleistocene. These sediments were graded as they were transported away from the front of the retreating ice to form the alluvial deposits that dominate the present-day landscape of the lower Tomah Stream. These basement sediments are now deeply buried by peat (International Joint Commission Report 1957).

The study site used for much of the information provided in this chapter is 1.6 km south of Route 6 (45°26′42″N, and 67°34′50″W), just north of the confluence of Tomah Stream and Beaver Creek (= "Tomah Stream study site"). Here the stream has a straight-walled channel ~6–8 m wide. Depths during low flow condition during midsummer range from ~0.3 to 2+ m. Substrata are sand-and-gravel. The floodplain at this site is on the west bank of the stream and has an area of 2.6 ha.

Hydrology and Thermal Regime

During much of the year (June–March) Tomah Stream is confined to its channel. During this period discharge may be as low as 0.3 m^{-3} s (measured on July 21, 1997). Between December and March the stream is usually covered by ice and snow; ice cover over the upper floodplain may be continuous with the soil. During late March or early April an increase in discharge, caused by the melting snow pack, causes the river to inundate its floodplain. The inundated area gradually decreases from April through May (although it may fluctuate dramatically depending on weather conditions). The stream usually returns to its channel by early June, and the floodplain dries. In some years, however, heavy rains may cause the floodplain to be briefly inundated at other times of the year. Maximum water depth on the floodplain during peak inundation is <1.5 m, and usually well below 1.0 m.

The long-term pattern of flooding at the Tomah Stream study site was predicted from a regression equation relating extent of inundation to discharge of the St. Croix River. Based on a 34-year record of discharge obtained from the USGS, the probability of inundation of the upper floodplain (e.g., within 20 horizontal m of the high-water mark observed in 1997) on any given day of the year was estimated (Fig. 16.1). The probability of inundation was 70–80 percent from March to May, but was usually below 20 percent during the remainder of the year, and well below 10 percent during summer. Fauna that require the continuous presence of surface water will generally be able to occupy the floodplain for a maximum period of ~2.5 months (late March–early June).

Floodplain water temperature was measured at hourly intervals at the Tomah Stream study site during 1997. The mean daily temperature from April 28 to June 9 was 10.0 ± 0.6°C (±SE). The minimum mean daily temperature was 3.0°C, measured on April 29; the maximum was 19.6°C, measured on June 9. The increase in mean daily temperature over the period of inundation was approximately linear. Daily fluctuation of temperature was low, ranging to only 3.4°C. Stream temperatures measured from June 4–9 were usually equal to or slightly warmer (<1°C) than floodplain temperatures.

Water Chemistry

Floodplain and stream water at the Tomah Stream study site are similar in chemistry, both being acidic, moderately to poorly buffered, and oligotrophic.

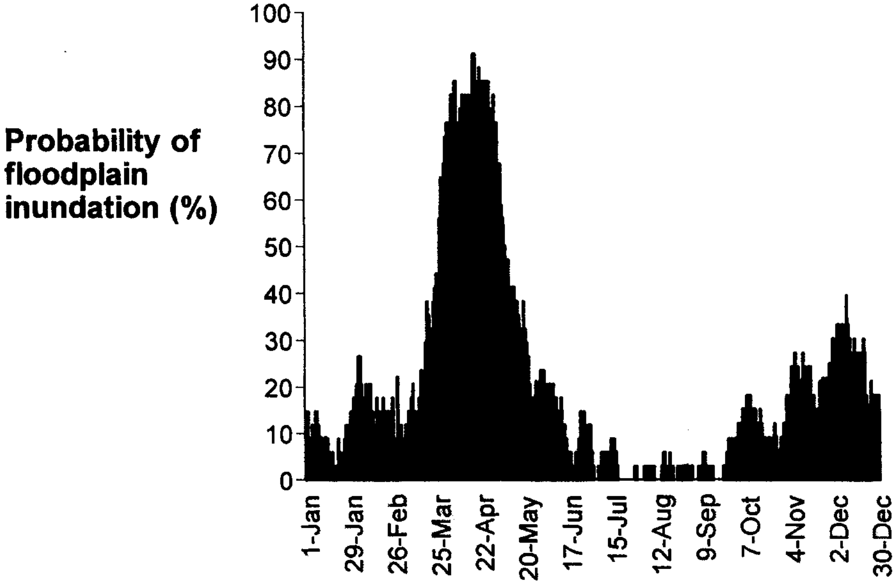

Fig. 16.1. Seasonal pattern of the probability of inundation of the upper floodplain at Tomah Stream.

From May 5 to June 10, 1997, pH was 6.3 ± 0.2 (mean + SE, four dates) on the floodplain and 6.2 ± 0.1 in the stream. Conductivity was 33 ± 8 μmho/cm on the floodplain and 25 ± 3 in the stream. Total alkalinity was 6.3 ± 0.2 mg $CaCO_3$/L on the floodplain and 6.5 ± 1.5 in the stream. Concentrations of soluble reactive phosphorous and of nitrate and ammonium in both floodplain and stream water were usually below 0.05 mg/L. Total phosphorus was slightly higher in floodplain (0.040 ± 0.013 mg/L) compared to stream water (0.023 ± 0.003).

Vegetation

At least 68 species of plants occur on the Tomah Stream floodplain: 34 forbs, 12 sedges and rushes, 5 grasses, 10 woody plants, and 7 ferns and allies. Sedges and rushes almost always comprise >50 percent of overstory vegetation, with woody plants comprising <10 percent. The remaining plants are primarily forbs, ferns, and grasses (Gibbs 1991). The understory vegetation consists of *Sphagnum* moss and detritus.

At the Tomah Stream study site tussock sedge (*Carex stricta*) is the most important (e.g., percent cover) plant species. The sedge *Carex vesicaria* is also abundant. Other major plant species are wool grass (*Scirpus cyperinus*), soft rush (*Juncus effusus*), and horsetails (*Equisetum*) (Gibbs 1989). The narrow leaves and stems of the tussock sedge form dense, broad tussocks that persist as dead leaves among new annual growth. During inundation the sedge tussocks tend to protrude from the water, with prostrate leaf detritus forming a dense meshwork between tussocks. During 1997 new growth from the sedge tussocks was not apparent until late May and was not a visually dominant feature until early June, when surface water on the floodplain was reduced to isolated pools.

FLOODPLAIN MACROINVERTEBRATES

Following initial inundation in March or April, until the floodplain dries in June, aquatic macroinvertebrates are abundant among clumps of living and dead sedge, with mayflies most obvious. Species of mayflies documented from the Tomah Stream floodplain include the siphlonurids *S. aerodromia* and *Siphlonurus mirus, S. alternatus,* and *S. quebecensis,* the metretopodid *Siphloplecton basale,* the arthropleid *Arthroplea bipunctata,* the ephemerellids *Eurylophella temporalis, Ephemerella subvaria,* and *E. septentrionalis,* the baetiscid *Baetisca laurentina,* and the leptophlebiids *Leptophlebia cupida, L. nebulosa,* and *L. johnsoni* (Gibbs and Mingo 1986, Burian and Gibbs 1991, Gibbs and Siebenmann 1996). Larval chironomids, Trichoptera (Limnephilidae: *Limnephilus*), Coleoptera (Dytiscidae: *Hydroporus,* Helophoidae: *Helophorus*), Hemiptera (Corixidae: *Sigara*), and the amphipod *Hyalella azteca* have also been variously reported (Gibbs and Mingo 1986, Gibbs and Siebenmann 1996).

Community Structure

During 1997 ice over the floodplain had melted sufficiently to allow sampling at the Tomah Stream study site by April 25. Macroinvertebrates were sampled at weekly intervals thereafter with a cylinder sampler (area = 0.13 m^2, n = 5 samples per date). The mesh size of the net used to clear the cylinder was 500 μm and defines the lower size limit for macroinvertebrates in this study. Information about community structure reported here is from samples collected on April 27 (~ two weeks after ice melt), May 13 (~ four weeks after ice melt), and June 3 (shortly before complete drying of surface water). On June 3 surface water occurred as isolated pools on the upper floodplain and an oxbow swale in the lower floodplain. Data describing community structure are reported as biomass.

On April 27 total macroinvertebrate biomass was 745 mg dry mass (= DM) m^{-2}. *Leptophlebia* spp. contributed 85 percent of the total biomass (Table 16.1). The mayflies *Siphlonurus* spp., and *S. aerodromia* and mosquito larvae *Aedes* sp. were also major contributors (range = 2–6 percent of total biomass; Table 16.1). On May 13 total macroinvertebrate biomass was 4082 mg DM m^{-2}. *Leptophlebia* spp. remained the major contributor (61 percent) (Table 16.1). The mayflies *Siphlonurus* spp., and *S. aerodromia,* mosquito larvae *Aedes* sp., caddisfly larvae *Limnephilus* cf. *indivisus,* and pea clams *Pisidium* were also important contributors (range = 4–6 percent of total biomass; Table 16.1). On June 3 total macroinvertebrate biomass was 11,828 mg DM m^{-2}. Biomass was dominated by the mayfly *Siphlonurus* spp, which contributed 45 percent (Table 16.1). The mayflies *Leptophlebia* spp., *S. aerodromia,* and *Eurylophella* and limnephilid caddisflies (*Anabolia, Limnephilus* cf. *indivisus*) were also major contributors (range = 9–17 percent of total biomass; Table 16.1). Large numbers of *Leptophlebia* emerged during the week prior to sampling, which may explain the relatively lower contribution of this taxon to total biomass on this date.

Macroinvertebrate biomass at the Tomah Stream study site showed a dramatic 16-fold increase from April to June, which translates into substantial daily instantaneous growth rate of 7.5 percent. The meaning of these statistics in terms of production dynamics of floodplain fauna is difficult to interpret, however, because the area of surface water fluctuated greatly during the study. During late April the floodplain was completely inundated and the abundance of individuals on a m^{-2} basis was relatively diluted. On May 13, however, the wetted perimeter of the inundated floodplain had moved ~16 m toward the stream channel (measured along a permanent transect placed perpendicular to the stream channel). By June 3 the wetted perimeter had moved ~68 m toward the stream channel compared to its position on April 27. This resulted in a concentrating effect toward the end of the season as larvae

TABLE 16.1. Biomass of Common Macroinvertebrates on the Tomah Stream Floodplain (Maine) during Inundation in the Spring of 1997[a]

	April 27, 1997		May 13, 1997		June 3, 1997	
	mg DM m^{-2}	Percent	mg DM m^{-2}	Percent	mg DM m^{-2}	Percent
River-floodplain fauna						
Leptophlebia (E)	629.0 (108.9)	84.5	2475.2 (988.5)	60.6	2017.3 (587.8)	17.1
Siphlonisca (E)	23.7 (15.7)	3.2	243.8 (105.8)	6.0	1418.5 (386.6)	12.0
Siphlonurus (E)	44.8 (29.4)	6.0	261.2 (92.3)	6.4	5377.1 (3104.9)	45.5
Floodplain fauna						
Aedes (D)	14.7 (6.5)	2.0	186.7 (138.5)	4.6	— (—)	
Anabolia (T)	— (—)		19.0 (11.0)	0.5	216.3 (64.5)	1.8
Donacia (larvae) (C)	— (—)		3.1 (3.1)	0.1	1.7 (1.7)	0.0
Limnephilidae (T)	— (—)		10.3 (7.2)	0.3	180.1 (89.2)	1.5
Limnephilus (T)	2.5 (0.8)	0.3	174.5 (75.2)	4.3	1173.9 (196.4)	9.9
Phalacrocera (D)	— (—)		1.0 (1.0)	0.0	— (—)	
Pisidium (B)	1.3 (0.8)	0.2	222.5 (64.8)	5.5	28.6 (13.2)	0.2
Podonominae (D	0.2 (0.2)	0.0	38.4 (22.1)	0.9	— (—)	
Source habitat uncertain						
Acarina	0.2 (0.0)	0.0	7.5 (2.7)	0.2	0.5 (0.2)	0.0
Agabus (larvae) (C)	— (—)		— (—)		6.5 (6.5)	0.1
Arthroplea (E)	2.0 (0.8)	0.3	71.2 (69.7)	1.7	141.7 (19.1)	1.2

TABLE 16.1. (Continued)

	April 27, 1997		May 13, 1997		June 3, 1997	
	mg DM m^{-2}	Percent	mg DM m^{-2}	Percent	mg DM m^{-2}	Percent
Atrichopogon (D)	— (—)		4.6 (4.6)	0.1	— (—)	
Banksiola (T)	2.4 (1.8)	0.3	3.4 (2.1)	0.1	62.8 (49.6)	0.5
Ceratopogonidae (D)	— (—)		10.1 (4.7)	0.2	1.1 (1.1)	0.0
Chironominae (D)	0.1 (0.1)	0.0	2.2 (1.4)	0.1	60.8 (16.0)	0.5
Eurylophella (E)	1.9 (0.8)	0.3	58.2 (38.8)	1.4	1058.6 (110.2)	9.0
Fossaria (P)	7.5 (3.6)	1.0	96.0 (29.9)	2.4	— (—)	
Hirudinea	— (—)		— (—)		25.7 (15.7)	0.2
Hydrocanthus (adult) (C)	— (—)		6.3 (3.9)	0.2	— (—)	
Laccophilus (adult) (C)	— (—)		— (—)		86.2 (86.2)	0.7
Lymnaea (P)	— (—)		— (—)		47.3 (28.9)	0.4
Nematoda	— (—)		2.5 (1.3)	0.1	0.4 (0.2)	0.0
Oligochaeta	7.1 (3.8)	1.0	26.8 (10.8)	0.7	0.7 (0.7)	0.0
Orthocladiinae (D)	6.9 (2.4)	0.9	101.4 (30.1)	2.5	6.4 (4.0)	0.1
Physa (P)	— (—)		— (—)		25.9 (15.9)	0.2
Polycentropus (T)	— (—)		— (—)		60.2 (51.3)	0.5
Psychodidae (D)	— (—)		2.3 (2.3)	0.1	— (—)	
Ptilostomis (T)	— (—)		33.7 (21.6)	0.8	— (—)	
Sigara (adult) (H)	— (—)		2.1 (2.1)	0.1	10.9 (6.9)	0.1
Sympetrum (O)	0.6 (0.2)	0.1	3.9 (3.3)	0.1	14.8 (14.8)	0.1
Tanypodinae (D)	0.2 (0.2)	0.0	1.7 (0.6)	0.0	67.7 (22.4)	0.6
Total biomass	744.7 (127.3)		4,082.3 (1,110.7)		11,827.5 (3,428.2)	

[a] Only macroinvertebrates that contributed 0.1% or more to total biomass on at least 1 date are included. Taxa are arranged by probable source habitat. Values in parentheses are standard errors (n = 5). DM = dry mass. B = Bivalvia, C = Coleoptera, D = Diptera, E = Ephemeroptera, H = Hemiptera, P = Pulmonata, O = Odonata, T = Trichoptera.

crowded into the diminishing surface water. The concentration of mayfly larvae in floodplain pools during early June was striking, being sufficient to produce turbulence at the water's surface when the mayflies were disturbed. Rapid fluctuations in area of surface water in floodplain wetlands are an important and dynamic factor whose effects must be interpreted simultaneously with individual biomass and rates of growth and mortality when production of floodplain invertebrate communities is studied.

Regardless of problems in interpreting population dynamics from these data, it is clear that the community biomass is dominated by the mayflies *Leptophlebia, Siphlonurus,* and *Siphlonisca,* which together comprised 73–94 pecent of total macroinvertebrate biomass over the entire period of inundation.

Trophic Structure

The trophic structure of the macroinvertebrate community at the Tomah Stream study site is simple, consisting of collector-gathers and shredders, as primary consumers, and their predators. The majority of primary consumers are collector-gatherers (Merritt and Cummins 1996) and so feed on biofilms and fine particles of organic matter that accumulate among submerged sedge leaves and on the benthos. This includes two of the dominant mayflies, *Leptophlebia* and *Siphlonurus,* as well as other relatively important contributors to biomass such as *Eurylophella, Aedes,* and *Pisidium. Aedes* can filter small particles from the water, but usually feeds as a collector-gatherer by brushing particles from substrata (Clements 1992). Like *Aedes, Pisidium* is also a filter-feeder, but as infauna it probably feeds on organic detritus or interstitial bacteria from sediments rather than the water column and is probably best considered a collector-gatherer as well (McMahon 1991). Collector-gatherers contributed 74 percent (June 3) to 96 percent (April 27) to community biomass. The major shredders on the floodplain are the limnephilid caddisflies *Limnephilus* and *Anabolia,* which consume vascular plant detritus, presumably decaying sedge leaves. Shredders contributed <1 percent (April 27) to 13 percent (June 3) to community biomass.

The major macroinvertebrate predator was the mayfly *S. aerodromia,* which apparently functions as a collector-gatherer early in larval development but becomes predacious as development proceeds (Gibbs and Mingo 1986). The most common prey are larvae of *Siphlonurus,* but *Leptophlebia, Eurylophella,* and midge larvae are also consumed (Gibbs and Mingo 1986). *Siphlonurus* is apparently omnivorous (Edmunds et al. 1976), but the relative importance of animal prey compared to biofilm and organic particles is unknown, and it is considered a collector-gatherer for present purposes. Adult and larval dytiscids, larvae of phryganeid caddisflies, *Polycentropus,* Ceratopogonidae, and Tanypodinae, and leeches and mites are also predators. Their biomass was relatively small compared with that of *S. aerodromia* (Table 16.1), however. Predators collectively contributed 4 percent (April 27) to 15 percent (June 3) to community biomass. *Siphlonisca aerodromia* alone contributed 3.2–12.0 percent to total biomass on these dates.

Vertebrates that feed on aquatic macroinvertebrates are conspicuous during floodplain inundation at the Tomah Stream study site. Their quantitative effect on the floodplain macroinvertebrate fauna, however, is unknown. The common shiner (*Notropis cornutus*), the three-spine stickleback (*Gasterosteus aculeatus*), the chain pickerel (*Esox niger*), and the common white sucker (*Catostomus commersoni*) have all been reported from the Tomah Stream study site during April and May. The direct examination of gut contents from these species and from brook trout (*Salvelinus fontinalis*) captured from the stream shows that they feed heavily on macroinvertebrates from the floodplain, especially mayflies (Gibbs and Mingo 1986).

Terrestrial vertebrates also feed on invertebrates from the floodplain. Common snipe (*Capella gallinago*), for example, were almost continuously present at the Tomah Stream study site during inundation in 1997. These birds are predators of wetland invertebrates and have been specifically reported to feed on mayfly larvae (Terres 1980). The black duck (*Anas rubripes*) is also a predator of mayfly larvae. As much as 50 percent of the diet of adult female black ducks during egg laying in Maine consists of mayflies (Reinecke 1977). Although present elsewhere along Tomah Stream during April and May 1997, black ducks were not observed at the study site.

Energy Base

Sources of carbon used for macroinvertebrate production at the Tomah Stream study site were investigated by stable isotope analysis (Hershey and Peterson 1996). This method assumes that ratios of stable isotopes of carbon (^{12}C:^{13}C) composing the tissue of consumers reflects their food sources. This assumption is generally valid, and changes in ratios of stable carbon isotopes through successive trophic levels appear to be minor (~1‰, Hershey and Peterson 1996). Providing there is sufficient discrimination among potential food sources—terrestrial versus aquatic primary production, for example—isotope ratios of consumers will indicate which food source is actually being assimilated. Stable isotope ratios are reported relative to a standard, and the units of measure (δ-^{13}C) represent departures (‰) from the standard. Negative δ-values indicate a lower proportion of ^{13}C compared to the standard (^{13}C "depleted"); positive δ-values indicate relative "enrichment" (Hershey and Peterson 1996). δ-^{13}C values were measured for potential food sources (sedge and grass detritus, sediment [particle size <100 μm], and periphyton) and consumers from the Tomah Stream study site during April and May 1997 (Fig. 16.2). Samples were analyzed at the Sawyer Environmental Laboratory at the University of Maine, Orono.

Consumers at the Tomah Stream study site were substantially depleted in ^{13}C, compared with obvious food sources—sedge and grass detritus, sediment, and periphyton (Fig. 16.2a). *Leptophlebia* larvae collected from above the ice layer before floodplain inundation and within two weeks following ice melt were substantially less depleted in ^{13}C compared to larvae collected

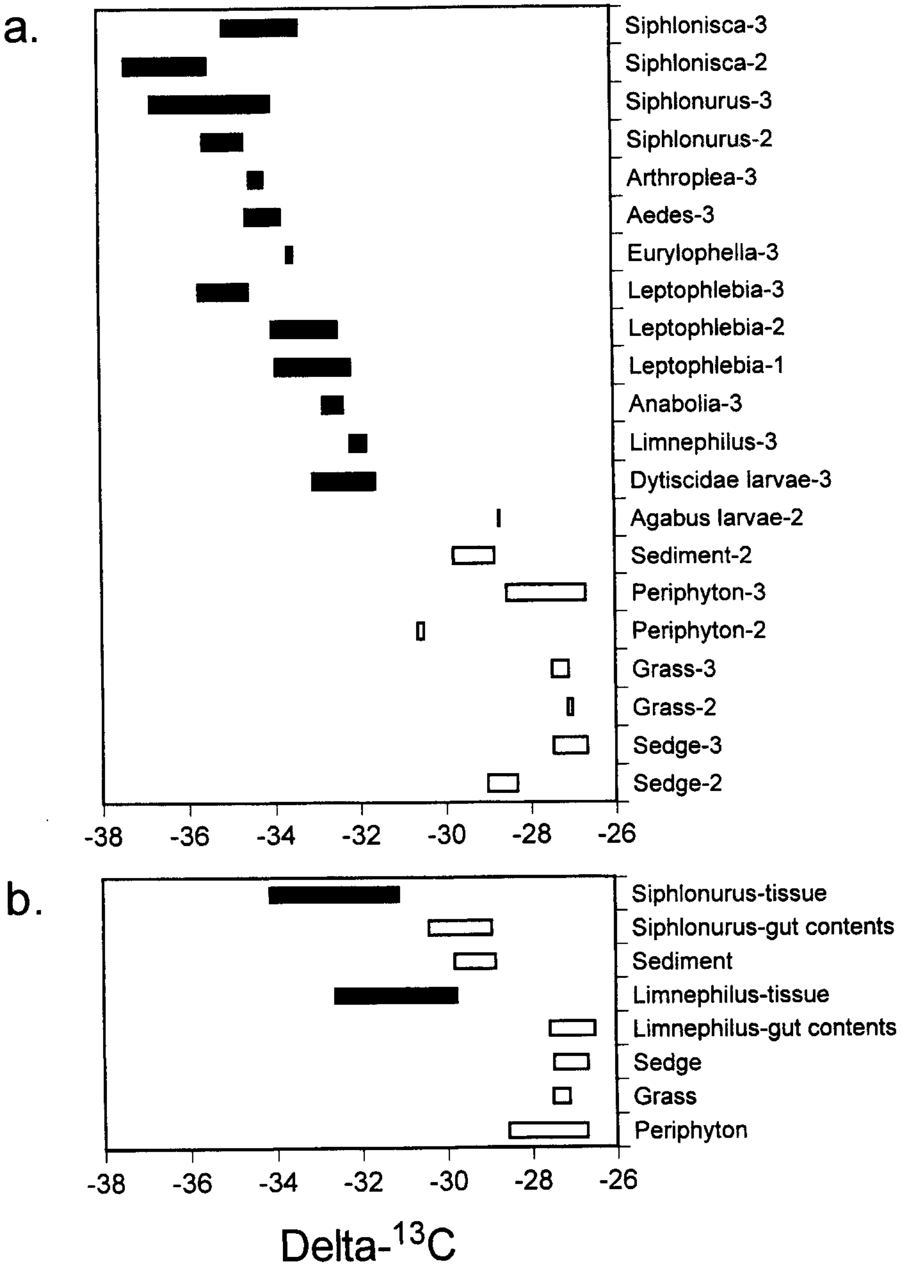

Fig. 16.2. δ-^{13}C values measured for (*a*) potential food sources and tissues of selected consumers and (*b*) potential food sources, gut contents, and tissues of *Limnephilus* and *Siphlonurus* collected at the Tomah Stream study site. Numbers associated with individual categories refer to date sampled during 1997 (1 = April 5, 2 = April 25, 3 = May 27). Specimens used for analysis of gut contents were collected May 27. Bars represent the maximum and minimum values measured. Sample size ranged from 1 to 7. Individual samples consisted of 3–10 specimens.

during the later phase of floodplain inundation (Fig. 16.2*a*). As the season progressed, larvae were apparently using a carbon source on the floodplain that was substantially more depleted than obvious food sources such as sedge or grass detritus, which are the most abundant source of organic matter on the floodplain, or periphyton, as shown for wetland foodwebs both in tropical (Hamilton et al. 1992) and temperate (Keough et al. 1996) regions. This result is almost identical to the results of Bunn and Boon (1993), who studied the foodweb in Australian oxbow lakes (billabongs).

For determining whether invertebrates were ingesting abundant sources of organic matter, but perhaps selectively assimilating material that is depleted in ^{13}C, both tissue and gut contents were analyzed from *Siphlonurus* and *Limnephilus*. The gut content of *Siphlonurus* had δ-^{13}C values that matched those of sediments, a likely food source for a collector-gatherer (Fig. 16.2b). The δ-^{13}C value for the gut content of *Limnephilus,* a shredder, also matched that of the appropriate food source—vascular plant material and attached periphyton (Fig. 16.2*b*). The tissues of these consumers, however, were substantially more depleted than the gut contents (Fig. 16.2*b*). These results, although preliminary, indicate that a small fraction of the ingested material is assimilated and that some of this material is highly depleted in ^{13}C. This material would have to make up a small proportion of the ingested material, otherwise the overall stable isotope ratio would be more strongly skewed. Providing that larval gut contents are turned over rapidly, assimilation of only a small proportion of the ingested food could result in tissue-stable carbon ratios that varied from food ratios.

Although this is speculative, a likely candidate for highly ^{13}C-depleted material in the "assimilated fraction" are bacteria that scavenge biogenic methane released from wetland sediments (methanotrophic bacteria) (Bunn and Boon 1993). Since biogenic methane is both abundant in wetlands and highly depleted in ^{13}C (δ-^{13}C < -52), Bunn and Boon (1993) suggested that methanotrophic bacteria should be depleted in ^{13}C to the degree that assimilation of relatively small quantities of their carbon by consumers could significantly influence isotope ratios of their tissues. Calculations based on a simple two-source mixing model (Araujo-Lima et al. 1986), indicate that δ-^{13}C values measured for *Limnephilus* (~ -31) would result if larvae obtained 20 percent of their tissue carbon from methanotrophic bacteria (assuming $\delta-^{13}$C values $= -52$) and 80 percent from vascular plant tissue (δ-^{13}C ~ -27). A similar ratio was obtained for *Siphlonurus* feeding on sediment.

Sources of Community Members

The floodplain community at Tomah Stream floodplain is derived from two general sources: the floodplain and the stream. Macroinvertebrates that are major contributors to community biomass and permanent residents of the floodplain ("floodplain fauna") include the mosquito *Aedes,* the caddisflies *Limnephilus* cf. *indivisus* and *Anabolia,* and the pea clam *Pisidium* (Table

16.1). Macroinvertebrates that colonize the floodplain from the stream ("river-floodplain fauna") include the mayflies *Leptophlebia* spp., *S. aerodromia,* and *Siphlonurus* spp. (Table 16.1).

Life Cycles of Floodplain Fauna

Floodplain fauna life cycles contrast with those of river-floodplain fauna because they must survive the dry period during summer, which may be punctuated by brief periods of inundation and a long period of ice and snow during winter, before rapidly completing growth, development, and reproduction during April and May. The general life histories of macroinvertebrates in intermittent aquatic habitats have been well documented (Wiggins 1973, Wiggins et al. 1980, Ward 1992, Williams 1987), but detailed information about the life cycles of many taxa found at the study site is lacking. Information about the life cycles of *Aedes, Limnephilus,* and *Pisidium,* however, is abundant and indicates that these taxa are probably permanent residents of the floodplain.

Aedes, Limnephilus, and *Anabolia,* as well as *Pisidium,* contain species that are able to pass through summer and winter as eggs (*Aedes*), as aestivating juveniles or adults (*Pisidium*), or as terrestrial adults in reproductive diapause (*Limnephilus* and possibly *Anabolia*) (Wiggins 1973, Clarke 1981, Ward 1992). In the latter case, adults survive the summer dry period and deposit egg masses in areas that are likely to be flooded in the spring. Winter is passed in the egg stage (Wiggins 1973). *Pisidium* is abundant in damp *Sphagnum* moss and sedge detritus on the Tomah Stream floodplain throughout the dry period. Although not major contributors to total biomass, *Lasiodiamesa* (Podonominae) and *Phalacrocera* (Tipulidae) occur in pockets of *Sphagnum* moss (Alexander and Byers 1981, Brundin 1983) and so form a special group within the floodplain fauna.

Life Cycles of River-Floodplain Fauna

Although remarkable in their complexity, life histories that span both river and floodplain habitats are not unusual for mayflies on the Tomah Stream floodplain. The life history of *S. aerodromia* has been intensively studied (Gibbs and Mingo 1986, Gibbs and Siebenmann 1996) and provides a general example of the life cycle of river-floodplain fauna (Fig. 16.3). Larvae of *S. aerodromia* first appear beneath the ice of the stream channel during November. Larvae remain in the stream, growing slowly at water temperatures ~0°C until snowmelt during March or April. Following snowmelt, larvae migrate onto the inundated floodplain (Fig. 16.3), where they become closely associated with patches of tussock sedge (Gibbs 1991). Most larval growth and development occurs during this period, and larvae enter their final instar in late May and early June (Fig. 16.3). The emergence period in early June is short (9–10 days) and synchronous and occurs only when water temperature is >11°C (Gibbs and Siebenmann 1996). Oviposition by females is completed

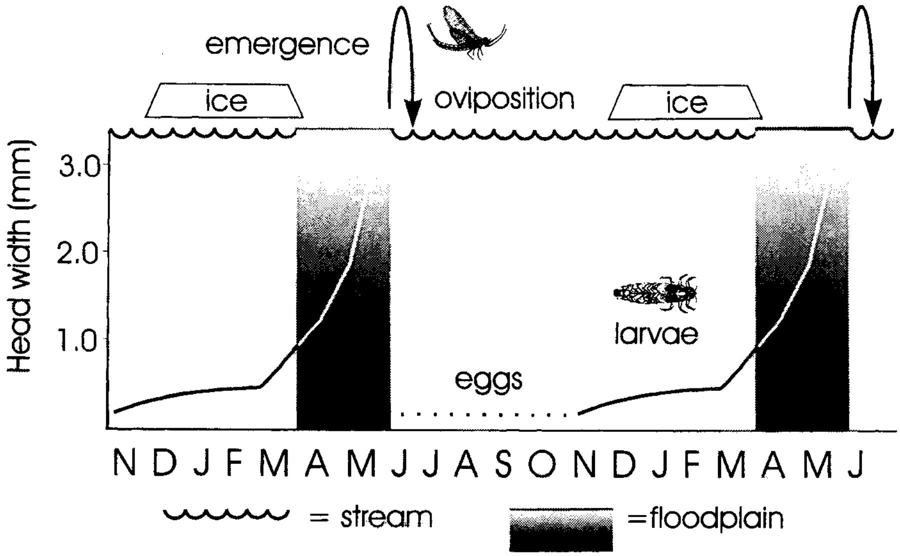

Fig. 16.3. Diagram showing details of the life cycle of *Siphlonisca aerodromia* at the Tomah Stream study site (for more information see Gibbs and Mingo 1986).

by mid-June. Standing water has usually disappeared from the floodplain at this time, and females return to the stream channel, where they deposit eggs on the water's surface. Eggs hatch in the stream the following November and December (Fig. 16.3).

The life cycles of other common mayflies at the study site, *Siphlonurus mirus* and *Leptophlebia cupida,* have been documented from river-floodplain complexes similar to Tomah Stream (Neave 1930, Hayden and Clifford 1974, Voshell 1982). The life cycles of these mayflies generally follow the pattern described for *S. aerodromia.* Adult females of both *S. mirus* and *L. cupida* oviposit in river channels, following emergence from floodplain marshes and ponds in early summer. Larvae appear in the river channel during autumn and migrate onto floodplains to complete growth and development during the spring. Upon emergence and mating, females return to the river channels to oviposit. *Siphlonurus* is also known to survive dry periods as resistant eggs (Wiggins et al. 1980, Voshell 1982). It is not known if any of the species occurring at Tomah Stream are able to use this strategy. Larvae collected shortly after inundation were relatively large (7–9 mm in length), and it is assumed that these migrated from the stream. Early instars became increasingly abundant as the season progressed, however, and it is possible that these were derived from eggs deposited on the floodplain the previous year.

Synchronized migrations of *L. cupida,* from river to floodplain following snowmelt, have been well documented (Neave 1930, Hayden and Clifford 1974). During early April in 1997 *Leptophlebia* nymphs were observed in water over ice that covered the floodplain at Tomah Stream. At this time ice on the floodplain was ~0.5-m thick and was continuous with the floodplain soil. The larvae had apparently escaped from the stream channel through holes in the ice and migrated over the ice toward the river margins as described by Hayden and Clifford (1974) for a population in Alberta. Similar migratory behavior was described for the mayfly *Paramaletus chelifer* in a Norway river-floodplain system (Olsson and Soderstrom 1978, Soderstrom and Nilsson 1987), and we assume that *S. aerodromia* and *Siphlonurus* spp. show migratory behavior at Tomah Stream.

MACROINVERTEBRATE COMMUNITIES AND RIVER-FLOODPLAIN INTERACTION

The biomass of the macroinvertebrate community on the Tomah Stream floodplain is largely composed of mayflies that are able to use the stream as a refuge during the dry period of the summer and the freezing temperatures of winter, and the floodplain during a short but critical period of rapid growth and development during spring. Compared to the contributions by this river-floodplain fauna, those by floodplain fauna to community biomass seem remarkably small. Because nothing is presently known about possible competitive interactions among members of these two assemblages, however, speculation about this factor seems unwarranted. The proximity and interconnection of the river and floodplain, however, are clearly required for the development of the characteristic floodplain community structure during the short period of inundation.

Given that river-floodplain life cycles of mayflies are relatively common, it is not surprising that there has been long interest in factors contributing to the evolution of this strategy. Most authors agree that the major risk for organisms that colonize floodplains during inundation is death because of desiccation before completing development (Neave 1930, Soderstrom and Nilsson 1987, Gibbs and Siebenemann 1996). Compared to proposed risks, explanations of the advantages of this strategy are more diverse and generally fall into the following categories (modified from Soderstrom and Nilsson 1987):

1. Avoidance of fish and invertebrate predators (Neave 1930, Olson and Soderstrom 1978, Soderstrom and Nilsson 1987, Gibbs and Siebenemann 1996);
2. Avoidance of high water velocity and ice in channel during spring floods (Neave 1930, Hayden and Clifford 1974, Olson and Soderstrom 1978);
3. Food supplies on floodplain abundant compared to river (Neave 1930, Gibbs and Siebenmann 1996);
4. Water temperatures on the floodplain more optimal for growth (Olson and Soderstrom 1978, Gibbs and Siebenmann 1996, Siebenmann and Gibbs 1996); and

5. Emergence sites in river inadequate (Soderstrom and Nilsson 1987, Gibbs and Siebenmann 1996).

Soderstrom and Nilsson (1987) tested the first of these explanations by using a combination of field observations and laboratory experiments. These authors showed that larvae of *Parameletus* that migrated from river channels to floodplain ponds in Norway were subject to lower risk of fish predation than were larvae that remained in the river channel. Although this study indicated lower risk from fish predation, Soderstrom and Nilsson (1987) conceded that the risk of predation by other invertebrates (Dytiscidae) and wetland birds might have actually been higher on the floodplain. Tomah Stream provides a similar situation because *S. aerodromia,* one of the major mayfly taxa that colonize the floodplain, is a predator of the other mayflies. The remaining explanations remain speculative, presumably because of logistical difficulties in devising experiments required for rigorous testing, and also because the different categories of explanation are not mutually exclusive. Perhaps they are also overly complex.

In the review of those factors suggested as being important in the evolution of the river-floodplain life cycle, it was apparent that there was perhaps an overemphasis on proposing adaptive explanations for movements from river-to-floodplain rather than floodplain-to-river. There is at least one critical evolutionary advantage for movements from floodplain to river by adults. If the eggs of a given species are not desiccation resistant or cannot withstand freezing, oviposition and eventual hatching of larvae in the stream channel may simply provide the only option for completing the life cycle for organisms otherwise adapted to wet meadow habitats.

Other research concerning macroinvertebrates of river-floodplain systems has concentrated on their potential role in translocating biomass between the stream and floodplain (Smock 1994). In a study of movements of macroinvertebrates in forested river-floodplain system in Virginia, Smock (1994) shows that movements across the channel-floodplain boundary were minimal and that these low numbers suggest that movements of invertebrates between the channels and floodplains would have little effect on the trophic dynamics of these systems. Although probably true when only the aquatic life history stages are considered over relatively short time intervals (<1 year), this conclusion overlooks other properties of the river-floodplain community.

At Tomah Stream the migrations of mayfly larvae onto the floodplain are rapid and extensive. Although most of the growth and production probably occurs on the floodplain (e.g., Fig. 16.3), the individuals that cross the river-floodplain boundary to colonize the floodplain eventually dominate community biomass and almost certainly do play a major role in the trophic dynamics of the floodplain community. Consideration of the exchange of biomass alone overlooks this important qualitative factor. The fate of the biomass produced on the floodplain involves aerial movements to the stream channel that are also overlooked when only larval movements are considered (e.g., Smock 1994). During the emergence of *S. aerodromia* at Tomah Stream, Gibbs and

Siebenemann (1996) observed intense fish predation on ovipositing female imagos in the stream channel and striking numbers of dead imagos of *Leptophlebia* spp. originating from the floodplain accumulated on the surface of Tomah Stream following oviposition in late May and June of 1997. The quantitative importance of aerial translocations of biomass from floodplain to river and their effect on trophic dynamics of the entire complex are unknown, but should not be ruled insignificant without further study.

MANAGEMENT AND CONSERVATION ISSUES

Prior to European colonization, streams with extensive riparian sedge-meadows were abundant in Maine and elsewhere in the Northeast. Where records exist, these systems are reported to have supported a rich and diverse fauna of wildlife (Widoff 1988). The damming of rivers for mills, water storage, and transporting timber has been a central feature in the history and development of Maine since the earliest days of European settlement, and thousands of dams have been built (Hasbrouck 1984). These dams have created numerous lakes on reaches of rivers formerly bordered by meadows and drastically altered the normal seasonal flow patterns of rivers (Widoff 1988).

Because of a complex life cycle that spans both river and floodplain habitats, *S. aerodromia* and other members of the sedge-meadow community are vulnerable to activities which alter the seasonal discharge patterns of rivers. Increased flow following snowmelt is essential to produce the inundated floodplain habitat in April and May. Threats to habitat by the building of dams are ongoing and are exemplified by a recent proposal to construct a dam on Tomah Stream (Anonymous 1990). Such a dam would threaten the most abundant and predictable population of *S. aerodromia* known. The disappearance of *S. aerodromia* from the Sacandaga River in New York following construction of the Sacandaga Reservoir confirms that dam construction is a serious threat to the species and to the entire river-floodplain community (Gibbs and Siebenmann 1993, McCafferty and Edmunds 1997).

Seasonally inundated floodplains support a wide variety of plants and animals, and their value as habitats is little understood (Ward 1992). The discovery of *S. aerodromia* has provided a focus for efforts to conserve these habitats in Maine. *Siphlonisca aerodromia* has been officially recognized as a threatened species in Maine (M. McCollough, Maine Department of Inland Fisheries and Wildlife, personal communication), and as such it may act as an umbrella that will provide protection for other members of the riparian sedge meadow community.

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