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THE EDGE EFFECT:

LATERAL HABITAT ECOLOGY OF AN ALLUVIAL RIVER FLOOD PLAIN

By

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The edge effect: Lateral habitat ecology of an alluvial river flood plain

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ABSTRACT:

We describe the ecology of off-channel or "lateral" habitats as key attributes of the Shifting Habitat Mosaic (SHM) of a river flood plain at the Nyack Research Natural Area in northwestern Montana. Our working hypothesis was that lateral habitats are important to the cycling of energy and materials within the SHM and contribute greatly to the productivity and biodiversity of the floodplain ecosystem. We produce a quantitative description of temperature variation across aquatic and terrestrial habitats at Nyack. Thermal patterns across lateral habitats indicate vast differences exist between lateral habitats in habitat suitability for aquatic organisms over an annual cycle. Existing thermal regimes favor life history diversification. We further document the impacts of flood disturbances on organic matter accumulation by aquatic primary producers in off-channel environments. We were able to show that the annual flood pulse disturbance was the major force controlling periphyton community biomass, nutrient status, and species composition, with secondary control by surface and groundwater mediated water chemistry fluctuations during lower flow periods. We end with a study relating biodiversity pattern and process to lateral habitat heterogeneity. Data supported our prediction that densities and diversity of organisms and food webs of the flood plain would be greatly increased if off-channel habitats as well as main channel habitats were included. Collectively, lateral habitats uniquely support 50% of the total documented aquatic biodiversity of the entire floodplain. We conclude that lateral habitats contribute significantly to the biocomplexity of alluvial floodplain ecosystems.

DEDICATION

This work is dedicated to:

Nate Stevenson, who taught me that becoming a dedicated scientist and an admirable person is possible in a single lifetime. You are with us always.

The Dalimata family, to whom I extend my deep gratitude for inviting me to spent time on their land and in their excellent company. My best days at Nyack I spent with you.

And for Jed, who knows the way home.

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CHAPTER 1:

A REVIEW OF ECOSYSTEM RESEARCH IN ALLUVIAL FLOOD PLAINS

In the last 35 years ecologists have recognized that river ecosystems must be viewed as the integration of stream channels and the surrounding catchments (Hynes 1975). This understanding of streams as features integrated with the terrestrial landscape led to the development of key hypothesis about river ecosystem structure and function. The River Continuum Concept (RCC, Vannote et al 1980) is applicable to entire stream networks while the Flood Pulse Concept (FPC, Junk et al. 1989), the 4-D nature of lotic ecosystems (Ward 1989), and the Shifting Habitat Mosaic (SHM, Stanford et al. 2005) provide more specific insight into floodplain ecosystems. The SHM describes naturally dynamic processes that form and maintain a complex suite of interactive habitats in flood plains. This comes as a consequence of short and long term effects of catchment hydrology, cut and fill alluviation and plant succession. As an emergent property of natural river-flood plains, the SHM links processing of water, heat and materials to biogeochemical cycles. This becomes the stage upon which biotic communities are organized, influencing organismal life histories, biological productivity and food web interactions.

Prior to the 1980's, most well-studied systems were smaller, lower order streams, tropical floodplains, or rivers that had been modified heavily (Bayley 1995, Ward et al. 2001). This inhibited our ability to predict ecosystem-level processes associated with the SHM and guide restoration and preservation in large, temperate rivers. The increase in alluvial floodplain ecosystem studies worldwide over the past 20 years has been instrumental in revealing the structure and function of natural and impacted rivers. A case study of major worldwide gravel-bed river floodplain study sites was conducted to synthesize across the major research findings of these investigations (Table 1). While studies did exist in other large river-floodplain systems, notably the Hoh River in Washington and the Taeri River in New Zealand, these sites were not included in this analysis. This body of work was excluded as these investigations lacked the long-term dedication to interdisciplinary, landscape scale research observed at the sites that were included in the synthesis.

One of the oldest river-flood plains that has been continuously studied is the Tanana River within the Bonanza Creek LTER site outside of Fairbanks, Alaska (Table 1). The Tanana is a glacial-fed, permafrost river with a history of floodplain research dating back to the 1970's. This site exhibits a clear successional chronosequence of vegetation limited by soil nitrogen, phosphorous, temperature and moisture (Viereck et al. 1993). Nearly all studies of the Tanana are focused on vegetation and soil subsystems of the flood plain, with succession serving as the framework for research questions. Investigators have explored chemical links between soil processes and vegetation dynamics, with some additional consideration of the impacts of climate on permafrost and browsing animal effects on vegetation. Studies of flood processes have highlighted the influence of the hydrograph in shaping nutrient cycling, soil structure, and vegetation successional dynamics.

Research on the Danube River stretches back centuries, but has only recently coalesced in a systematic way to address ecosystem scale questions (Table 1). Since the 1990's, researchers have monitored restoration of lowland, urban reaches of the Danube in Austria (Schiemer et al. 1999). These studies continued a tradition of aquatic research on the Danube but have broadened beyond fisheries to include nutrient cycling (Hein et al. 2003), algal production (Hein et al. 1999) and benthic invertebrate diversity (Ward et al. 1999). Key findings stressed the dual source and sink nature of the floodplain in relation to nutrients, and support the hypotheses that flooding interacts with floodplain primary production, respiration, nutrient cycling and aquatic species' life histories.

In the last decade the Val Roseg floodplain and the series of floodplains on the Fiume Tagliamento have been active sites for research by investigators from European universities (Universite Claude Bernard Lyon in France, Kings College and the University of Birmingham in the UK, the Royal Veterinary and Agricultural University in Denmark) and the Swiss Federal Institute for Environmental Science and Technology (EAWAG/ETH). These two rivers each originate from different glacial systems in the Alps and share the flashy hydrograph and unstable gravel channels typical of glacial rivers. The river and aquifer are the primary ecosystem components considered at these sites.

The Val Roseg floodplain is part of a 2nd order watershed in the Swiss Alps, draining 67 km^2 and ranging in elevation from 4,000 m to 1,750 m elevation (Tockner et al. 2002). Research at Val Roseg (Table 1) illustrated the importance of nutrients and fungi to in-stream litter decomposition, and the key role of glacial melt-water runoff in developing habitat complexity, recycling nutrients and biotic productivity.

The Tagliamento, the last major intact free-flowing river in Europe, is a 7th order watershed originating in the Italian Alps that drains an area of 2580 km^2 (Tockner et al. 2003). The Tagliamento ranges in elevation from the headwaters at 2700 m to sea-level where it drains into Adriatic Sea. Research on the Tagliamento (Table 1) has occupied six floodplain reaches that vary in geomorphology from constrained to island-braided to meandering in progression downstream (Arscott et al. 2001). The main research findings at the Tagliamento mirrored the results from work at the Val Roseg. The Tagliamento studies also revealed the stabilizing effect of LWD in forming vegetated islands in unstable glacial streams (Edwards et al. 1999), energy sources in the river derived from instream algal and microbial production and soil organic materials (Kaiser et al. 2004), and the high rate of consumption by terrestrial arthropods of emergent aquatic insects (Paetzold & Tockner 2005).

Our survey of world-wide floodplains ends with Nyack flood plain in northwestern Montana, a core study site for researchers and graduate students of the Flathead Lake Biological Station since the 1980's (Table 1). The SHM concept has been shaped and reinforced by +20 years of studies at the Nyack flood plain, which consistently links non-linear physical and biological processes to illustrate the biocomplexity of the SHM. It is also the main study site investigated in this dissertation. Access to unpublished documents from undergraduate and graduate student projects makes coverage of research at this site more comprehensive than was possible for other floodplain projects described. The most obvious feature of the Nyack studies is the depth and breadth of work distributed and linked across all subsystem components of the floodplain ecosystem, from river to aquifer to soils to terrestrial vegetation.

Work at Nyack has crossed all scales of research questions in ecology, from organization of microbial communities to ecosystem carbon cycling. In the 1980's and 1990's, work by research scientists and graduate students from the Flathead Lake Biological Station (FLBS) initially described the 4-dimensional nature of this river-flood plain. Over the last decade, two multi-year projects operating at a whole ecosystem scale have been conducted in the Nyack flood plain. Each project helped synthesize existing information and create a new framework for hypothesis testing in this system.

The Nyack Biocomplexity Project began in 2003 and involved a group of researchers from diverse disciplines. The Biocomplexity Project was designed to model the dynamic biophysical processes making this flood plain a regional center of ecological organization. The project's chief goal was creation of a process model linking water, heat and materials flux and retention to the physical and biological organization of the SHM (Poole et al. 2004, 2006). Nested within the larger objectives of the Biocomplexity Project, investigators pursued focused studies of hydrology, forest structure and geomorphic dynamics (Harner and Stanford 2003, Whited et al. 2007, Mouw et al. submitted), along with the aquatic biota of parafluvial ponds (Chilcote 2004) and the aquifer (Reid 2007). Short-term studies were also pursued in the summers of 2003-2007 by students enrolled in the Research Experiences for Undergraduates (REU) Program administered by FLBS scientists (A. McKee, personal communication). REU projects examined a broad spectrum of research topics, including nutrient cycling, vegetation dynamics, and aquatic community structure.

The Nyack Microbial Observatory Program was established in 2004 to explore microbial diversity in the hyporheic zone of the aquifer. The intent of this project is to characterize microbial diversity in the context of factors influencing community structure using innovative molecular, microbial and hydrologic techniques. As part of this research, Nyack Microbial Observatory Program investigators explore linkages between the microbial community and higher organisms such as insects and plants. To these ends a grid of over 100 wells, some of which also informed the Biocomplexity Project aquifer studies, are currently being used to monitor hydrologic condition and as a source of microbes.

While the initial phases of the Biocomplexity Project and Microbial Observatory Program have ended or are coming to a close, research activity at Nyack continues to expand. New studies place an even greater emphasis on biogeochemical cycling, which supports the modeling efforts of Stanford, Poole, Kimball and Wright (in prep). Their ecosystem model will link water, nutrients and energy fluxes in three dimensions in order to predict the biological productivity in specific habitats. The model has great potential as a tool for testing novel hypotheses and guiding river conservation and restoration planning. The research presented herein also supports these modeling efforts by defining elements of abiotic and biotic structure that are poorly resolved in off-channel habitats.

The three papers in this dissertation provide a foundation for concluding off-channel or “lateral” habitats are ecological attributes essential to SHM structure and function. Lateral habitats interact variably with main channel, riparian, and hyporheic zones as these habitats occur at different elevations across the floodplain. This enhances the likelihood of off-channel areas exhibiting abiotic and biotic complexity (Moore and Gregory 1988, Junk et al. 1999). Our working hypothesis is that lateral habitats are import to the cycling of energy and materials within the SHM and contribute greatly to the productivity and biodiversity of the Nyack floodplain ecosystem.

Each of the three papers examines a different aspect of how hydrologic change impacts the physical structure and biotic composition of Nyack lateral habitats. The first paper (Chapter 2) provides a quantitative description of temperature variation across aquatic and terrestrial habitats at Nyack, providing data to support the hypothesis that the SHM determines floodplain heat flux and storage. Arrays of temperature recorders were installed in air, soil, surface water and groundwater environments to monitor spatial and temporal variability in thermal regimes across the floodplain. Daily, seasonal and annual fluctuation in heat was compared to known thermal preferences of floodplain biota.

The second paper (Chapter 3), documents the impacts of disturbances by large and small floods on organic matter accumulation by aquatic primary producers. We evaluated evidence for the hypothesis that lateral habitats are influenced by different frequencies and intensities of disturbances, governing water chemistry flux and periphyton community metrics. We predicted that the annual flood pulse disturbance was the major force controlling periphyton community biomass, nutrient status and species composition, with secondary control by fluctuations in surface water and groundwater chemistry during lower flow periods.

The final paper (Chapter 4) focuses on the influence of habitat heterogeneity within the SHM on taxonomic diversity of aquatic organisms and the complexity of food webs. We relate biodiversity pattern and process to habitat heterogeneity created by flooding of the shifting habitat mosaic (SHM) of this river-flood plain. We predicted densities and diversity of organisms and food webs of the flood plain would be greatly increased if off-channel habitats as well as main channel habitats were analyzed. We examined spatial and temporal changes in biotic community composition (density, diversity metrics) and organization (food web structure, functional feeding groups, energy sources) across the aquatic components of the habitat catena.

The more we study river floodplains perhaps the more we may understand how societal choices impact the environment. The rate of processes and change that operate in a flood plain fits within our ability to observe relative to our life spans. Taken together, these three papers underscore the importance of expanding analyses beyond a narrow focus on main channel processes and communities. This research demonstrated the role of frequency and intensity in flooding as a driver for temperature and nutrient cycling. The manifestation of flood effects and abiotic structure depends largely on the geographic location of habitats. The physical features of habitats in turn regulate rates of biomass accumulation and states of biodiversity and life history expression that vary across the flood plain. Lateral habitats add significantly to habitat heterogeneity, aquatic primary production and overall aquatic biodiversity of the entire floodplain ecosystem. It remains to be seen how well this view can be integrated with recent theory regarding river ecosystem processes (Riverine Ecosystem Synthesis; Thorp et al. 2006). It seems likely that the biocomplexity we demonstrate herein for lateral habitats is vital to creating and maintaining ecosystem goods and services. If we hope to maintain healthy and productive flood plains, we must protect lateral features and the processes sustaining these habitats.

LITERATURE CITED

Adams, S. 2006. Microbes, stoneflies and fish: trophic interactions in aquatic ecosystems. M. S. Thesis, University of Montana, Missoula, Montana, USA.

Arscott, D. B., K. Tockner, J. V. Ward. 2000. Aquatic habitat diversity along the corridor of an alpine floodplain river (Fiume Tagliamento, Italy). Archiv fuer Hydrobiologie **149**: 679-704.

Arscott, D. B., K. Tockner, J. V. Ward. 2001. Thermal heterogeneity along a braided floodplain river (Tagliamento River, Northeastern Italy). Canadian Journal of Fisheries and Aquatic Sciences **58**: 2359-2373.

Arscott, D. B., K. Tockner, D. van der Nat, J. V. Ward. 2002. Aquatic habitat dynamics along a braided river ecosystem (Tagliamento River, Northeastern Italy). Ecosystems **5**: 802-814.

Arscott, D. B., K. Tockner, J. V. Ward. 2003. Spatio-temporal patterns of benthic invertebrates along the continuum of a braided Alpine river. Archiv fuer Hydrobiologie **158**: 431-460.

Arscott, D. B., K. Tockner, J. V. Ward. 2005. Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. Journal of the North American Benthological Society **24**: 934-954.

Bansak, T. 1998. The influence of vertical hydraulic exchange on habitat heterogeneity and surficial primary production on a large alluvial floodplain. M.S. Thesis. University of Montana, Missoula, Montana, USA.

Bergherr, P., J. V. Ward, R. Glatthaar. 2001. Diversity, distribution and seasonality of the Simuliidae fauna in a glacial stream system in the Swiss Alps. Archiv fuer Hydrobiologie **152**: 19-37.

Brenner, R. E., R. D. Boone, J. B. Jones, K. Lajtha, and R. W. Ruess. 2006. Successional and physical controls on the retention of nitrogen in an undisturbed boreal forest ecosystem. Oecologia **148**: 602-611.

Brown, K. R., D. B. Zobel, and J. C. Zasada. 1988. Seed dispersal, seedling emergence, and early survival of *Larix laricina* (DuRoi) K. Koch in the Tanana Valley, Alaska. Canadian Journal of Forest Research **18**: 306-314.

Brouwer, B. O., J. K. Caves, M. R. Morris and J. A. Stanford. In prep. Changes in soil and hyporheic nitrogen fertility with riparian succession on the Nyack Floodplain, MT: Implications for riparian vegetation.

Bryant, J. P. 1987. Feltleaf willow-snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology **68**: 1319-1327.

Case, G. L. 1995. Distribution and abundance of zoobenthos in channel, springbrook and hyporheic habitats of an alluvial floodplain, M.S. Thesis, University of Montana, Missoula, Montana, USA.

Cavallo, B. J. 1997. Floodplain habitat heterogeneity and the distribution, abundance, and behavior of fishes and amphibians in the Middle Fork Flathaed River Basin, Montana. M.S. Thesis, University of Montana, Missoula, Montana, USA.

Chilcote, S. 2004. The ecology of parafluvial ponds on a Rocky Mountain floodplain. Ph.D. Dissertation, University of Montana, Missoula, Montana, USA.

Chovanec, A., F. Schiemer, A. Cabela, S. Gressler, C. Grotzer, K. Pascher, R. Raab, H. Teufl and R. Wimmer. 2000. Constructing inshore zones as river corridors through urban areas-the Danube in Vienna: preliminary results. Regulated Rivers: Research and Management **16**: 175-187.

Craft, J. A., J. A. Stanford, and M. Pusch. 2002. Microbial respiration within a floodplain aquifer of a large gravel-bed river. Freshwater Biology **47**: 251-261.

Diehl, C. J. 2004. Controls on the magnitude and location of groundwater/surface water exchange in a gravel dominated alluvial floodplain system, northwestern Montana. M.S. Thesis. University of Montana, Missoula, USA.

Dyrness, C. T. and K. Van Cleve. 1993. Control of surface soil chemistry in early-successional floodplain soils along the Tanana River, interior Alaska. Canadian Journal of Forest Research **23**: 979-994.

Edwards, P. J., J. Kollmann, A. M. Gurnell, G. E. Petts, K. Tockner, and J. V. Ward. 1999. A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. Wetlands Ecology and Management **7**: 141-153.

Ellis, B. K., J. A. Stanford and J. A. Ward. 1998. Microbial assemblages and production in alluvial aquifers of the Flathead River, Montana, USA. Journal of the North American Benthological Society **17**: 382-402.

Gafner, K and C. T. Robinson. 2007. Nutrient enrichment influences the responses of stream macroinvertebrates to disturbance. Journal of the North American Benthologicla Society **26**: 92-102.

Gessner, M. O., Robinson, C. T., and J. V. Ward. 1998. Leaf breakdown in streams of an alpine glacial flood plain: dynamics of fungi and nutrients. Journal of the North American Benthological Society **17**: 403-419.

Gurnell, A. M. and G. E. Petts. 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. Freshwater Biology **47**: 581-600.

Gurnell, A., K. Tockner, P. Edwards, G. Petts. 2005. Effects of deposited wood on biocomplexity of river coordiors. Fronteirs in Ecology and the Environment **3**: 377-382.

Hammond, T. and Yarie, J. 1996. Spatial prediction of climatic state factor regions in Alaska. Ecoscience **3**: 490-501.

Harner, M. J. and J. A. Stanford. 2003. Differences in cottonwood growth between a losing and gaining reach of an alluvial floodplain. Ecology **84**: 1453-1458.

Harner, M. J., P. W. Ramsey and M. C. Rillig. 2004. Protein accumulation and distribution in floodplain soils and river foam. Ecology Letters **7**: 829-836.

Harrison, N. E. 2004. Gravity, radar and seismic investigations to help determine geologic, hydrologic, and biologic relations in the Nyack valley, northwestern Montana. M.S. Thesis, University of Montana, Missoula, Montana, USA.

Hawkins, C. R. 2003. Imaging the shallow subsurface using ground penetrating radar at the Nyack floodplain, Montana. M.S. Thesis, University of Montana, Missoula Montana, USA.

Heiler, G., T. Hein, F. Schiemer, and G. Bornette. 1995. Hydrological connectivity and flood pulses as the central aspects for the integrity of a river-floodplain system. Regulated Rivers: Research and Management **11**: 351-361.

Hein, T., G. Heiler, D. Pennetzdorfer, P. Riedler, M. Schagerl, and F. Schiemer. 1999. The Danube Restoration Project: functional aspects and planktonic productivity in the floodplain system. Regulated Rivers: Research and Management **15**: 259-270.

Hein, T. C., Baranyi, G. J. Herndl, W. Wanek, and F. Schiemer. 2003. Allocthanous and autocthanous particulate organic matter in floodplains of the River Danube: the importance of hydrological connectivity. Freshwater Biology **48**: 220-232.

Hynes, H. B. 1975. The stream and its valley. Verhein Internationale Vereinigung Limnologie **19**: 1-15.

Jacobus, L. M., R. L. Newell and W. P. McCafferty. 2006. First adult and egg descriptions of *Caudatella edmundsi* (Ephmemeroptera: Ephemerellidae), from Montana (U.S.A.), with habitat observations. Entomological News **117**:175-180.

Johnson, A. N. 2003. Preliminary hydrogeological and ground penetrating radar investigation of preferential flow zones in a gravel dominated floodplain, northwest Montana. M.S. Thesis, University of Montana, Missoula, Montana, USA.

Jorgenson, M. T., C. H. Racine, J. C. Walters, and T. E. Osterkamp. 2001. Permafrost degradation and ecological changes associated with a warming climate in central Alaska. Climatic Change **48**: 551-579.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems, in D. P. Dodge (ed.), *Proceedings of the International Large River Symposium*, pp. 110-127, Canadian Special Publications in Fisheries and Aquatic Sciences **106**.

Kaiser, E., D. B. Arscott, K. Tockner and B. Sulzberger. 2004. Sources and distribution of organic carbon and nitrogen in the Tagliamento River, Italy. Aquatic Sciences **66**: 103-116.

Karaus, U., L. Alder, and K. Tockner. 2005. " Concave islands": habitat heterogeneity of parafluvial ponds in a gravel-bed river. Wetlands **25**: 26-37.

Kaye, J. P., D. Brinkley, and C. Rhoades. 2003. Stable soil nitrogen accumulation and flexible organic matter stoichiometry during primary floodplain succession. Biogeochemistry **63**: 1-22.

Klingensmith, K. M., and K. Van Cleve. 1993a. Denitrification and nitrogen fixation in floodplain successional soils along the Tanana River, interior Alaska. Canadian Journal of Forest Research **23**: 956-963.

Klingensmith, K. M., and K. Van Cleve. 1993b. Patterns of nitrogen mineralization in floodplain successional soils along the Tanana River, interior Alaska. Canadian Journal of Forest Research **23**: 964-969.

Krasny, M. E., K. A. Vogt, and J. C. Zasada. 1984. Root and shoot biomass and mycorrhizal development of white spruce seedlings naturally regenerating in interior Alaskan floodplain communities. Canadian Journal of Forest Research **14**: 554-558.

Langhans, S. D., and K. Tockner. 2006. The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy). Oecologia **147**: 501-509.

Machura, M. in prep. Ph.D. Dissertation. University of Montana, Missoula, Montana, USA.

Malard, F., K. Tockner, and J. V. Ward. 1999. Shifting dominance of subcatchment water sources and flow paths in a glacial floodplain, Val Roseg, Switzerland. Arctic, Antarctic and Alpine Research **31**: 135-150.

Malard, F., K. Tockner, and J. V. Ward. 2000. Physico-chemical heterogeneity in a glacial landscape. Landscape Ecology **15**: 679-2000.

Malard, F., A. Mangin, U. Uehlinger, and J. V. Ward. 2001a. Thermal heterogeneity in the hyporheic zone of a glacial floodplain. Canadian Journal of Fisheries and Aquatic Sciences **58**: 1319-1335.

Malard, F., M. Lafont, P. Burgherr, and J. V. Ward. 2001b. A comparison of longitudinal patterns in hyporheic and benthic oligochaete assemblages in a glacial river. Arctic, Antarctic and Alpine Research **33**: 457-466.

Malard, F., U. Uehlinger, R. Zah, and K. Tockner. 2006. Flood-pulse and riverscape dynamics in a braided glacial river. Ecology **87**: 704-716.

Mann, D. H., C. L. Fastie, E. L. Rowland, N. H. Bigelow. 1995. Spruce succession, disturbance, and geomorphology on the Tanana River floodplain, Alaska. Ecoscience **2**: 184-199.

Marion, G. M., K. Van Cleve, and C. T. Dryness. 1993. Calcium carbonate precipitation-dissolution along a forest primary successional sequence on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research **23**: 923-927.

Marion, G. M., K. Van Cleve, C. T. Dryness, and C. H. Black. 1993. The soil chemical environment along a forest primary successional sequence on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research **23**: 914-922.

McKee, A. 2007. personal communication, regarding Research Experiences for Undergraduates Program studies conducted at the Nyack flood plain, 2003-2007.

Meier, C. 2008. Cottonwood establishment in a gravel-bed river. Ph.D. Dissertation. University of Montana, Missoula, Montana, USA.

Miserendino, L., and J. A. S. Stanford. In prep. Life histories, abundance and distribution of stoneflies in the Flathead River, Montana (USA): Comparison of 1972-3 and 2001-2 data.

Moore, K.M.S., and S.V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (Salmo clarki) in Cascade Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences **45**: 1921-1930.

Mouw, J. E. B. and P. Alaback. 2003. Putting floodplain hyperdiversity in a regional context: an assessment of floodplain connectivity in a montane environment. Journal of Biogeography **30**: 87-103.

Mouw, J. E. B., J. A. Stanford, and P. Alaback. In review. Influences of flooding and hyporheic exchange on floodplain plant richness and productivity. River Research and Applications.

Osterkamp, T.E. 1994. Evidence for warming and thawing of discontinuous permafrost in Alaska. EOS, Transactions of the American Geophysical Union **75**: 85.

Osterkamp, T. E. and V.E. Romanovsky. 1996. Characteristics of changing permafrost temperatures in the Alaskan Arctic. Arctic and Alpine Research **28**: 267-273.

Osterkamp, T. E. and V. E. Romanovsky. 1997. Freezing of the active layer on the coastal plain of the Alaskan Arctic. Permafrost and Periglacial Processes **8**: 23-44.

Osterkamp, T. E., V. E. Romanovsky, T. Zhang, V. Gruol, J. K. Peterson, T. Matava, and G. C. Baker. 1997b. EOS, Transactions of the American Geophysical Union **78**: F270.

Osterkamp, T. E, L. Viereck, Y. Shur, M. T. Jorgenson, C. Racine, A. Doyle, R. D. Boone. 2000. Observations of thermokarst and its impacts on boreal forests in Alaska, U.S.A. Arctic, Antarctic, and Alpine Research **32**: 302-315.

Paetzold, A. and K. Tockner. 2005. Effects of riparian arthropod predation on the biomass and abundance of aquatic insect emergence. Journal of the North American Benthological Society **24**: 395-402.

Pepin, D. M. and F. R. Hauer. 2002. Benthic responses to groundwater-surface water exchange in two alluvial rivers in northwestern Montana. Journal of the North American Benthological Society **21**: 370-383.

Petts, G. E., A. M. Gurnell, A. J. Gerrard, D. M. Hannah, B. Hansford, I. Morrissey, P. J. Edwards, J. Kollman, J. V. Ward, K. Tockner, and B. P. G. Smith. 2000. Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. Aquatic Conservation: Marine and Freshwater Ecosystems **10**: 249-266.

Poole, G. C. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biology **47**: 641-660.

Poole, G. C. J. A. Stanford, S. W. Running, C. A. Frissell, W. W. Woessner and B. K. Ellis. 2004. A patch hierarchy approach to modeling surface and subsurface hydrology in complex flood-plain environments. Earth Surface Processes and Landforms **29**: 1259-1274.

Poole, G. C., J. A. Stanford, S. W. Running, C. A. Frissell. 2006. Multiscale geomorphic drivers of groundwater flow paths: subsurface hydrologic dynamics and hyporheic habitat diversity. Journal of the North American Benthological Society **25**: 288-303.

Racine, C. H. and J. C. Walters. 1994. Groundwater-discharge fens in the Tanana Lowlands, interior Alaska. **26**: 418-426.

Reid, B. 2007. Energy flow in a floodplain aquifer ecosystem. Ph. D. Dissertation. Uniersity of Montana, Missoula, Montana, USA.

Robinson, C. T., M. O. Gessner and J. V. Ward. 1998. Leaf breakdown and associated macroinvertebrates in alpine glacial streams. Freshwater Biology **40**: 215-228.

Robinson, C. T. and M. O. Gessner. 2000. Nutrient addition accelerates leaf breakdown in an alpine springbrook. Oecologia **122**: 258-263.

Robinson, C. T., M. O. Gessner, K. A. Callies, C. Jolidon, and J. V. Ward. 2000. Larch needle breakdown in contrasting streams of an alpine glacial floodplain. Journal of the North American Benthological Society **19**: 250-262.

Robinson, C. T., K. Tockner, and P. Burgherr. 2002. Seasonal patterns in macroinvertebrate drift and seston transport in streams of an alpine glacial flood plain. Freshwater Biology **47**: 985-993.

Robinson, C. T., K. Tockner, and P. Burgherr. 2004. Drift benthos relationships in the seasonal colonization dynamics of alpine streams. Archiv fuer Hydrobiologie **160**: 447-470.

Schiemer, F. C. Baumgartner, and K. Tockner. 1999. Restoration of floodplain rivers: the ‘Danube Restoration Project’. Regulated Rivers: Research and Management **15**: 231-244.

Schimel, J. P., K. Van Cleve, R. G. Cates, T. P. Clausen, and P. B. Reichardt. 1995. Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: implications for changes in N cycling during succession. Canadian Journal of Botany **74**: 84-90.

Stanford, J. A. and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. Nature **335**: 64-66.

Stanford, J. A. and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society **12**: 48-60.

Stanford, J. A., J. V. Ward, and B. K. Ellis. 1994. Ecology of the alluvial aquifers of the Flathead River, Montana (USA), pp. 367-390. In: Gilbert, J., D. L. Danielopol and J. A. Stanford (eds.), *Groundwater Ecology*. Academic Press, San Diego, California, USA.

Stanford, J. A., M. S. Lorang and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems, Verhein Internationale Vereinigung Limnologie **29**: 123-136.

Stanford, J. A., F. R. Hauer, J. S. Kimball and M. S. Lorang. 2001. Biocomplexity-dynamic controls on emergent properties of river floodplains: revised project summary.

Thorp, J. H. M. C. Thoms, M. D. Delong. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. River Research and Applications **22**: 123-147.

Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: Present state and future trends. Environmental Conservation **29**:308-330.

Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer, and J. V. Ward. 1999. Hydrologic connectivity, and the exchange of organic matter and nutrients in a dynamic river floodplain system (Danube, Austria). Freshwater Biology **41**: 521-535.

Tockner, K., F. Malard, and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes **14**:2861-2883.

Tockner, K., F. Malard, U. Uelinger and J. V. Ward. 2002a. Nutrients and organic matter in a glacial river-floodplain system (Val Roseg, Switzerland). Limnology & Oceanography **47**: 266-277.

Tockner, K., J. V. Ward, P. J. Edwards, and J. Kollmann. 2002b. Riverine landscapes: an introduction. Freshwater Biology 47: 497-500.

Tockner, K., J. V. Ward, D. B. Arscott, P. J. Edwards, J. Kollmann, A. M. Gurnell, G. E. Petts, and B. Maiolini. 2003. The Tagliamento River: a model ecosystem of European importance. Aquatic Sciences **65**: 239-253.

Uliassi, D. D. and R. W. Ruess. 2002. Limitations to symbiotic nitrogen fixation in primary succession on the Tanana River Floodplain. Ecology **83**: 83-103.

Van Cleve, K. Energy and biomass relationships in alder (Alnus) ecosystems developing on the Tanana River floodplain near Fairbanks, Alaska. Arctic and Alpine Research **5**: 253-260.

Van Cleve, K., C. T. Dyrness, G. M. Marion and R. Erickson.1993. Control of soil development on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research **23**: 941-955.

Van Cleve, K., J. Yarie, R. Erickson and C. T. Dyrness.1993. Nitrogen mineralization and nitrification in successional ecosystems on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research **23:** 970-978.

Van Cleve, K., J. Yarie, L. A. Viereck and C. T. Dyrness.1993. Conclusions on the role of salt-affected soils in primary succession on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research **23:** 1015-1018.

van der Nat, D., A. P. Schmidt, K. Tockner, P. J. Edwards, and J. V. Ward. 2002. Inundation dynamics in braided floodplains: Tagliamento River, Northeast Italy. Ecosystems **5**: 636-647.

van der Nat, D., K. Tockner, P. J. Edwards, J. V. Ward, and A. M. Gurnell. 2003. Habitat change in braided flood plains (Tagliamento, NE-Italy). Freshwater Biology **48**: 1799-1812.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Science **37**: 130-137.

Viereck, L. A., C. T. Dyrness, and M. J. Foote. 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. Canadian Journal of Forest Research **23:** 889-898.

Viereck, L. A., K. Van Cleve, P. C. Adams, and R. E. Schlentner. 1993. Climate of the Tanana River floodplain near Fairbanks, Alaska. Canadian Journal of Forest Research **23**: 899-913.

Walker, L. R. and F. S. Chapin III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology **67**: 1508-1523.

Walker, L. R., J. C. Zasada and F. S. Chapin III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. Ecology **67**: 1243-1253.

Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society **8**: 2-8.

Ward, J. V. and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems, in T. D. Fontaine and S. M. Bartell (eds*.), Dynamics of Lotic Ecosystems*, pp. 29-42. Ann Arbor Science Publishers, Ann Arbor, Michigan, USA.

Ward, J. V., F. Malard, K. Tockner and U. Uehlinger. 1999. Influence of ground water on surface water conditions in a glacial flood plain of the Swiss Alps. Hydrological Processes **13**: 277-293.

Whited, D. C., M. S. Lorang, M. J. Harner, F. R. Hauer, J. S. Kimball, J. A. Stanford. 2007. Hydrologic disturbance and succession: Drivers of floodplain pattern. Ecology **88**: 940-953.

Wondzell, M. 1992. Vegetation patterns along the Middle Fork of the Flathead River, Glacier National Park, Montana. M.S. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Wyatt, K. H. 2005. The influence of hyporheic-surface water exchange on benthic algal biomass, abundance, and community composition in the Middle Fork Flathead River, Montana. M.S. Thesis. University of Southern Mississippi, Mississippi, USA.

Wyatt, K. H., F. R. Hauer and G. F. Pessoney. 2008. Benthic algal response to hyporheic-surface water exchange in an alluvial river. Hydrobiologia **607**: 151-161

Yarie, J. 1993. Effects of selected forest management practices on environmental parameters related to successional development on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research **23**: 1001-1014.

Yarie, J., K. Van Cleve, C. T. Dyrness, L. Oliver, J. Levison, and R. Erickson. 1993. Soil-solution chemistry in relation to forest succession on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research **23**: 928-940.

Zah, R. and U. Uehlinger. 2001. Particulate organic matter inputs to a glacial stream ecosystem in the Swiss Alps. Freshwater Biology **46**: 1597-1608.

Table 1. Synthesis of ecosystem research conducted on floodplains world-wide, 1973-2008. Floodplain area estimates of maximum inundation are listed in parentheses. N = nitrogen, C = carbon, P = phosphorous, POC = particulate organic carbon, DOC = dissolved organic carbon, CPOM = course particulate organic matter, FPOM = fine particulate organic matter, DOM = dissolved organic matter, LWD = large woody debris

Floodplain	**Ecosystem Study Findings**	**Source**
Tanana, Bonanza Cr. LTER, Alaska, USA (taiga, ~100 km^2)	Described a successional chronosequence at Tanana: bare gravel to willow to willow-alder to balsam-poplar to white spruce to black spruce. As succession progressed terrace height, distance to water table, amount of forest floor moss and depth of permafrost all increased. 80 % of total energy content in stands was in living material while total energy increased with stand age due to greater biomass and a change in species composition.	Van Cleve (1973), Viereck et al. a, b (1993), Mann (1995)
	White spruce seedling biomass was greatest on bare gravel and lowest under the spruce canopy. White spruce root: shoot and seed dispersal of all species was highest on bare gravel. Willow and polar seedlings grew fastest and growth was enhanced by the presence of N fixing alder. Only spruce colonized mid-late successional surfaces where litter and shade inhibit other species. Tamarack seedling germination peaked mid-summer. Early tamarack seedling survival was highest on bare gravel and was more influenced by water table elevation than soil temperature	Krasny et al. (1985), Walker & Chapin (1986), Walker et al. (1986), Brown (1988)
	Willow C:N was affected by soil fertility and light intensity. Snowshoe hare browsing increased twig biomass but decreased willow height, making willows susceptible to shade and increasing their palatability.	Bryant (1987)
	Tanana has groundwater fed wetlands of floating macrophytes free of Sphagnum. A decomposed root matrix extend 0.5-1 m below the surface. When white spruce stands were clear-cut more radiation reached the ground, increasing evaporation rates, soil pH and salts. Litter biomass decreased along with spruce foliage decomposition and N, P mobility.	Yarie (1993), Racine & Walters (1994)

Table 1 (cont.).

Floodplain	Ecosystem Study Findings	Source
Tanana, (cont.)	Tanana newly flood-deposited silts were high in salts and pH. The main salts were $CaCO_3$, Mg, and SO_4. Phosphate mobility was constrained by $CaCO_3$. As succession progressed surface salt mobilization was retarded by decreased evaporation and increased organic acids from litter.	Dyrness & Van Cleve (1993), Marion et al 1993 a-b
	Soil N was 85-95% in the stable, non-labile pool. Stable N increased with stand age and was correlated with stable C, while labile N increased with soil depth and river infiltration. Denitrification and nitrogen fixation rates in all stands were low and limited by low temperatures, soil moisture, and C, N availability. N cycling was highest on newly deposited silts immediately after a flood and in alder stands. The system became N limited as alder graded to poplar, in part from tannin N immobilization.	Klingensmith & Van Cleve (1993 a-b), Van Cleve et al. (1993 a-d), Schimel et al. (1996), Kaye et al. (2003), Brenner et al. (2006)
	In experimentally manipulated alder plots, adding P increased root nodule biomass while adding N did not appear to change nodule nitrogenase activity. The presence of a poplar overstory did not alter alder N cycling. In controls, alder leaf area was correlated with the total amount of N fixed.	Uliassi & Ruess (2002)
	Climate data showed a warming trend for Alaska indicated by the northward trend of the 0^{o} C isocline from the 1960's to 1980's. Permafrost temperatures are on the rise (1-2^{o}C) except in areas insulated by moss or thick organic soil. Permafrost temperature rise began in the late 1970's.	Osterkamp et al. (1994), Hammond & Yarie (1996), Osterkamp & Romanovsky (1996), Romanovsky & Osterkamp (1997), Osterkamp et al. (1997), Osterkamp et al. (2000), Jorgenson et al. (2001)

Table 1 (cont.).

Floodplain	Ecosystem Study Findings	Source
Danube (AZNP), Austria, EU (lowland, 93 km^2)	Fish species utilized different floodplain habitats over their life cycle. The floodplain was a sink for sediment, POC, and nitrogen. The floodplain was a source for DOC, algae, and CPOM. Phytoplankton production reacted positively to flood pulse nutrient influx. Flooding and hydrologic connectivity controlled aquatic species' richness, production: respiration, 1^{o} production, carbon sources and nutrient cycling. Restored lateral habitats on Danube island were colonized by dragonflies and amphibians	Schiemer & Spindler (1989), Ward et al. (1999), Tockner et al. (1999a), Hein et al. (1999), Heiler et al. (1995), Tockner et al.(1999b, 2000), Chovanec (2000), Hein et al. (2003)
Val Roseg, Switzerland, EU (glacial, 50 km^2)	Alder leaf and larch needle decomposition and colonization by fungi and macroinvertebrates varied between habitats and tended to be slower near glaciers and faster in high nutrient experimental treatments and habitats. Allochthonous inputs to glacial streams increased with distance downstream.	Robinson et al. (1998, 2000a-b), Gessner et al. (1998), Zah and Uehlinger (2001)
	Groundwater flowpaths were critical to subsurface routing of glacial melt-water, base flow surface-water volume and water temperature variation.	Malard et al. (1999, 2001a)
	Glacial melt-water runoff period produced the highest annual habitat complexity, and replenished floodplain inorganic and organic nutrients.	Malard et al. (2000), Tockner et al. (2002)
	Surface-water groundwater connected habitats, particularly groundwater channels, had high abundance, biomass, and diversity of oligochaetes, Simulidae and aquatic drift. This contributed to downstream colonization.	Burgherr et al. (2001), Malard et al. (2001b), Robinson et al. (2002, 2004)
	Runoff induced variability in habitat size and location limited aquatic macroinvertebrate dispersal and 1^{o} production. Stream experiments revealed nutrient enrichment yielded a macroinvertebrate community dominated by chironomids and less impacted by disturbance.	Malard et al. (2006), Gafner and Robinson (2007)

Table 1 (cont.).

Floodplain	**Ecosystem Study Findings**	**Source**
Fiume Tagliamento, Italy, EU (glacial,150 km^2)	Glacial floodplains viewed as vegetated island mosaics formed by LWD mediated sediment accrual. Substrate size decreased while substrate heterogeneity increased downstream. Deposition of living driftwood fostered sediment deposition and development of islands characterized by high habitat and biological diversity and rare taxa.	Edwards et al. (1999), Petts et al. (2000), Gurnell et al. (2005)
	Thermal and habitat variability was greatest in the mid-gradient island floodplain, with greatest thermal variation in floodplain water bodies, in summer and fall from groundwater and tributary inflows.	Arscott et al. (2000, 2001), Karows et al. (2005)
	Summer glacial melt created a flashy hydrograph. During high flows, channel braiding and connectivity increased and pond area decreased. When coupled with slope, sediment supply and land use, flow variation increased habitat turnover while maintaining a steady-state habitat mosaic.	Arscott et al. (2002), van der Nat et al. (2002, 2003)
	Benthic macroinvertebrate densities were highest in summer, increased downstream, and were dominated by mobile, quickly reproducing taxa.	Arscott et al. (2003, 2005)
	Riparian arthropods ingested 45% of all emerging aquatic insects, with ground beetles consuming stoneflies and spiders consuming caddisflies.	Paetzold & Tockner (2005)
	The FPOM, DOM sources in the floodplain were a mix riverine bacteria, microalgae and soil derived organics. FPOM amplified remineralization rates. Algal biomass and POC were greatest in bar-braided floodplains.	Kaiser et al. (2004), Arscott et al. (2000)
	Populus leaf breakdown increased in winter and with flood duration. Invertebrate and fungal density increased with inundation duration.	Langhans & Tockner (2006)

Table 1 (cont.).

Floodplain	**Ecosystem Study Findings**	**Source**
Nyack, Middle Fork, Flathead R. Montana, USA (postglacial, 20 km^2)	The hyporheic corridor concept related the life histories of fauna living in the aquifer to surface waters adult reproduction. Aquifer microbial productivity was orders of magnitude higher than benthic production. An aquifer carbon limitation gradient formed lateral to the river channel and was correlated with lower microbial biomass. Fungal hyphae were common in well samples. Algae of river origin were entrained in the aquifer kilometers from the main channel. Aquifer low oxygen hotspots correlated with high invertebrate production. Aquifer invertebrate respiration scaled ½, not ¾ as predicted by metabolic theory. Aquifer stoneflies were found to be infected with a fish pathogen.	Stanford and Ward (1988, 1993), Stanford et al. (1994, 2005), Ellis et al. (1998), Craft et al. (2002), Adams (2006), Reid (2007)
	Evidence for an aquifer paleochannel network was mixed. A 3-D link node network computer models accurately routed surface and groundwater. This model showed hyporheic flows responded abruptly and non-linearly to seasonal changes in river discharge when floodplain topography and stratigraphy were heterogeneous. Field groundwater hydraulic conductivity varied from 1-1000 m/d. Two separate flow networks existed in the aquifer: long, deep and short, shallow flowpaths.	Poole et al. (2002, 2004, 2006), Johnson (2004), Diehl (2004), Harrison (2004), Hawkins (2005)
	Plant communities differed in flood inundation frequency by elevation. Cottonwood growth, C:N:P ratios, and plant diversity on the floodplain responded to surface and groundwater interactions. 63% of the total plant species pool for Nyack watershed was found in the floodplain. Proteins of mycorrhizae accumulated in older soils and river foam. Vegetation structure was in steady-state, influenced by climate acting in concert with hydrology. Bar sediment structure controlled cottonwood establishment. Total N increased in soils but stayed the same in hyporheic water along a forest succession gradient, while measures of N cycling were static.	Wondzell (1992), Mouw and Alaback (2003), Harner et al (2003, 2004), Whited et al. (2007), Meier (2008), Mouw et al. (2008), Brouwer et al. (in prep)

Table 1 (cont.).

Floodplain	**Ecosystem Study Findings**	**Source**
Nyack (cont.)	Flood disturbance influenced surface water, groundwater and nutrient flux, which correlated with algal biomass, productivity, and diversity.	Bansak (1998), Wyatt (2005, 2008)
	Aquatic macroinvertebrate community composition overlapped across habitats while species abundances differed between habitats. Aquatic macroinvertebrates responded to gradients in surface water, groundwater, and algal abundance. Pond habitats had unique biotic communities, contributing to overall floodplain aquatic diversity. Stonefly emergence varied widely in species identity and abundance (1972-2002). Nyack provided unique species life history records (*Caudatella edmundsi*).	Case (1995), Pepin and Hauer (2002), Chilcote (2004), Miserendino and Stanford (in prep), Jacobus et al. (2006)
	Lateral habitats were utilized by fish and amphibian species to reproduce and rear, particularly by non-native brook trout. All fish exhibited diel activity variation. Pond-dwelling brook trout out-competed native trout.	Cavallo (1997), Chilcote (2004), Machura (in progress)
(REU studies)	Aquatic vertebrate habitat associations	Smith, Pendergast (2003), Gibson (2007),
	Aquatic macroinvertebrate communities habitat differences	Watts (2003), Kendrick (2005), Huang (2006),
	Groundwater-surface water interactions, nutrients and algae	Marsh, Fehrer, McGill (2005),
	Terrestrial arthropods, leaf litter and herbivory	Spivav, Steinweden (2003),
	Carbon cycling	Walton (2006), McNamara (2007),
	Vegetation structure and successional dynamics	Chipko (2005), Emery and Walton (2006)

CHAPTER 2:

THERMAL VARIABILITY AND THE PHENOLOGY OF AQUATIC ORGANISMS ON AN ALLUVIAL FLOOD PLAIN

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ABSTRACT

Temperature is a master variable determining the distribution, abundance and phenology of aquatic ectotherms. Daily, seasonal and annual temperature patterns were documented in aquatic and terrestrial habitats at the Nyack Flood Plain Research Natural Area, located on the Middle Fork of the Flathead River in northwestern Montana. We were interested in establishing the extent of temperature variation in habitat types located lateral to the main channel. These habitats extend through the expansive aquatic-terrestrial transition zone created by riparian areas of the flood plain. Temperature patterns in these habitats were related to published temperature criteria influencing the phenology of ectotherms.

We found spatial variance in temperature was greatest in terrestrial habitats while the least occurred in aquatic habitats substantially influenced by groundwater inputs. Temperature fluctuations were the most extreme in spring and summer, when diel variability was as large as annual temperature change. Habitats strongly coupled to surface water flow from the river exhibited a temperature peak (16-17^{o}C) within 3 ½ weeks of the peak air temperature. Habitats influenced by groundwater or upslope water peaked at a much lower temperatures (11-13 ^{o}C) that varied in timing over 2 months. In summer, we recorded river temperatures within the optimal thermal range for growth of most fish species found at Nyack. By late fall and over the entire winter the maximum and minimum temperatures hovered below 1.0^{o}C, a value that is at or near the lower lethal limit for all adult fish species and mollusks in this system. Analysis of the degree-day requirements for aquatic insect and fish growth showed that the minimum necessary for growth could be reached in most habitats in most seasons. What varied between habitats was the duration of time in different seasons of the annual cycle spent above the degree-days required for growth. It appears that thermal variation helps shape floodplain landscape diversity, contributing to maintenance of the Shifting Habitat Mosaic. Herein we review evidence for the hypothesis that temperature is a both a niche separating mechanism and a constraint on population dynamics.

Keywords: river; temperature; floodplain; Shifting Habitat Mosaic; invertebrate; fish; phenology

INTRODUCTION

Temperature is well known as a primary determinant of the productivity and phenology of ecotherms inhabiting river ecosystems (Cummins 1974). Distribution, growth, and reproduction of molluscs (Dewitt 1955, Kilgour and Mackie 1991), amphibians (Welch and MacMahon 2004, Carey et al. 2005), and fish (Torgersen et al. 1999, 2001) have been correlated with temperature patterns in freshwater environments. The majority of aquatic and semi-aquatic insects possess a limited capacity to thermoregulate and exhibit life cycles controlled in large part by temperature (Vannote and Sweeney 1980, Ward and Stanford 1982).

In rivers, temperatures vary three dimensionally and are influenced by strong seasonal effects. The magnitude of this variation can be great in expansive flood plains of gravel-bed rivers as a function of habitat specific abiotic factors such as light and water depth. River flood plains are dynamic environments owing to natural flood cycles and cut and fill alluviation as affected by woody plant succession that combine with sediment transport to create a complex array of aquatic and terrestrial habitats in addition to the primary channel network (Stanford et al. 2005). Habitat patch dynamics considered in a biocomplexity context (Michener et al. 2002) involve short and long time scales (10's to 100's of years) due to flood pulse variability (Arscott et al. 2002; Amoros and Bornette 2002; Latterell et al. 2003, Whited et al. 2007). Regional biodiversity appears to maximize on flood plains, presumably due to heterogeneity of physical processes and habitat structure (Ward et al. 2002, Stanford et al. 2005). Despite their importance for energy transformation and biodiversity, flood plains are the most endangered landscapes on earth, owing to dams, diversions and the plethora of other human influences (Tockner and Stanford 2002). An understanding of natural temperature variation across the entire flood cycle in these landscapes is needed to assess threats to ecosystem goods and services posed by intensive river regulation, landscape conversion and climate change (Tockner et al. 2000, Harper and Peckarsky 2006).

An examination of thermal heterogeneity in alluvial flood plains invokes measurements in three spatial dimensions over hourly to seasonal time scales (Fig. 1). Heat flows at variable rates and multiple directions between terrestrial, soil, aquatic and aquifer subsystems of the flood plain. Models of heat transfer must incorporate both the method (conduction, convection, radiation) by which heat is transported and the medium (air, water, sediment) through which it is carried. For example, upon entering the aquifer water temperatures equilibrate as the length of the interstitial flow path increases. This is due to the conductance of heat between down welling water and the surrounding substrate in the aquifer. Water exits the aquifer and returns to surface channels at constant temperatures that can strongly influence heating and cooling of surface waters.

The method and medium of heat transport are modified by environmental factors such as wind speed, snowpack, water depth, water velocity, stream width, substrate type and riparian shading vary widely across floodplain surfaces; each has the potential to influence temperature dynamics (Poole et al. 2001, Poole and Berman 2001). Many of the environmental attributes that influence heat transport are observed to fluctuate seasonally in flood plains as the amount of solar radiation, surface flows and water table elevations change. This in turn shifts the magnitude and direction of hydrologic interactions, and thus thermal regimes (Huggenberger et al 1998) in both a linear and non-linear fashion. A strong linear relationship between air and surface water temperatures has been observed in rivers (Ward 1985, Langan 2000), but this relationship varies in off-channel habitats that are more heterogeneous and influenced by terrestrial processes (Malcolm et al. 2004). Shifts in river discharge frequently induce abrupt, non-linear exchanges of water and heat with the alluvial aquifer system in flood plains (Poole et al. 2004, 2006). In turn water temperatures can influence streamflow by mediating evapotranspiration rates (Constanz 1998). Thus, thermal heterogeneity exists in a process feedback loop with habitat heterogeneity as a fundamental attribute of the Shifting Habitat Mosaic in flood plains.

Biota inhabiting flood plains, especially ectotherms, must modify their behavior in relation to the thermal complexity of their environment. Thus, the degree of thermal heterogeneity within and between habitats should be a strong determinant of species assemblages occupying different areas of the flood plain. The spatial and temporal range of thermal pattern is poorly understood in lateral (i.e., off-channel) areas that contribute significantly to habitat diversity in alluvial flood plains. Abundant off-channel or lateral habitats (e. g., springbrooks, ponds and wetlands) occur in both the actively-flooded parafluvial (annually scoured) zones and higher elevation orthofluvial (mainly depositional) zones of the flood plain.

We examined the relationship between habitat type, temperature variability and the thermal experience of organisms found in surface and subsurface habitats. This was quantified over daily, seasonal and annual cycles in an expansive alluvial flood plain. We related temperature variation in specific habitats to known thermal constraints on life history expression for a suite of aquatic biota. We expected that temperature metrics (degree days, diel, seasonal and annual maximum and minimum temperatures) would vary between habitat types and that these metrics would correlate with habitat selection by ectotherms. The temperature signature of lateral habitats is expected to be quite distinct from the main channel, as off-channel zones are substantially influenced by riparian canopies as well as ground- and surface water interactions. Parafluvial sites, unless modified by regular groundwater inputs, were expected to have warmer temperatures because of shallow water depths and greater exposure to solar heating. In contrast orthofluvial sites are expected to have cooler temperatures owing to a constant source of groundwater influx and more shading by riparian vegetation.

METHODS

Study Area

The Nyack flood plain (hereafter referred to as Nyack) is located in the 2300 km^2 catchment of the Middle Fork of the Flathead River, a fifth-order, free-flowing river in northwest Montana (Fig. 2). The flood plain is 10 km long x 2 km wide, encompassing active river channels, springbrooks, ponds, abandoned channels and riparian benches; habitat diversity is a function of the legacy of flood-mediated scour and fill processes interacting with drift wood and riparian plant succession (Stanford et al. 2005). Timing, duration and magnitude of annual peak flood events are governed by basin-wide winter snow accumulation and spring melt coupled with stochastic spring and fall rain events, all of which is further moderated by regional climate cycles operating under the influence of the Pacific Decadal Oscillation (Whited et al. 2007). The annual flood period is late May through June, with floods attaining bankfull magnitude (465 m^3/s discharge) at a return interval of 1-3 years. In the last 10 years, river flows in the annual range of flooding (105 m^3/s discharge) occur 60-100 days per year, while floods of bankfull magnitude typically last less than 20 days (Anderson Chapter 3).

The Nyack flood plain is situated between two bedrock constrained canyons that form an upstream and downstream knickpoint. In essence, glaciation scoured a basin out of the bedrock that subsequently filled with alluvium composed of sand, gravel and cobble above laucustran clays. As a function of this hydrogeology, approximate 30 % of the river downwells into the aquifer at the top the flood plain, recharging the alluvial aquifer with upwelling of groundwater occurring predominately in the lower end of the flood plain (Stanford et al. 2005 Fig. 4). However, there are meso-scale losses and gains of equivalent scale throughout the longitudinal length of the flood plain (Stanford et al. 2005 Fig. 4). Thus the upper third of the flood plain is generally downwelling and the rest of the system is exhibits regional upwelling or downwelling depending upon location (Stanford et al. 2005).

Aquatic species assemblages and productivity have been observed to vary dramatically among floodplain habitats at Nyack, in part related to the differential influence of hyporheic groundwater (Pepin and Hauer 2002, Chilcote 2004, Wyatt 2005, Anderson Chapter 4). The hyporheic zones of coarse grained gravel-bed rivers like the Middle Fork can be defined in a zoological context as the upper portion of the unconfined aquifer occupied by organisms that migrate to the surface waters to complete some stage in their life cycle (Brunke and Gonser 1997). The biota (i.e., the hyporheos) are composed of species unique to the alluvial aquifer and also species, such as stoneflies, with an obvious affinity for the river because they migrate from the aquifer to the channel to emerge and reproduce (Stanford and Ward 1988). At the Nyack, the aquifer and its' hyporheic zone are comprised of geologically recent alluvial and colluvial deposits (silt, sand, clay, gravel) 26-100+ meters deep (Harrison 2004), in which dynamic water exchange and most biotic activity occurs in the top 4 meters (Reid 2007). Groundwater chemistry, hydraulic conductivity (<1-1000 m/d; average 400 m/d) and residence time (1 hour-1.5 years) varies widely across the floodplain (Johnson 2004, Diehl 2004).

Floodplain forest composition and productivity at Nyack are influenced by elevation relative to the river thalweg and the groundwater table, underlying sediment structure, groundwater-soil water flux, and stream power associated with overbank floods influnced in part by regional climate patterns (Harner and Stanford 2003, Whited et al. 2007, Mouw et al. 2008). Annual flooding causes scour and fill in the lower elevation parafluvial zone, followed by colonization with grasses, forbs, willows (> 10 *Salix* spp.) and cottonwood (*Populus balsamifera*) seedlings. In the higher elevation areas of the parafluvial zone, flood deposition of sediments mediates the establishment of dense pole stands of cottonwood mixed in with secondary successional stands of willows and alder (*Alnus incana*). These regeneration tree stands develop during decades with large magnitude floods and greater frequency of moderate floods that correspond with cooling phases of the PDO (Whited et al. 2007). Orthofluvial areas are fully inundated at intervals greater than 10 years and receive scouring flows only during rare, large flood events. Orthofluvial benches support diverse, mature gallery forests dominated by mature cottonwood and spruce (*Picea engelmanni*). Parafluvial gravel bars are often devoid of overhead canopy cover (0-5%) while canopy cover on orthofluvial benches is between 20-40% (Anderson Chapter 4).

Site Selection and Instrumentation

We selected a suite of lateral habitats to encompass the expected spatial variation in temperature across the lateral habitats of the entire flood plain (Figure 2). Habitats were grouped in relation to degree of surface water connectivity at river base flow. Groups included permanently connected main channel areas, springbrooks that flowed in flood channels, ponds isolated in scour pools, and the alluvial aquifer. Connected main channel areas were further segregated into shallow shorelines along the permanent channel edge and backwater pocket eddies. Springbrooks and ponds were found in both parafluvial and orthofluvial zones.

Aquifer monitoring well-sites were categorized as either hyporheic (short exchange time on the order of days) or phreatic (long residence time on the order of months) based on the slope of the regression of well water level versus river discharge (Ferris et al. 1962). In hyporheic sites water levels increased rapidly with rising river discharge, creating a steep slope in the relation between river discharge and water table in the well. In phreatic well water table elevations responded slowly to changes in river discharge; as such the slope between river discharge and water table in the well was categorically less.

Arrays of thermister-loggers (Vemco TR, Onset Stowaway or Maxim Integrated Products iButton), 10 minute recording interval) were deployed in the suite of aquatic habitats (calibration and field placement after Malard et al. 2001 and Johnson et al. 2005). For aquifer water temperatures, we deployed arrays of temperature sensors in selected monitoring wells at surveyed elevations to enable correlation with water table and river stage elevations (Diehl 2004, Reid 2007). Two (parafluvial and orthofluvial) weather stations fitted with Campbell Scientific data loggers collected hourly air temperature, humidity (HUMICAP HMP45C sensors), precipitation, wind speed and direction, soil moisture and soil temperature (Vitel probes) data. River stage and discharge was determined from streamflow statistics reported for USGS gauge #12358500, located 10 km downstream.

Temperature influences on selected biota

We selected a suite of commonly-occurring taxa of conservation concern found at Nyack for which we were able to document thermal criteria for various life stages (Table 1). Thermal characteristics researched for each group of organisms included the range of temperatures associated with optimal activity and growth, acute upper and lower lethal temperature limits (ULTL; LLTL) associated with organism mortality and degree-day thresholds for growth and reproduction. These metrics were used to evaluate responses to temperature patterns recorded in the various habitat types on the flood plain.

Data analysis

In order to compare spatial and temporal variation in temperatures across sites we calculated the average, phase shift, pulse, rate of change, and degree-days in daily time steps after Arscott et al. (2001) studies of the Tagliamento. Formulas used to compute metrics for daily, monthly, seasonal and annual change are reported in Table 2; all metrics were calculated with SPSS 12.0 (SPSS Inc., Chicago, Illinois). Average daily seasonal temperatures were calculated over 6 week intervals in summer (July 15-August 31), fall (Oct 1-Nov 15), winter (Jan 15-Feb 29), and spring (April 1-May 15) for sites where complete data records existed. Data gaps in some of the temporal records were related to losses of thermisters from flood scour and deposition along with human interference. Short gaps were reasonably filled by extrapolation from nearby sites. In cases of longer data gaps we replaced missing data by modeling water temperatures at the site in the week before and after the data gap either to air temperature records or water temperature records from another site within the same habitat type. Models were considered adequate to generate replacement data only if they met criteria of an $R^2 \geq 0.70$. Data produced to fill in gaps was used solely to estimate annual degree-days. We chose not to model degree-days at shallow shoreline and backwater sites in the spring runoff period owing to rapid changes in river stage which resulted in data gaps. All other analyses described above are based on actual measured temperature values at sites.

Phase shift is a metric comparing the date on which the maximum temperature for the year was reached in different habitats. This metric is important to understanding the life history expression of organisms whose development is tied to an annual peak temperature cue. Temperature pulse and rate of thermal change were interpreted as measures of potential thermal stress experienced by organisms. Biota must acclimate to the amplitude of the temperature pulse and rate of changing temperatures. Degree-day calculations provided an approximation of the daily temperature exposure experienced by organisms in the different habitats. Degree-days estimates were compared to published rearing studies where degree days for developmental stages were explicit. We calculated degree-days at Nyack using an averaging method by summing the daily mean temperatures above 0^{o} C over monthly, seasonal and annual scales.

In order to assess thermal stress on aquatic vertebrates we compared optimal growth, critical maximum and critical minimum threshold temperature values to diel temperature distributions in different habitats. A series of habitat specific histograms were created to illustrate the distribution of hourly temperatures within the optimal and stressful temperature ranges on one of the warmest summer (August 10, 2003) and coldest winter (January 5, 2004) days observed at Nyack. We also examined differences between the seasonal degree day accumulations for habitats over the year by creating annual degree-day curves starting in different seasons. We compared the rate of change and asymptote of curves to published values (Table 1) of degree-day thresholds for the development of aquatic insects and brook trout eggs.

RESULTS

Inter-annual hydrologic and temperature variation

Floodplain organisms face metabolic and reproductive challenges posed by year to year variation in flood flows and temperature. We examined our longest record of air and river temperatures and flow at Nyack from July 2002 – 2005 to determine year to year stochasticity (Fig. 3) to underscore this important point. The interannual cycle of average daily temperature in the river was coherent with the discharge pattern throughout this period. During the early summer peak flow period, main channel water and air temperature tracked closely with changes in river discharge. Across years the river water temperature presented a fairly stable waveform that crested between 15.7 to 16.3°C during the period of August 9 – 18, a two to three month offset from the peak in the annual hydrograph.

Summer peak temperatures in the river were only slightly above the published optimal temperature ranges of most adult fish that inhabit Nyack (Table 1). Average daily air temperature took on a variable waveform that rose to a maximum of 21.1 to 23.1°C in mid-July to early August, slightly closer in time to the yearly hydrograph peak. This was within the optimal temperature range and growth period for many of the aquatic organisms selected for study, (cf. adult *Bufo boreas*) across years (Table 1). We observed no major difference between years in maximum air or water temperatures in the summer despite differences in peak discharge and timing. The only noticeable influence of peak flow variation was on the rate of thermal increase. In 2003 the shorter duration of flooding was consistent with a faster rise in early summer air and water temperatures than in the longer duration flood year of 2004.

In winter, constant baseflow conditions did not correspond closely with changes in water and, in particular, air temperature. The river temperature wave declined to <2 °C for much of the winter with a trough at 0.0 to 0.1°C that occured during mid-December to early January, thus reaching lethal limits for aquatic vertebrates across years (Table 1) if the river froze solid. A solid freeze was not observed in the field for most of the channel, possibly owing to friction heat of water flow and the capacity of snow cover to insulate the water below from changes in air temperature. The annual air temperature winter wave trough was extremely variable, dropping unpredictably from near freezing down to -19.4°C, -31.7°C, and -25.0°C in 2003, 2004, and 2005 respectively. Such cold temperatures were well below stated temperature minimums for *B. boreas,* underscoring why toads habitually are restricted to hibernation dens throughout the winter.

Intra-annual temperature variation

The amplitude and timing of the annual temperature wave reaching its crest differed between habitats as thermal energy dissipated unevenly throughout the floodplain SHM (Table 3). Air, soil and surface water site temperatures began to increase from winter minimums two to three weeks after the onset of spring flooding. Air (21.9°C) and soil (26.2°C) temperatures peaked in late July, followed by surface water peaks (11.2°C – 17.4°C) three to four weeks later. The time lag in well water temperature response was longer, with the maximum temperature rise in hyporheic wells occurring at some point in August and phreatic wells from September to October. Shoreline and parafluvial habitats strongly coupled to surface river water flow peaked in a narrow temperature range (16-17°C) within 3 ½ weeks of air temperature, while habitats influenced by phreatic water were lower in temperature (11-13 °C) and varied in peak timing over 2 months. An average of three months was required for temperatures at all sites to return to pre-flood states by mid-September to mid-December.

The annual pattern of maximum, minimum and average daily temperatures (Fig. 4, 5) coupled with average seasonal metrics (Table 4) showed that certain habitats experienced intervals of time within thermally stressful ranges for floodplain organisms. Air and soil temperatures reached summer thermal daily maximums ranging from 15-35°C, with a seasonal average of 30.0°C for air and 26.5°C for soil. This was typically within the optimal temperature range for "basking" behavior and growth of adult terrestrial *B. boreas*, but at times approached the lethal maximum range. These temperatures were also at or above the thermal maximum for aerial adult forms of some long-lived coldwater aquatic insects (Smith and Collier 2005). In fall and spring daily maximum air and soil temperatures fell as low as -10.0 °C, and varied up to 20.0°C from one day to the next. In winter maximum daily air temperatures were extremely variable, fluctuating between -23.5°C to 20.3°C over the course of the season, resulting in a maximum averaged for the season of 2.1°C. Winter soil temperatures never moved higher than 0.3°C and did not drop much below freezing, presumably owing to heat conduction from the alluvial aquifer and the insulating effect of continuous snow cover.

Surface water habitats displayed less extreme fluctuations in temperature than the surrounding air temperature even though many surface water areas were quite shallow; and, river temperatures were much more variable than in habitats influenced by ground water (Fig. 4, 5). In summer, we recorded thermal maximums averaging 16.1°C (range of 9-17°C) and minimums averaging 13.8°C (range of 8-15°C) in the river, within the optimal thermal range for growth of most fish species found at Nyack. Throughout the fall maximum and minimum river temperatures averaged 5.9 and 4.4^{o}C respectively, falling within the stressful range for the tail end of *B. boreas* tadpole growth and metamorphosis. By late fall and over the entire winter the maximum and minimum temperatures hovered below 1.0^{o}C, a value that is at or near the lower lethal limit for all adult fish species and mollusks should flow velocity drop enough to allow the habitat to freeze solid. Hyporheic well temperatures tracked with the river throughout the year but gave rise to a smoother temperature curve with lower daily maximum and higher daily minimum values.

Backwater and shallow shoreline habitats appeared to have similar and extremely variable thermal regimes. Alternating periods of optimal and stressful thermal conditions for biota could be found in each of these habitats. In summer, daily maximum temperatures averaged 17.3-17.8^{o}C with highs of up to 20.3^{o}C. This was near or at the lethal thermal maximums for most trout species. In contrast average minimum temperatures in summer descended to 12.2-12.4^{o}C, with lows down to 10.0^{o}C in September. These temperatures were within the optimal growth range for Nyack fish species but below the minimum tolerance values for *B. boreas* tadpoles. Quite commonly fall and winter maximum and minimum temperatures at these sites lingered near 0^{o}C, creating stressful conditions for amphibians, fish and mollusks.

Throughout the summer and fall, tributaries, parafluvial and orthofluvial springbrooks provided sub-optimal maximum and minimum temperatures (>14^{o}C) for *B. boreas* tadpole growth but optimal temperatures for fish growth. Fall and winter temperatures ranging from 2-6^{o}C along with spring temperatures ranging from 3-8^{o}C were the norm in parafluvial and orthofluvial springbrooks. These temperatures were within the optimal range for development of trout eggs. Aquifer well temperatures for the most part tracked with the orthofluvial springbrooks, although it is notable that aquifer well minimum temperatures in the fall were 1^{o}C higher per day than springbrooks.

Resistance to thermal change was measured in two ways: 1) annual pattern of daily temperature pulse variation and, 2) average seasonal rate of hourly TC $_{increase}$ and TC $_{decrease}$ within a day (Fig. 6, Table 4). Air and soil temperatures were the least resistant to change as measured by the annual maximum and minimum, with an absolute change in average daily temperature in air of 49^{o}C followed by soil temperatures variation of 21^{o}C. The change in shallow lateral habitats was 16^{o}C (backwater) to 17^{o}C (shallow shoreline), as opposed to more resistant sites that varied 10 – 12^{o}C in a year (parafluvial springbrook, river, tributary, strong interaction well). The greatest annual resistance (3 – 4^{o}C) was observed at orthofluvial springbrooks the aquifer. All values fell within the range of temperatures aquatic vertebrates should be able to acclimate to, depending on the rate of TC $_{increase}$ and TC $_{decrease.}$ TC $_{increase}$ and TC $_{decrease}$ were most variable in the summer when shallow shorelines, backwaters, tributaries and springbrooks all varied up to 0.8 to 1.4 ^{o}C hourly.

Degree days

Degree-day accumulation varied widely between seasons and habitats (Fig.7), of course, in relation to the annual temperature patterns. River, backwater and shallow shoreline achieved the most summer degree days (~1200). Across habitat types, main channel habitats were the most seasonally variable while lateral and groundwater habitats provided more continuity between seasons in degree-day accumulation. This was most apparent in the fall and winter when parafluvial and orthofluvial springbrooks and phreatic wells accumulated 200-300 more degree-days than main channel habitats. Differences between surface habitats moderated as flood waters of the spring spate inundated the flood plain and recharged the aquifer.

Analysis of the range in timing of degree-days for aquatic insects and fish showed that minimum requirements for growth could be reached in most habitats in most seasons (Fig 8). For insects beginning their development in the summer the 1100 to 1300 degree-day minimum required prior to emergence was reached between September to November in all habitats. Insects initiating development in summer that have a 2500 degree-day threshold were not able to achieve this point within a year unless they lived in the river or tributaries. Moreover, for insects beginning their development in the winter and spring the 1100 to 1300 degree-day window required for emergence was reached 5 to 8 months later in all habitats. The 2500 degree-day threshold was once again met at all sites other than tributaries. What varied between habitats was the duration of time spent above the threshold range within the annual cycle. Organisms with winter initiation of development ended an annual cycle with 3 months above the threshold range; this lengthened to 4 months above threshold for organisms with spring developmental initiation. Organisms beginning their development in fall spent the least amount of time in a single annual cycle above both the 1100-1300 and 2500 degree-day thresholds.

Brook trout, an invasive species at Nyack, spawn in springbrooks and ponds with high groundwater flux rates (Anderson chapter 3, 4). The developmental threshold of 630 degree-days needed for *S. frontinalis* eggs to hatch after being deposited in the fall was consistently passed by January or February in orthofluvial springbrooks and alevins were observed in those habitats in that time frame. Parafluvial springbrooks and tributaries converged on the threshold by March-April and alevins were observed in those habitats as well. But, main channel habitats did not surpass the critical threshold until May-June, which coincides with the period of annual peak flooding, which presumably would be problematic for alevin survival.

Daily temperature variation

Diel temperatures were much more variable across habitats on hot summer days than cold winter days (Fig. 9, Table 5). The summer diel cycle in backwater, shallow shoreline and parafluvial springbrook sites tracked closely with the sine wave of air temperature. River temperatures hit their daily peak and trough two to three hours after other surface water bodies while aquifer sites remained constant at 10.5^{o}C with no discernable diel cycle at all. On the coldest winter days when diel air temperatures ranged from -15 ^{o} to -35 ^{o}C, the surface habitats and soils were near freezing and did not display diel patterns while aquifer temperatures fluctuated 1-5 ^{o}C. This cycling of aquifer water temperatures may have been driven in part by the shallow depth of sensors in wells.

We compared the availability of optimal thermal conditions for fish species during a 24 hour period on an extreme warm and cold day. Histograms of hourly thermal data on August 10, 2003 and January 5, 2005 were produced to examine diel distribution of temperatures by habitat type (Fig. 10). Optimal ranges for different fish species were laid on top of histograms to examine the degree of overlap. On extreme warm days, main river channel habitats were continuously warmer than the native fish optimal thermal range; whereas lateral habitats produced 12-18 hours in the optimum range. The number of hours on August 10 falling within the optimal range of both native and non-native fish differed markedly between main river channel habitats (main river 4 hrs, shallow shoreline 7 hrs, backwater 11 hrs) and also varied widely from off-channel habitats (tributary 12 hrs, parafluvial springbrook 7 hrs, orthofluvial springbrook 6 hrs). Lateral habitats spanned briefer periods (0-2 hrs) in the thermal range preferred by non-native fish as opposed to main river channel habitats (16-20 hrs).

During midwinter, main river channel, shallow shoreline, backwater and tributary temperatures were at or near freezing for days to weeks without interruption, which of course is lethal if the habitat freezes solid and organisms cannot move into refuge in flowing surface habitats or aestivate in bed-sediments warmed by ground water. Indeed, temperatures were continually above 1-3 °C in the entire aquifer and the parafluvial and orthofluvial spring brooks. The parafluvial ponds mostly have enough groundwater flux that they also do not freeze to the bottom (Chilcote 2004).

DISCUSSION

Inter-annual hydrologic and temperature variation

As expected, the annual pattern of temperature in the river was coherent with flow; low, cold flows occurred in winter, followed by warming temperatures moderated via spring spates and warmest temperatures transpired as flows declined to base flow. Temperature seasonality was strongly influenced by year to year climate variation as in all rivers. Indeed, Whited et al. (2007) showed that flooding at the Nyack was strongly correlated with the climate record (Pacific Decadal Oscillation; PDO) of the North Pacific Ocean; the PDO determines wet (cool) and dry (warm) weather phases that reach far inland to the Continental Divide and are reflected in the year to year Nyack data.

However, the volume of the alluvial aquifer at Nyack is 1000x larger than all surface habitats combined. Owing to the heat capacity of the bed-sediments, aquifer temperature patterns do not vary much from year to year and groundwater-surface water exchange buffers climate driven dynamics in the river and in lateral habitats. Hence, the annual temperature patterns in habitats strongly influenced by groundwater were remarkably similar from year to year (cf. Fig. 2).

Moreover, the phenology of biotic assemblages in the river, including emergence times of insects, have not changed in over 30 years based on long term studies of Plecoptera, a hemimetabolous order that is notably sensitive to temperature patterns (Mesenderino and Stanford 2008). Nonetheless, the analysis showed that very warm and very cold years stress Nyack biota in some habitat types. On the other hand, annual temperature patterns in all of the aquatic habitats were far more stable than mean air temperatures. A wide range in annual pattern occurred between habitats owing to ground water buffering, allowing mobile biota to potentially avoid stressful conditions. Less mobile organisms assembled in the most favorable habitats resulting in big differences in food web structure among habitat types. This should persist from year to year unless a particular habitat was modified by flooding in ways that caused temperature patterns to change.

Intra-annual temperature variation

Examining the data seasonally among habitats revealed the influence of temperature variation associated with the SHM and attendant influence on organismal life histories in a floodplain (habitat selection) context. The annual temperature pulse moves through individual habitats at different rates (e.g., the temperature maximum in the aquifer is more than a month out of phase with the river), creating substantial thermal heterogeneity within the habitat catena of the flood plain. The ground water buffering effect (summer cool, winter warm) appeared to vary in relation to the amount of ground water input, but hydrologic evidence for this remains to be fully documented. Sudden spatial changes in temperature may themselves serve as strong indicators of ground water upwelling. If groundwater inputs are as variable as we suspect, this would provide a wide range of habitat alternatives to life in the permanently connected channel network. Evidence for highly localized groundwater effects in the main channel already exists (Wyatt 2005)

In any case, thermal heterogeneity clearly is a primary attribute of the habitat catena at Nyack. Biota that are widely distributed among the habitat catena have broad temperature tolerances, are able to utilize behavioral thermoregulation, or are very mobile and able to move from habitat to habitat as thermal limits are encountered. For example, aquatic vertebrates at Nyack are mobile enough to overwinter in warmer groundwater or the bed-sediments or move into winter-warm springbrooks. As summer approaches these animals redistribute into habitats that favor growth and reproduction. Boreal toads spawn and rear in the warmest parafluvial ponds where groundwater flux is limited by fine sediments on the bottom and exposure to solar heating drives temperatures toward 30^{o}C during the day. Tadpoles also congregate in the warmest areas of the ponds, using behavioral thermoregulation to maximize their temperature inputs (Chilcote 2004). Many of the native fishes spawn and rear in springbrooks probably because they are more thermally and hydrologically stable environments than the main river (Anderson Chapter 4).

Degree days

Analysis of degree days among the habitat types further elaborated conditions for aquatic insect metabolism and growth. All habitats except tributaries fell within cumulative degree-day requirements for growth of aquatic insects, even for those groups with high degree-day demands. Winter and summer ovipositors were able to achieve degree-days required for growth more quickly than in other seasons (Fig. 8). Insects emerging in summer and fall with high degree-day requirements were able to achieve growth targets within a single year but could not do so in cold orthofluvial habitats. These conditions however only describe minimal growth targets. Diapause break, hatching and emergence cues among the insects are often independent of degree-days, although the extent to which temperature plays a role in these life history transitions remains to be resolved for most species (Ward and Stanford 1982).

Daily temperature variation

Summer average daily temperature metrics (Fig. 4-6, Table 4) and temperature cycles within a day (Fig. 8) fluctuated widely. On hot summer days all habitats provided some hours within the optimal thermal range for all Nyack fishes, but tributaries and springbrooks were potentially more favorable owing to greater temperature buffering of ground water inputs.

The main river channel and its shallow shorelines experience protracted intervals of 5-6 hours a day within temperature ranges stressful to all fish during the warmest days of the year. In contrast, averaged temperatures were sub-optimal (too cold) for *Bufo* tadpole development in any of the available aquatic habitats. However, shallow shorelines of parafluvial ponds approached 30^{o}C whereas it appeared that groundwater flux cooled the bottom waters of the ponds and reduced the average pond temperatures below development threshold (Chilcote 2004).

In order to meet their degree-day requirements for metamorphosis, *Bufo* tadpoles have been observed seeking out warm temperatures at the water's edge in backwaters, shallow shorelines and ponds (Chilcote 2004). Air temperatures were favorable to adult *Bufo* growth throughout much of the day (Fig. 9), allowing adult *Bufo* more flexibility in their activity range.

It is difficult to judge temperature preferences for aquatic insects in summer as the literature on this subject remains sparse. The limited data we are aware of indicates that coldwater adapted aquatic insects become stressed in a 25-35^{o}C range rarely achieved in Nyack aquatic habitats. Theoretically insect foraging, growth and competitive interactions are not constrained by high summer water temperatures in most aquatic habitats at Nyack, although this may not be the case in extremely shallow microhabitats at the edge of water bodies such as ponds.

Influence of thermal heterogeneity in the SHM on phenology

At one time or another during the year, most of organisms we assessed experienced either optimal thermal conditions or stressful conditions in all of the habitats. This created a temporally variable checkerboard of thermal niche availability. For example, all surface water habitats exhibited suboptimal temperatures in winter for aquatic vertebrate feeding and growth. In comparison, aquatic insects can continue to grow at or near 0 °C and size at maturation varies in relation degree days in the optimum growth range and food supply. Annual temperature patterns in the main channel did not vary significantly from upstream to downstream through the flood plain. However, the downstream reach has been demonstrated to have higher productivity of trees (Harner and Stanford 2003) and periphyton (Anderson chapter 3). Pepin and Hauer (2002) showed that increased size of aquatic macroinvertebrates was commensurate with upwelling of hyporheic ground water and increased periphyton productivity and thus more food at the habitat patch scale.

Winter temperatures continually at or below freezing may contribute to depletion of energy reserves of aquatic vertebrates. This may explain why Nyack fishes predominately are summer or fall spawners. Springbrooks, tributaries and areas of the river with localized groundwater discharge provide salmonid eggs and adults with winter warmwater refugia (Fig. 4, 5, 9). Aggressive non-native brook trout may be displacing native fish from preferred springbrook environments, contributing to bull and cutthroat trout declines. Winter presents significant challenges to terrestrial soil organisms as well. In response to cold winter temperatures insects have been known to migrate deeper into soils to stay warm (Dowdy 1944).

Temperature exerts a substantial selective force on species by placing constraints on organisms' metabolic activity. In governing metabolism, temperature has been shown to influence population densities and growth rates (Brown et al. 2004), interspecific interactions between species (Thompson 1978), community biodiversity (Allen et al. 2002) and trophic dynamics (Teal 1957) in aquatic ecosystems. The Thermal Equilibrium Hypothesis (TEH; Vannote and Sweeney 1980) suggests stability of aquatic insect populations found within the overall geographic range of each species is a dynamic balance between temperature and life history constraints. At the species level we most often associate metabolism and temperature through Q_{10} approximations. This is an empirical graphic derivation of the relationship between an individual's respiration and temperature. Q_{10} can vary greatly within a species (*Pisidium amnicum* Q_{10} varies 1.5 to 5.6, Holopainen and Ranta 1977), indicating that some species may be adapted to different levels of thermal variation experienced in different habitats or during life history stages. Vannote and Sweeney's (1980) Developmental Rate Hypothesis further explains the mechanism for the inverse relationship of insect body size to maturation temperatures as the Q_{10} for maturation can be greater than the Q_{10} for somatic growth. This results in progressively smaller maturing adult metamorphs during the later, warmer portion of the emergence period.

Ectotherms reach maximum size under the coldest available thermal regimes within their environment (Hogue and Hawkins 1991). This trend is notable among the frogs (Berven 1982) and insects (Vannote and Sweeney 1980) and may be related to opposing effects of low temperature in increasing overall growth rate versus decreased differentiation during successive life history stages (Hogue and Hawkins 1991). In addition a trade-off exists within the thermal optimum range of most insects between increased metabolic activity and increased mortality at higher temperatures (Cabanita andAtkinson 2006). This implies that the temperature may exert a long term evolutionary selection pressure on nymphal aquatic insects to enter the groundwater system in winter in concert with other limiting factors such as oxygen and organic matter availability.

Conclusions and Implications

The fluxes proposed at the outset (Fig. 1) were strongly supported by the data presented herein. Extreme variation in the atmospheric and terrestrial subsystems is buffered by the heat capacity of the soil and aquifer subsystems with intermediate patterns in the river and lateral habitats. We conclude that thermal heterogeneity is a primary attribute of the habitat catena at Nyack.

At the floodplain scale, thermal heterogeneity, as a primary characteristic of the SHM, allows organisms to select from an array of habitat options either by direct movements (Fig. 1) or by broadcasting propagules widely. In either case persistence in that habitat will require attainment of a positive life history energy balance (*sensu* Hall et al. 1992) for the population or species in question. Thus we expect unique assemblages of aquatic ectotherms in the various habitat types as dictated by the prevailing temperature patterns.

Over the long term, habitat fidelity promotes phenotypic variation and maintains species richness. Typically the high level of temporal and spatial complexity in cold and warm water niches observed at Nyack has only been ascribed to an altitudinal gradient from headwaters (cold) to piedmont or coastal reaches (warm) in a large river system; or the range of variation observed at Nyack may be expressed in a suite of small streams at a regional scale (Hildrew and Edington 1979, Wehrly et al. 2003, Hauer et al. 2000). This is precisely why unit area biodiversity is very high at Nyack in comparison to adjacent landscapes (Mouw et al. 2008; Anderson chapter 4).

Moreover, thermal heterogeneity buffers short and long term climate change allowing species to persist in the flood plain environment by moving short distances, say from the river to a springbook, as opposed to long distance migrations that increase risk of mortality as temperatures change with climate warming. However, moderation afforded in aquatic habitats will not necessarily protect the terrestrial forms of vulnerable adult life history stages of amphibians and insects subject to air temperature volatility, highlighting the importance of riparian vegetation for providing cool terrestrial microclimates.

Temperature patterns shape the distribution and abundance of floodplain organisms at diel, seasonal, annual and interannual time scales and within the habitat catena of gravel bed flood plains. Managers must consider habitat complexity and thermal heterogeneity as an important goal for river restoration to maximize their chances of protecting multiple vulnerable species. Water quality administrators typically use only a few metrics such as daily or 7-day running averages of maximum or mean temperatures (Oregon DEQ, WA Ecology, EPA) to monitor temperature thresholds triggering management decisions. In most cases changes are triggered by temperatures rising above a 16 - 20^{o} C limit designed to protect salmonids alone. Managers need to appreciate the complexity of habitats and temperature regime of entire floodplain ecosystems in order to preserve all the biota within it, not just salmonids. The integrity of natural ecosystem processes needs to be maintained to support a diverse floodplain ecological community. This is best achieved for most rivers by reinstating a normative flow regime that can reshape damaged flood plains, gradually reconstructing the SHM and the thermal heterogeneity plus the associated biodiversity that comes with it.

LITERATURE CITED

Allen, A. P., J. H. Brown, and J. F. Gillooly. Global biodiversity, biochemical kinetics and the energetic-equivalence rule. Science **297**: 1545 – 1548.

Anderson, K. J. A. P. Allen, J. F. Gillooly, J. H. Brown. 2006. Temperature-dependence of biomass accumulation rates during secondary succession. Ecology Letters **9**: 673-682.

Arscott, D. B., K. Tockner, and J. V. Ward. 2001. Thermal heterogeneity along a braided floodplain river. Canadian Journal of Fisheries and Aquatic Sciences **58**: 2359-2373.

Bansak, T. 1998. The influence of vertical hydraulic exchange on habitat heterogeneity and surficial primary production on a large alluvial floodplain. M.S. Thesis. University of Montana, Missoula, Montana, USA.

Baxter, C. V. and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences **57**: 1470-1481.

Berven, K. A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica* I. An experimental study of life history traits. Evolution **36**: 962-983.

Briers, R. A., H. M. Cariss and J. H. R. Gee. 2003. Flight activity of adult stoneflies in relation to weather. Ecological Entomology **28**: 31 – 40.

Brown, L. R. 1989. Temperature preferences and oxygen consumption of three species of sculpin (*Cottus*) from the Pit River drainage, California. Environmental Biology of Fishes **26**: 223-236.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**: 1771 – 1789.

Brunke, M. and T. Gonser. 1997. The ecological significance of exchange processes between rivers and groundwater. Freshwater Biology **37**: 1 – 33.

Cabanita, R. and D. Atkinson. 2006. Seasonal time constraints do not explain exceptions to the temperature size rule in ectotherms. Oikos **114**: 431 – 440.

Case, G.L. 1995. Distribution and abundance of zoobenthos in channel, springbrook, and hyporheic habitats of an alluvial floodplain. Masters Thesis, The University of Montana, Missoula, MT. USA

Cather, M. R., and A. R. Gaufin. 1976. Comparative ecology of three *Zapada* species of Mill Creek, Wasatch Mountains, Utah (Plecoptera: Nemouridae). American Midland Naturalist **95**: 464-471.

Cavallo, B. 1997. Floodplain habitat heterogeneity and the distribution, abundance, and behavior of fishes and amphibians in the Middle Fork Flathead River basin, MT. Master's thesis, University of Montana, Missoula, Montana, USA.

Chilcote, S. D. 2004. The ecology of parafluvial ponds on a Rock Mountain flood plain. P.h.D. Dissertation. University of Montana. Missoula, Montana, USA.

Constantz, J. 1998. Interaction between stream temperature, stream flow and groundwater exchanges in alpine streams. Water Resources Research **34**: 1609-1615.

Cummins, L. K. 1974. Flathead Indian Reservation Forest Land: An Environmental Impact Assessment. EIA.

Dale, H. M. and T. Gillespie. 1977. Diurnal fluctuations of temperature near the bottom of shallow water bodies as affected by solar radiation, bottom color and water circulation. Hydrobiologia **55**: 87-92.

Diehl, C. J. 2004. Controls on the magnitude and location of groundwater/surface water exchange in a gravel dominated alluvial floodplain system, northwestern Montana. M.S. Thesis. University of Montana, Missoula, USA.

Dewitt, R. M. 1955. The ecology and life history of the pond snail *Physa gyrinia*. Ecology **36**: 40-44.

Dowdy, W. W. 1944. The influence of temperature on vertical migration of invertebrates inhibiting different soil types. Ecology **25**: 449-460.

Ellis, B. K., J. A. Stanford, and J. V. Ward. 1998. Microbial assemblages and production in alluvial aquifers of the Flathead River, Montana, USA. Journal of the North American Benthological Society **17**:382-402.

EPA. 1976. Quality criteria for water. U.S. Environmental Protection Agency, Washington, DC. 256 pp.

EPA. 1999. National recommended water quality criteria, correction. EPA 822-Z-99-001. U.S. Environmental Protection Agency, Washington, DC.

Gillooly, J. F. and S. I. Dodson. 2000. The relationship of egg size and incubation temperature to embryonic development time in univoltine and multivoltine aquatic insects. Freshwater Biology **44**: 595-604.

Haidekker, A., and D. Hering. 2007. Relationship between benthic insects (Ephemeroptera, Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized streams in Germany: a multivariate study. Aquatic Ecology online

Hall, C. A. S., J. A. Stanford, and F. R. Hauer. 1992. The distributional abundance of organisms as a consequence of energy balances along multiple environmental gradients. Oikos **65**: 377-390.

Hanrahan, T. P. 2007. Large-scale spatial variability of riverbed temperature gradients in Snake River fall Chinook salmon spawning areas. River Research and Applications **23**: 323-341.

Hargrave, B. T. 1969, Epibenthic algal production and community respiration in the sediments of Marion Lake. Journal of the Fisheries Research Board of Canada **26**: 2003-2026.

Harner, M. J., and J. A. Stanford. 2003. Differences in cottonwood growth between a losing and a gaining reach of an alluvial flood plain. Ecology **84**:1453–1458.

Harper, M. P. and B. L. Peckarsky. 2006. Emergence cues of a mayfly in a high-altitude stream ecosystem: potential response to climate change. Ecological Applications **16**: 612-621.

Harrison, N.E. 2004. Gravity, radar, and seismic investigations to help determine geologic, hydrologic, and biologic relations in the Nyack Valley, Northwestern Montana. Masters Thesis, The University of Montana, Missoula, Montana, USA.

Hauer, F. R., J. A. Stanford, J. J. Giersh, W. H. Lowe. 2000. Distribution and abundance patterns of macroinvertebrates in a mountain stream: an analysis along multiple environmental gradients. Verhein Internationale Vereinigung Limnologie **27**: 1485-1488.

Hawkins, C. P., J. N. Hogue, L. M. Decker, J. W. Feminella. 1997. Channel morphology, water temperature and assemblage structure of stream insects. Journal of the North American Benthological Society **16**: 728-749.

Heinonen, J., J. V. K. Kukkonen, I. J. Holopainen. 1999. The effects of parasites and temperatures on the accumulation of xenobiotics in a freshwater clam. Ecological Applications **9**: 475-481.

Hildrew, A. G., J. M. Edington. 1979. Factors facilitating the coexistence of Hydropsychid caddis larvae (Trichoptera) in the same river system. The Journal of Animal Ecology **48**: 557-576.

Hogue, J. N., and C. P. Hawkins. 1991. Morphological variation in adult aquatic insects: associations with developmental temperature and seasonal growth patterns. Journal of the North American Benthological Society **10**: 309-321.

Holopainen, I. J. and E. Ranta. 1977. Carbon dioxide output in the respiration of three Pisidium species (Bivalvia, Spaeriidae). Oecologia **30**: 1-8.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences **45**: 502-515.

Huggenberger, P., E. Hoehn, R. Beschta, and W. Woessner. 1998. Abiotic aspects of channels and floodplains in riparian ecology. Freshwater Biology **40**: 407-425.

Johnson, A. N. 2003. Preliminary hydrogeological and ground penetrating radar investigation of preferential flow zones in a gravel dominated floodplain, northwest Montana. M.S. Thesis, University of Montana, Missoula, Montana, USA.

Johnson, A. N., B. R. Boer, W. W. Woessner, J. A. Stanford, G. C. Poole, S. A. Thomas, S. J. O’Daniel. 2005. Evaluation of an inexpensive small-diameter temperature logger for documenting ground water-river water interactions. Ground Water Monitoring and Remediation. **25**: 68-74.

Keleher, C. J. and F. J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. Transactions of the American Fisheries Society **125**: 1-13.

Kelly, C. F., T. E. Band, and H. Heitman Jr. 1954. The role of thermal radiation in animal ecology. Ecology **35**: 562-569.

Kilgour, B. W. and G. L. Mackie. 1991. Relationship between demographic features of a pill clam (*Pisidium casertanum*) and environmental variables. Journal of the North American Benthological Society **10**: 68 – 80.

Kishi, D., M. Murakami, S. Nakano and K. Maekawa. 2005. Water temperature determines strength of top-down control in a stream food-web. Freshwater Biology **50**: 1315 – 1322.

Knispel, S. and M. Sartori. 2006. Egg development in the mayflies of a Swiss glacial floodplain. Journal of the North American Benthological Society **25**: 430-443.

Labbe, T. R. and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications **10**:1774-1791.

Langan, S. J., L. Johnston, M. J. Donaghy, A. F. Youngson, D. W. Hay, C. Soulsby. 2000. Variation in river water temperatures in an upland stream over a 30-year period. The Science of the Total Environment **265**: 195-207.

Lillehammer, A, J. E. Brittain, S. Jakob Saltveit, P. S. Nielsen. Egg development, nymphal growth and life cycle strategies in Plecoptera. Holarctic Ecology **12**: 173 – 186.

Lorang, M.S. 2006. Chapter 7: Fluvial geomorphic processes, pp. 145-168 in “Methods in stream ecology”, 2nd edition, F. R. Hauer and G. A. Lamberti, eds., Elsevier Inc., San Diego, California, USA.

Lowe, W. H. and F. R. Hauer. 1999. Ecology of two large, net-spinning caddisfly species in a mountain stream: distribution, abundance, and metabolic response to a thermal gradient. Canadian Journal of Zoology **77**: 1637-1644.

Malard, F., A. Mangin, U. Uehlinger, and J. V. Ward. 2001. Thermal heterogeneity in the hyporheic zone of a glacial floodplain. Canadian Journal of Fisheries and Aquatic Sciences **58**: 1319-1335.

Malcolm, I. A., D. M. Hannah, M. J. Donaghy, C. Soulsby, and A. F. Youngson. 2004. The influence of riparian woodland on the spatial and temporal variability of stream water temperatures in an upland salmon stream. Hydrology and Earth System Sciences **8**: 449-459.

Mellina, E., R. D. Moore, S. G. Hinch, J. S. Macdonald, and G. Pearson. 2002. Stream temperature responses to clearcut logging in British Columbia: the moderating influences of groundwater and headwater lakes. Canadian Journal of Fisheries and Aquatic Sciences **59**: 1886 – 1900.

Milner, A. M., J. E. Brittain, E. Castellas, and G. E. Petts. 2001. Trends of macroinvertebrate community tructure in glacier-fed rivers in relation to environmental conditions: a synthesis. Freshwater Biology **46**: 1833 – 1847.

Michener, W. K., T. J. Baerwald, P. Firth, M. A. Palmer, J. L. Rosenberger, E. A. Sandlin and H. Zimmerman. 2002. Defining and unraveling biocomplexity. BioScience **51**: 1018–1023.

Mohensi, O. and H. G. Stefan. 1999. Stream temperature/air temperature relationship: a physical interpretation. Journal of Hydrology **218**: 128 – 141.

Mouw, J. E. B. and P. B. Alaback. 2003. Putting floodplain hyperdiversity in a regional context: an assessment of terrestrial-floodplain connectivity in a montane environment. Journal of Biogeography **30**: 87-103.

Parsons, H. and D. Gilvear. 2002. Valley floor landscape change following almost 100 years of flood embankment abandonment on a wandering gravel-bed river. River Research and Applications **18**: 461-479.

Pearson, W. D., R. H. Kramer and D. R. Franklin. 1968. Macroinvertebrates in the Green River below Flaming Gorge Dam, 1964-65 and 67. Utah Academy of Sciences **33**: 113 – 119.

Pepin, D. M. and F. R. Hauer. 2002. Benthic responses to groundwater-surface water exchange in two alluvial rivers in northwestern Montana. Journal of the North American Benthological Society **21**: 370-383.

Poole, G. C. and C. H. Berman. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management **27**: 787-802.

Poole, G., J. Dunham, M. Hicks, D. Keenan, J. Lockwood, E. Materna, D. McCullough, C. Mebane, J. Risley, S. Sauter, S. Spaulding, D. Sturdevant. 2001. Scientific issues relating to temperature criteria for salmon, trout, and char native to the Pacific Northwest, as summary report submitted to the Policy Workgroup of the EPA Region 10 Water Temperature Criteria Guidance Project. EPA 910-R-01-007.

Poole, G. C., J. A. Stanford, S. W. Running, C. A. Frissell, W. W. Woessner and B. K. Ellis. 2004. A patch hierarchy approach to modeling surface and subsurface hydrology in complex flood-plain environments. Earth Surface Processes and Landforms **29**: 1259-1274.

Poole, G. C., J. A. Stanford, S. W. Running, C. A. Frissell. 2006. Multiscale geomorphic drivers of groundwater flow paths: subsurface hydrologic dynamics and hyporheic habitat diversity. Journal of the North American Benthological Society **25**: 288-303.

Reid, B.L. 2007. Energy flow in a floodplain aquifer ecosystem. P.h.D. Dissertation, The University of Montana, Missoula, Montana, USA.

Ross, D. H. and R. W. Merritt. 1978. The larval instars and population dynamics of five species of black flies (Diptera: Simuliidae) and their responses to selected environmental factors. Canadian Journal of Zoology **56**: 1633-1642.

Stanford, J. A. and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. Nature **335**: 64–66.

Stanford, J. A., F. R. Hauer, J. S. Kimball and M. S. Lorang. 2001. Biocomplexity-dynamic controls on emergent properties of river floodplains: revised project summary.

Stanford, J. A., M. S. Lorang and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems, Verhein Internationale Vereinigung Limnologie **29**: 123-136.

Sweeney, B. W. and J. A. Schnack. 1977. Egg development, growth and metabolism of Sigara alternate (say) (Hemiptera: Corixidae) in fluctuating thermal environments. Ecology **58**: 265 – 277.

Teal, J. M. 1957. Community metabolism in a temperate cold spring. Ecological Monographs **27**: 283-302.

Thompson, D. J. 1978. Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. The Journal of Animal Ecology **47**: 757 – 767.

Tockner, K., F. Malard and J.V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes **14**: 2861-2883.

Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: Present state and future trends. Environmental Conservation **29**: 308-330.

Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of Chinook salmon in northeastern Oregon. Ecological Applications **9**: 301-319.

Vannote, R. L. 1978. A geometric model describing a quasi-equilibrium of energy flow in populations of stream insects. Proceedings of the National Academy of Sciences **75**: 381 – 384.

Vannote, R. L. and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. The American Naturalist **115**: 667-695.

Ward, J. V. 1985. Thermal characteristics of running waters. Hydrobiologia **125**: 31-46.

Ward, J. V. and J. A. Stanford. 1982. Thermal response in the evolutionary ecology of aquatic insects. Annual Review of Entomology **27**: 97-117.

Ward, J. V., K. Tockner, D. B. Arscott, and C. Claret. 2002. Riverine landscape diversity. Freshwater Biology **47**: 517-539.

Wehrly, K. E., M. J. Wiley, and P. W. Seelbach. 2003. Classifying regional variation in thermal regime based on stream fish community patterns. Transactions of the American Fisheries Society **132**: 18 – 38.

Welch, N. E. and J. A. McMahon. 2004. Identifying habitat variables important to the rare Columbia spotted frog in Utah (USA): an information-theoretic approach. Conservation Biology **13**: 473 – 481.

Whited, D. C., M. S. Lorang, M. J. Harner, F. R. Hauer, J. S. Kimball, J. A. Stanford. 2007. Hydrologic disturbance and succession: Drivers of floodplain pattern. Ecology **88**: 940-953.

Wondzell, M. 1992. Vegetation patterns along the Middle Fork of the Flathead River, Glacier National Park, Montana. M.S. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Wyatt, K. H. 2005. The influence of hyporheic-surface water exchange on benthic algal biomass, abundance, and community composition in the Middle Fork Flathead River, Montana. M.S. Thesis. University of Southern Mississippi, Mississippi, USA.

Table 1. Thermal requirements of select organisms found at the Nyack flood plain. Min = lower lethal temperature range (°C), Opt = optimal growth range (°C), Max = upper lethal temperature range (°C). See appendix for references.

Organism	Generation time	Growth period	Min	Opt	Max	Degree days
Amphibian						
Bufo boreas						
tadpole[1, 2, 3]	2-3 months	Spring-Fall	10-14	27-28	37	1200-1800
adult[3, 4]	2-5 years	Summer	<1	20-27	35-45	-
Fish						
Salvelinus fontinalis						
egg[5]	2-4 months	Fall-Winter	<1	6	15	220-525
adult[6, 7, 8, 9]	1-2 years	Spring-Fall	3	12-16	22-30	-
Salvelinus confluentus						
egg[12, 13]	2-3 months	Fall-Winter	1.2	2-6	10	450-1000
adult[7, 9, 10, 11, 12]	3-5 years	Spring-Fall	?	9-14	19-23	-
Oncorhynchus clarki lewisi						
egg[14]	2-3 months	Spring-Summer	<1	4	13	630-800
adult[7, 8, 15, 16, 17, 18]	3-4 years	Spring-Fall	3	10-17	19-24	-
Prosopium williamsoni[6, 19]	2-3 years	Spring-Fall	unknown	unknown	23-24	-
Cottus spp.[8, 20, 21, 26]	1-2 years	Spring-Fall	<1	9-14	24-26	3800
Mollusc						
Pisidium sp. (embryo)[22]	70-140 days	April-Sept	-	-	-	900-1300
Insect (larvae)						
Ameletus similior[23]	1 year	April-July	-	-	-	250-350
Ameletus celer[23]	1-2 years	Aug-June	-	-	-	800-1350
Neophylax/Nemouridae[24, 26, 27]	1 year	Sept-May	-	-	-	1300-1900
Baetidae/Heptageniidae[26, 27, 28]	multi/yr	Sept-May	-	-	20-30	1300-2300
Pteronarcella/Taenionema[24, 25, 30]	1 year	July-May	-	-	32-34	2200-2300
Glossosomatidae[26]	multi/yr	April-Aug	-	-	-	2500-2600
Perlidae[26]	1-3 years	Sept-Aug	-	-	-	3800

Table 2. Thermal metrics used for analysis. Equations used to compute metrics, time period over which metric was calculated, and a description of the relationship between thermal metrics and biotic indicators is provided. Biotic indicator listings of metabolic optimum derived from Hall et al. (1992) and developmental threshold after Ward and Stanford (1982).

Metric	Equation	Period	Biotic indicator
Daily average temperature:	$\overline{T}_{\mathrm{d}} = \frac{\sum_{i=1}^{n} X_i}{n}$	day, season	metabolic optimum
Temperature phase shift:	$\mathrm{TPS} = \mathrm{date}, \overline{T}_{\max, site} - \mathrm{date}, \overline{T}_{\max, air}$	annual	life history
Temperature pulse:	$\mathrm{TP} = T_{\max} - T_{\min}$	day, season, annual	thermal tolerance
Rate of thermal change:	$\mathrm{TC} = \frac{T_2 - T_1}{t}$	season	thermal tolerance
Degree days:	$\mathrm{DD} = \frac{\sum_{i=1}^{n} \overline{T_d}}{n}$	month, season, annual	developmental threshold

Table 3. Phase shift in annual peak values for average daily temperature (^oC) across floodplain habitats in 2003. Phase shift days are measured in relation to air temperature peak on July 18, 2003. Values are ± 1 standard deviation (±1 SD).

	n	Temperature (^oC)	Days
Air	2	21.9±0.4	0±3
Soil	2	26.2±0.9	10±5
Orthofluvial springbrook	3	11.2±3.0	18±12
River	1	17.4	23
Tributary	2	13.9±3.9	23±2
Backwater	3	16.0±4.0	25±7
Shallow shoreline	4	16.5±0.5	26±10
Parafluvial springbrook	3	13.1±3.8	28±12
Aquifer	3	13.1±1.1	51±24

Table 4. Average daily values of thermal metrics for floodplain habitats in summer, fall, winter, and spring 2003-2004. Thermal metric calculations are described in Table 1. Values are averaged over 6 week intervals and reported in ^{o}C (± 1 SE, except when n=1 in which case values are ^{o}C ± 1 SD).

Habitat	n	Mean	Max	Min	Pulse	$TC_{increase}$	$TC_{decrease}$
<u>Summer</u>							
Air	2	18.1 (±1.9)	30.0 (±2.9)	7.3 (±2.1)	22.7 (±3.8)	4.9 (±1.0)	-4.6 (±0.9)
Soil	2	20.6 (±1.8)	26.5 (±2.4)	15.7 (±1.5)	10.8 (±1.9)	1.9 (±0.3)	-1.3 (±0.2)
River	1	14.9 (±1.0)	16.1 (±1.1)	13.8 (±1.0)	2.4 (±0.4)	0.4 (±0.1)	-0.2 (±0.1)
Shallow shore	4	15.0 (±0.6)	17.8 (±0.8)	12.6 (±0.5)	5.3 (±0.6)	1.2 (±0.2)	-0.8 (±0.1)
Backwater	3	14.6 (±0.6)	17.3 (±0.9)	12.2 (±0.5)	5.2 (±0.9)	1.2 (±0.3)	-0.8 (±0.2)
P. springbrook	3	11.4 (±0.4)	14.2 (±0.8)	9.8 (±0.3)	4.4 (±0.7)	1.1 (±0.3)	-1.0 (±0.2)
O. springbrook	3	10.5 (±0.2)	12.3 (±0.4)	9.1 (±0.2)	3.2 (±0.5)	0.6 (±0.1)	-0.5 (±0.1)
Tributary	2	11.1 (±0.5)	13.6 (±0.6)	8.8 (±0.6)	4.8 (±0.7)	1.4 (±0.7)	-1.3 (±0.7)
Hyporheic	0	-	-	-	-	-	-
Aquifer	3	9.9 (±0.6)	10.6 (±0.4)	9.1 (±0.8)	1.5 (±0.5)	0.2 (±0.1)	-0.1 (±0.0)
<u>Fall</u>							
Air	2	2.3 (±5.0)	9.2 (±6.5)	-3.1 (±4.6)	12.3 (±4.6)	2.9 (±1.0)	-2.5 (±1.1)
Soil	2	4.9 (±2.9)	6.1 (±3.4)	3.8 (±2.5)	2.3 (±1.3)	0.5 (±0.3)	-0.3 (±0.1)
River	1	5.1 (±2.0)	5.9 (±2.2)	4.4 (±1.8)	1.4 (±0.6)	0.3 (±0.1)	-0.3 (±0.1)
Shallow shore	4	5.3 (±1.7)	6.5 (±2.0)	4.4 (±1.5)	2.1 (±0.7)	0.6 (±0.2)	-0.3 (±0.1)
Backwater	4	6.3 (±1.4)	7.3 (±1.6)	5.5 (±1.3)	1.8 (±0.4)	0.5 (±0.1)	-0.3 (±0.1)
P. springbrook	3	7.3 (±0.9)	8.3 (±1.1)	6.7 (±0.8)	1.6 (±0.4)	0.5 (±0.1)	-0.3 (±0.1)
O. springbrook	3	8.7 (±0.7)	9.5 (±0.8)	8.0 (±0.7)	1.4 (±0.3)	0.4 (±0.1)	-0.2 (±0.1)
Tributary	3	6.0 (±1.2)	7.1 (±1.4)	5.0 (±1.1)	2.1 (±0.5)	0.7 (±0.2)	-0.8 (±0.2)
Hyporheic	3	7.9(±1.5)	8.1 (±1.5)	7.7 (±1.5)	0.4 (±0.1)	0.1 (±0.0)	-0.1 (±0.0)
Aquifer	4	10.4 (±0.4)	11.4 (±0.3)	9.2 (±0.6)	2.1 (±0.5)	0.6 (±0.3)	-0.1 (±0.1)

Table 4. (cont.)

Habitat	n	Mean	Max	Min	Pulse	$TC_{increase}$	$TC_{decrease}$
Winter							
Air	2	-3.1 (±3.2)	2.1 (±2.4)	-6.9 (±4.4)	9.0 (±4.0)	1.9 (±0.8)	-1.7 (±0.7)
Soil	2	0.0 (±0.2)	0.0 (±0.2)	-0.0 (±0.2)	0.0 (±0.1)	0.0 (±0.0)	0.0 (±0.0)
River	1	0.8 (±0.8)	1.1 (±1.0)	0.6 (±0.7)	0.4 (±0.5)	0.2 (±0.1)	-0.1 (±0.1)
Shallow shore	2	0.6 (±0.4)	0.3 (±0.1)	0.2 (±0.1)	0.1 (±0.0)	0.3 (±0.1)	-0.2 (±0.1)
Backwater	3	0.7 (±0.5)	1.0 (±0.6)	0.4 (±0.4)	0.5 (±0.3)	0.2 (±0.1)	-0.1 (±0.0)
P. springbrook	2	3.0 (±3.0)	3.9 (±0.9)	2.5 (±0.4)	1.4 (±0.7)	0.5 (±0.3)	-0.4 (±0.2)
O. springbrook	3	4.0 (±0.2)	4.6 (±0.2)	3.6 (±0.3)	1.0 (±0.2)	0.3 (±0.1)	-0.2 (±0.0)
Tributary	3	3.6 (±0.6)	4.8 (±0.7)	2.1 (±0.5)	2.7 (±0.4)	0.2 (±0.1)	-0.1 (±0.0)
Hyporheic	3	0.4 (±0.2)	0.5 (±0.2)	0.4 (±0.2)	0.1 (±0.1)	0.1 (±0.0)	-0.1 (±0.0)
Aquifer	4	4.0 (±0.3)	4.1 (±0.3)	3.7 (±0.3)	0.4 (±0.1)	0.3 (±0.1)	-0.4 (±0.1)
Spring							
Air	2	5.8 (±2.2)	13.8 (±3.6)	-1.2 (±1.9)	15.0 (±4.1)	3.2 (±0.8)	-2.9 (±0.8)
Soil	2	5.8 (±3.0)	8.5 (±4.4)	3.5 (±2.0)	5.0 (±2.7)	1.1 (±0.5)	-0.6 (±0.3)
River	1	4.9 (±0.9)	6.1 (±1.1)	3.9 (±0.9)	2.2 (±0.8)	0.5 (±0.2)	-0.3 (±0.1)
Shallow shore*	0	-	-	-	-	-	-
Backwater*	0	-	-	-	-	-	-
P. springbrook	4	5.1 (±0.6)	6.7 (±0.8)	4.0 (±0.4)	2.7 (±0.6)	0.8 (±0.1)	-0.4 (±0.1)
O. springbrook	2	5.7 (±0.8)	7.3 (±1.0)	4.5 (±0.6)	2.9 (±0.7)	0.7 (±0.2)	-0.5 (±0.1)
Tributary	3	5.0 (±0.4)	7.3 (±0.5)	2.9 (±0.4)	4.4 (±0.6)	0.7 (±0.2)	-0.8 (±0.3)
Hyporheic	2	4.2 (±0.9)	4.6 (±0.9)	3.9 (±0.9)	0.7 (±0.3)	0.2 (±0.1)	-0.2 (±0.1)
Aquifer	3	3.4 (±0.2)	3.5 (±0.2)	3.3 (±0.2)	0.2 (±0.1)	0.2 (±0.1)	-0.2 (±0.1)

Table 5. Floodplain temperatures, August 10, 2003 and January 5, 2004. Values are ± 1 SE, except for the river which is ± 1 SD. * No data available on these dates.

Habitat	n	Mean	Max	Min	Pulse	$TC_{increase}$	$TC_{decrease}$
August 10, 2003							
Soil	2	22.6 ± 2.9	29.9 ± 5.0	17.0 ± 1.3	12.9 ± 3.7	2.3 ± 0.6	-1.7 ± 0.7
Air	2	21.0 ± 0.4	34.9 ± 0.0	8.6 ± 0.2	26.3 ± 0.2	6.3 ± 0.7	-6.9 ±1.4
River	1	16.1 ± 0.9	17.4	14.8	2.6	0.5	-0.3
Shallow shore	4	16.4 ± 0.2	19.7 ± 0.6	13.7 ± 0.4	6.0 ± 0.9	1.2 ± 0.2	-1.0 ± 0.3
Backwater	3	15.6 ± 2.1	19.3 ± 2.6	13.0 ± 1.6	6.2 ± 1.5	1.3 ± 0.4	-1.1 ± 0.3
P. springbrook	3	11.9 ± 2.7	15.3 ± 3.6	10.3 ± 2.2	5.0 ± 1.4	1.4 ± 0.2	-1.4 ± 0.3
O. springbrook	3	10.9 ± 1.6	13.0 ± 2.7	9.3 ± 0.7	3.7 ± 2.3	0.8 ± 0.4	-0.6 ± 0.2
Tributary	2	11.8 ± 1.3	13.7 ± 1.1	9.5 ± 1.5	4.1 ± 0.5	0.8 ± 0.1	-0.5 ± 0.1
Hyporheic*	0	-	-	-	-	-	-
Aquifer	3	10.5 ± 0.8	10.6 ± 0.8	10.5 ± 0.7	0.1 ± 0.1	0.1 ± 0.1	-0.1 ± 0.1
January 5, 2004							
Soil	1	0.1 ± 0.0	0.1	0.1	0.0	0.0	0.0
Air	2	-31.2 ± 0.5	-23.5 ± 0.1	-35.5 ± 0.8	12.0 ± 0.9	3.0 ± 0.4	-2.3 ±0.7
River	1	0.1 ± 0.0	0.1	0.1	0.0	0.0	0.0
Shallow shore	2	0.0 ± 0.0	0.1 ± 0.0	-0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	-0.1 ± 0.0
Backwater	2	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	-0.1 ± 0.1
P. springbrook	2	1.2 ± 1.4	1.4 ± 1.5	1.1 ± 1.4	0.3 ± 0.1	0.2 ± 0.0	-0.2 ± 0.0
O. springbrook	3	4.8 ± 0.7	5.0 ± 0.6	4.7 ± 0.7	0.3 ± 0.1	0.1 ± 0.1	-0.1 ± 0.1
Tributary	3	0.3 ± 0.7	0.4 ± 0.6	0.3 ± 0.7	0.1 ± 0.1	0.0 ± 0.1	0.0 ± 0.1
Hyporheic	3	0.5 ± 0.3	0.6 ± 0.3	0.5 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Aquifer	4	3.3 ± 1.6	3.4 ± 1.5	3.3 ± 1.6	0.2 ± 0.1	0.1 ± 0.1	-0.1 ± 0

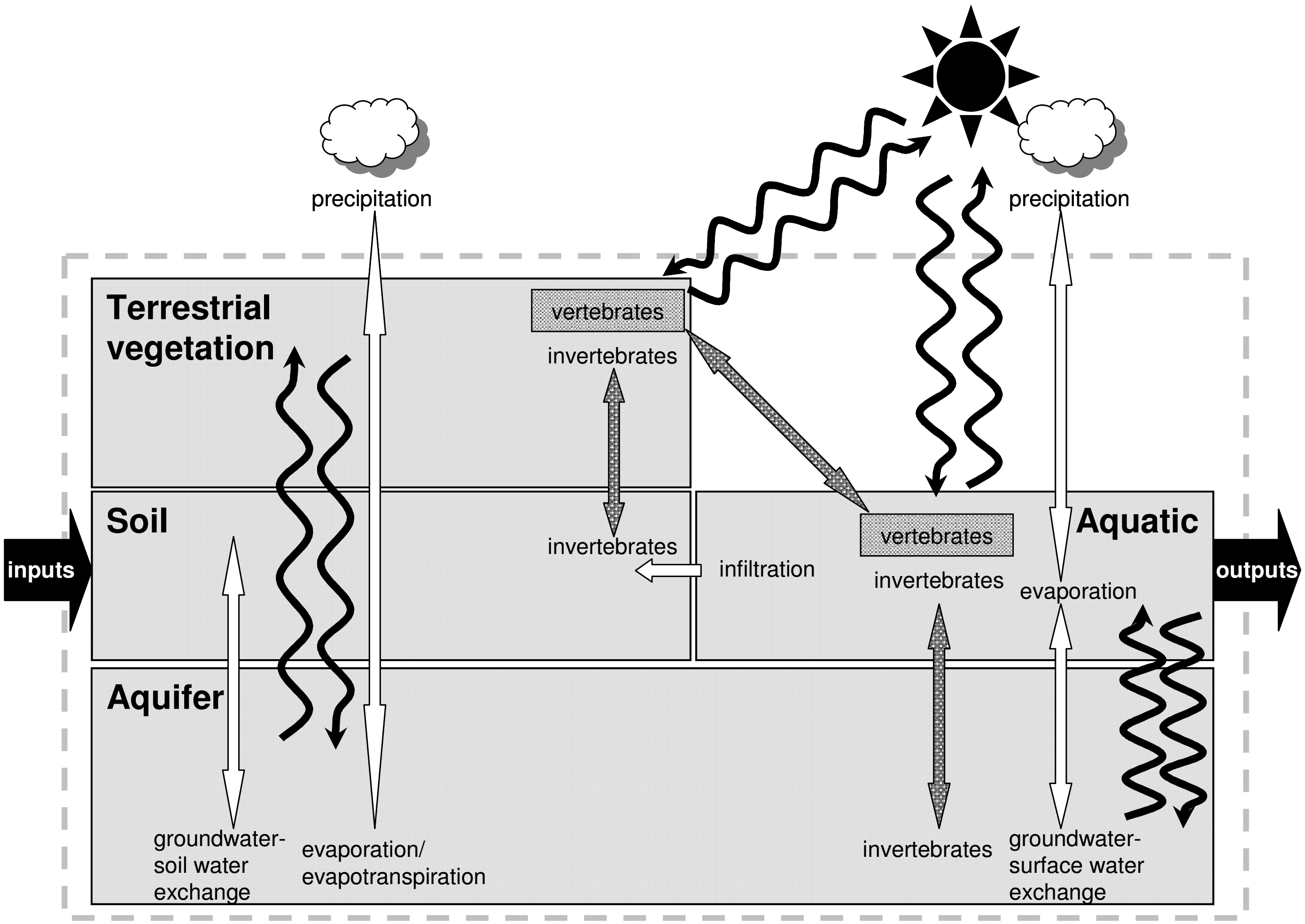

Figure 1. Conceptual process model of the floodplain ecosystem in the context of temperature dynamics. Arrows indicate pathways of exchange for water (open arrows), heat (solid wavy arrows) and biota (hatch marked arrows). Large boxes are subsystems of the flood plain interacting via the pathways of exchange. Small boxes are organisms that remain within a subsystem to complete their life cycle.

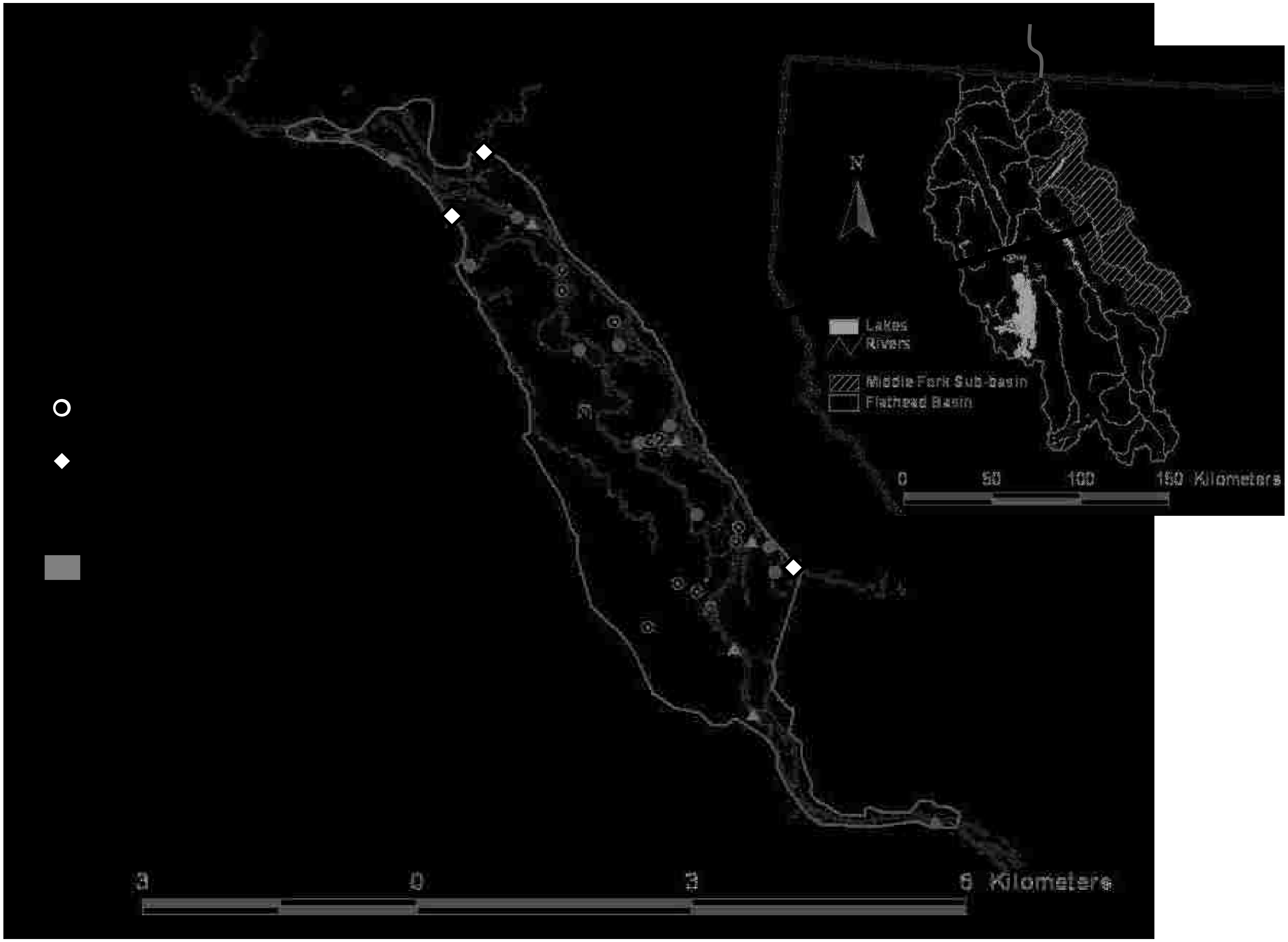

Figure 2. Temperature study site locations on the Nyack flood plain.

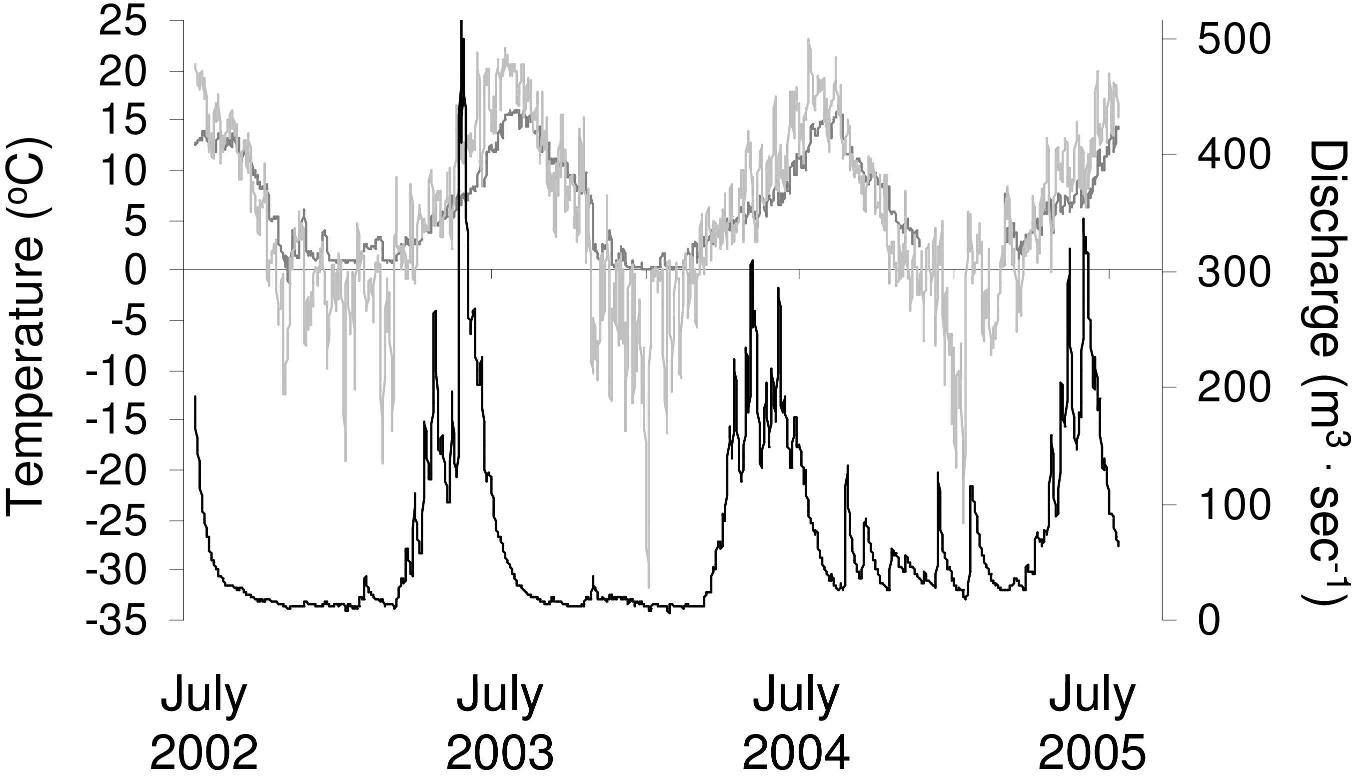

Figure 3. Annual temperature pattern at Nyack in relation to discharge in the river (black line). Parafluvial air temperature (light gray line) and main river channel temperature (dark gray line) are shown.

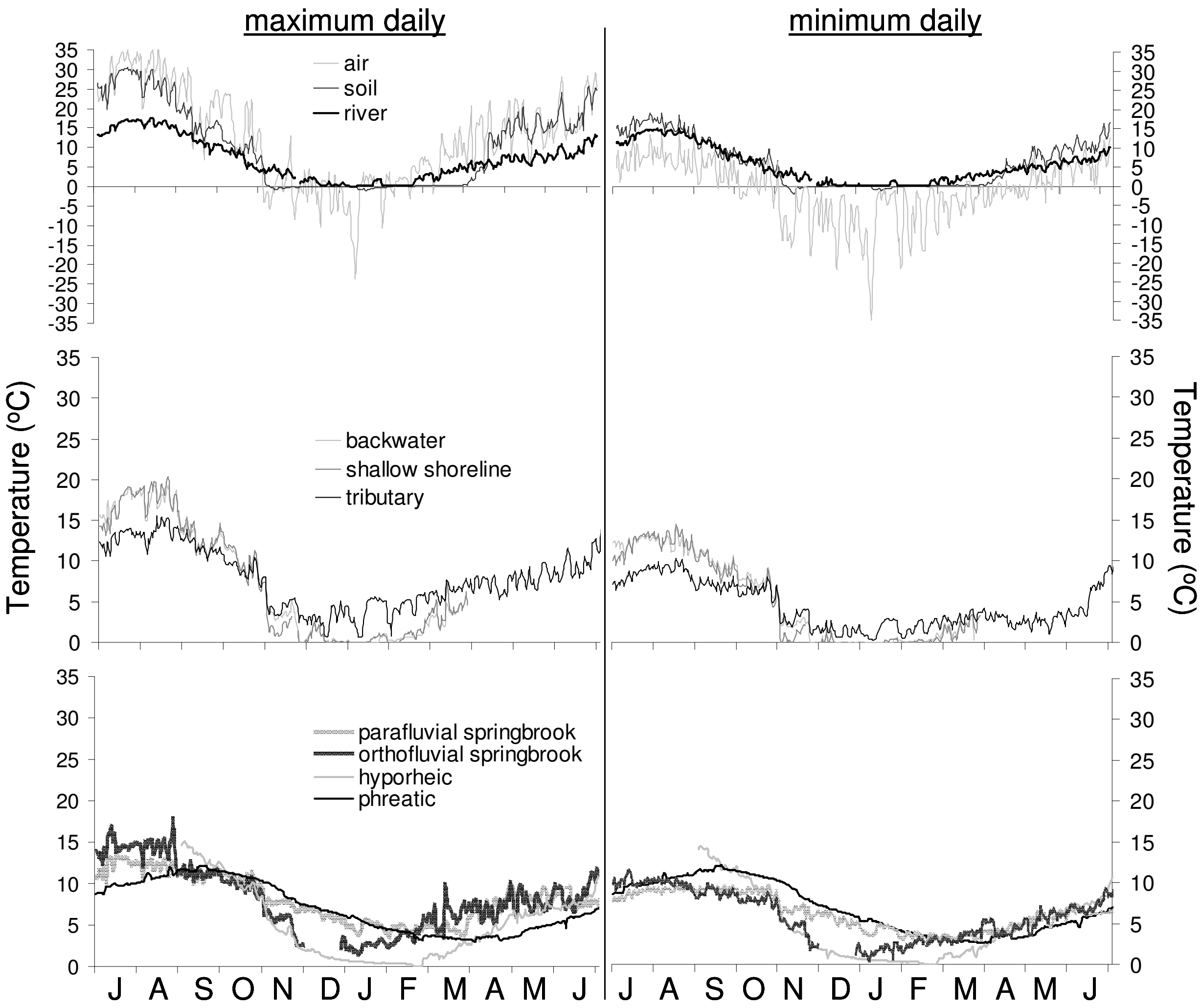

Figure 4. Annual temperature patterns for various Nyack habitats comparing maximum and minimum daily data. Note the moderating effect of the aquifer on springbrooks.

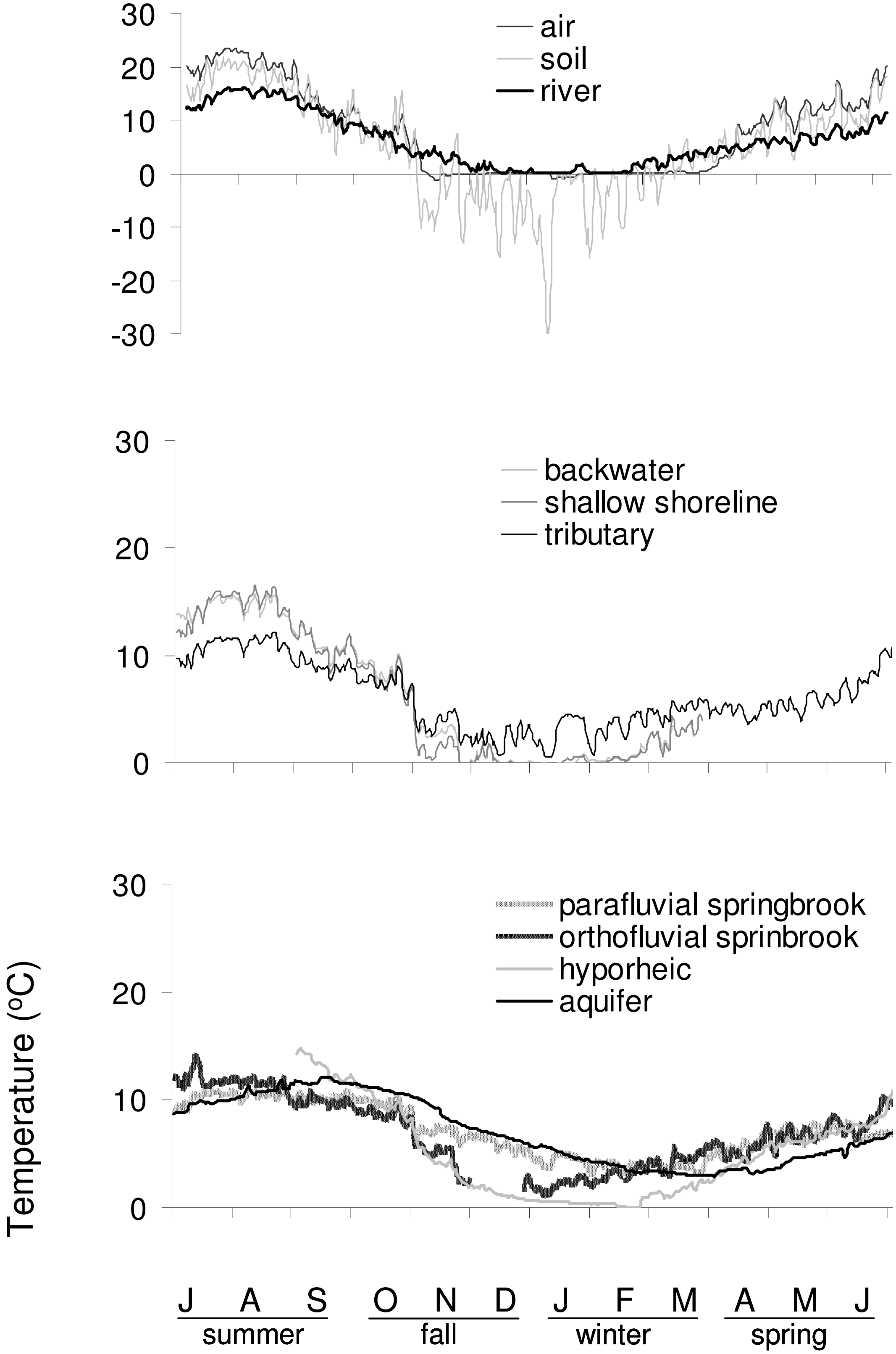

Figure 5. Daily average temperatures in various habitats over an annual cycle at Nyack.

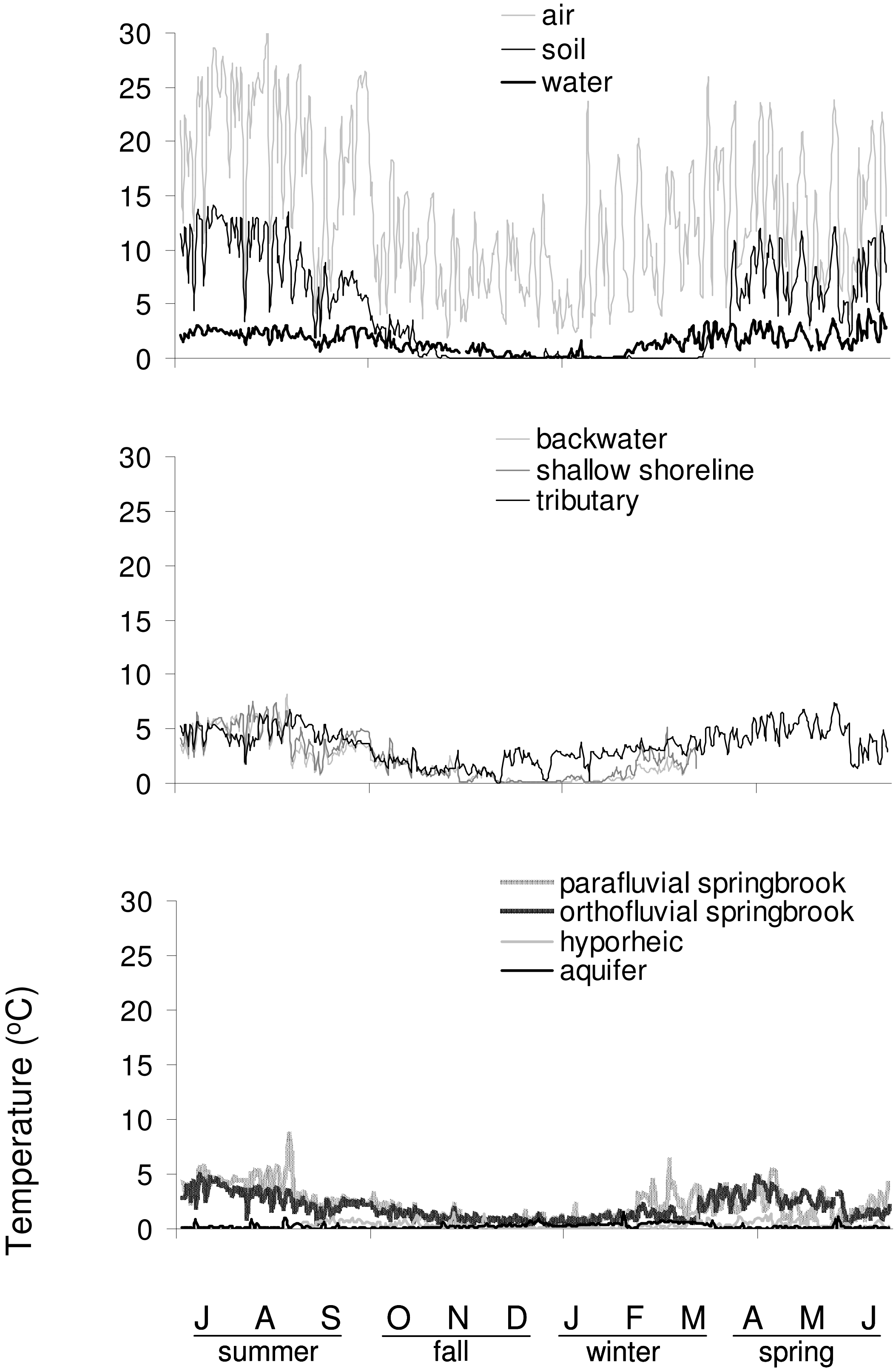

Figure 6. Daily temperature pulse in various habitats over an annual cycle at Nyack.

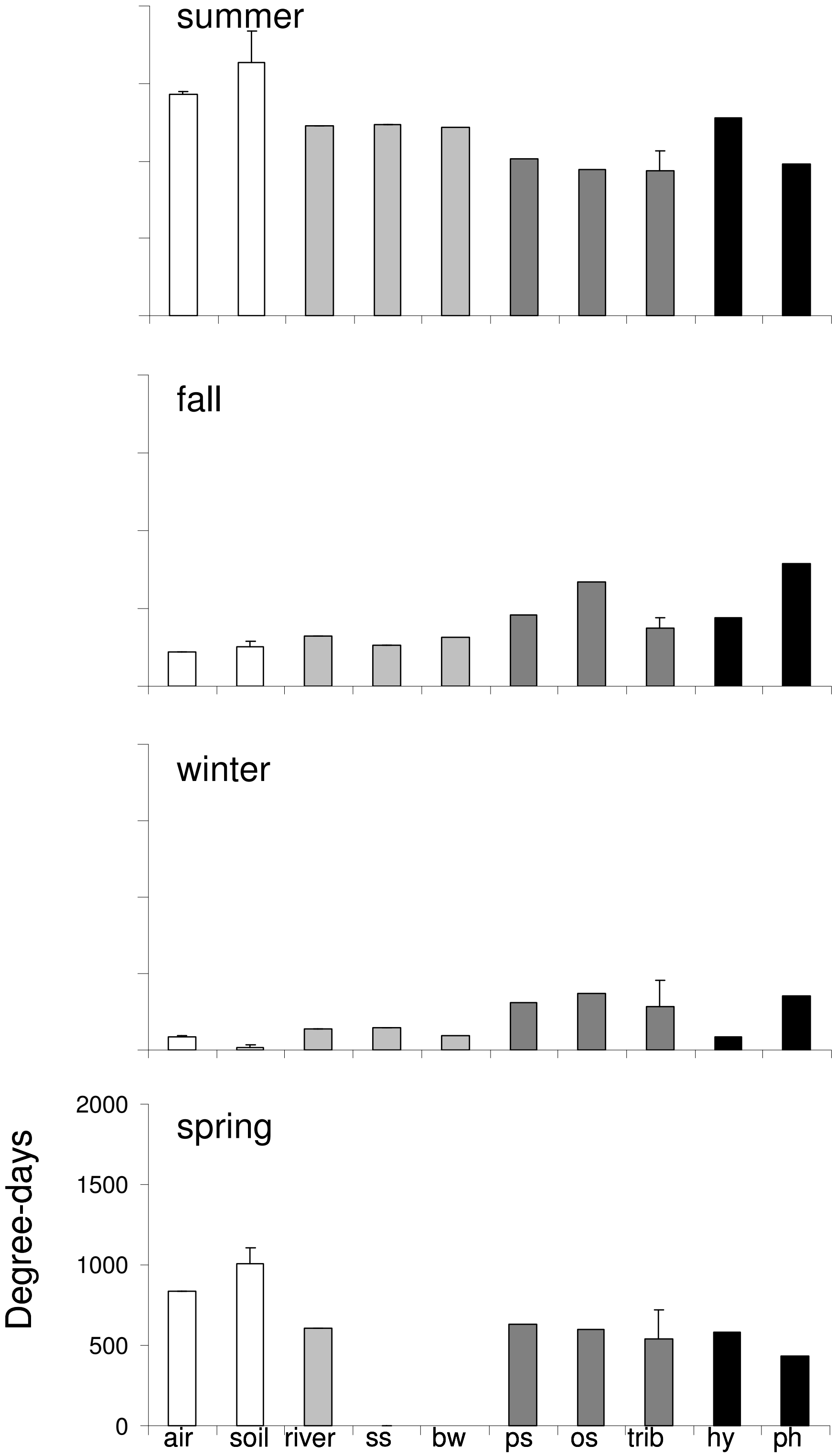

Figure 7. Comparative annual degree-days in various habitats at Nyack. ss = shallow shoreline, bw = backwater, ps = parafluvial springbrook, os = orthofluvial springbrook, trib = tributary, hy = hyporheic, ph = phreatic

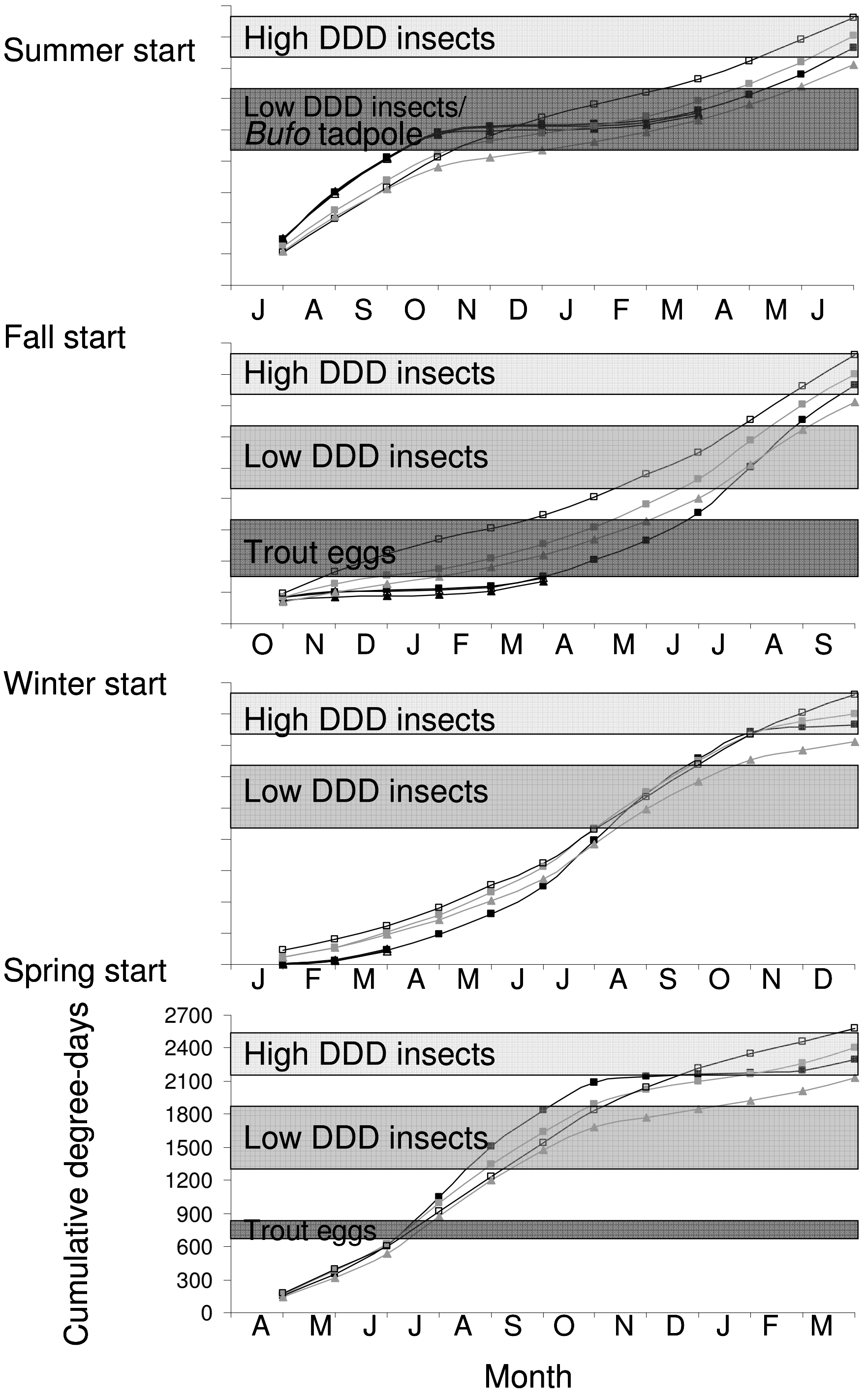

Figure 8. Degree-day accumulations in various habitats at Nyack over an annual cycle. Shaded areas are minimum degree-days required for aquatic insect maturation to emergence and for hatching of brook trout eggs. △= backwater, ▲= shallow shoreline ■ = river, ▨ = parafluvial springbrook, □ = orthofluvial springbrook, △ = tributary

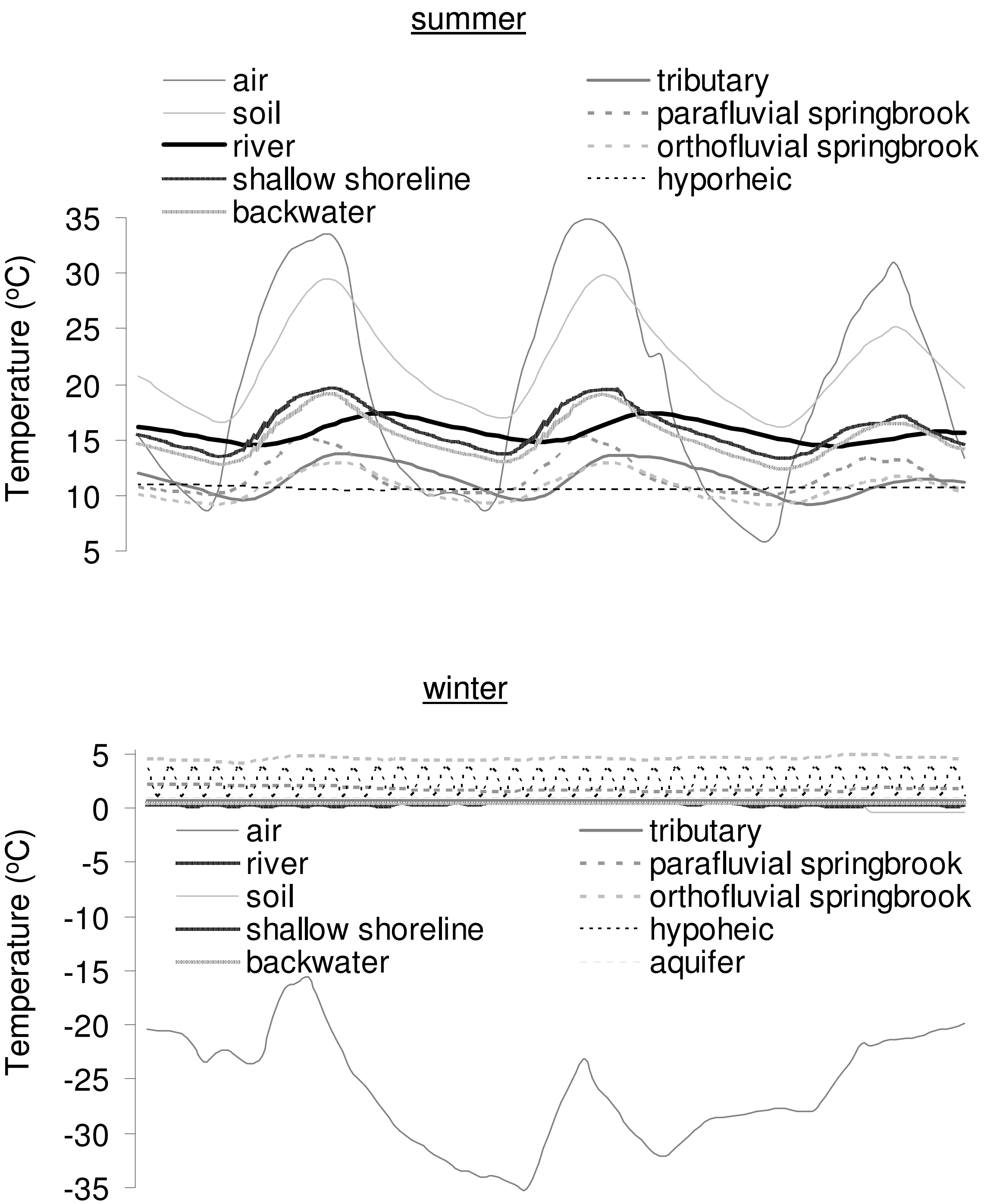

Figure 9. Diel temperature variation in various habitats of the flood plain on August 10, 2003 (summer), and January 5, 2004 (winter).

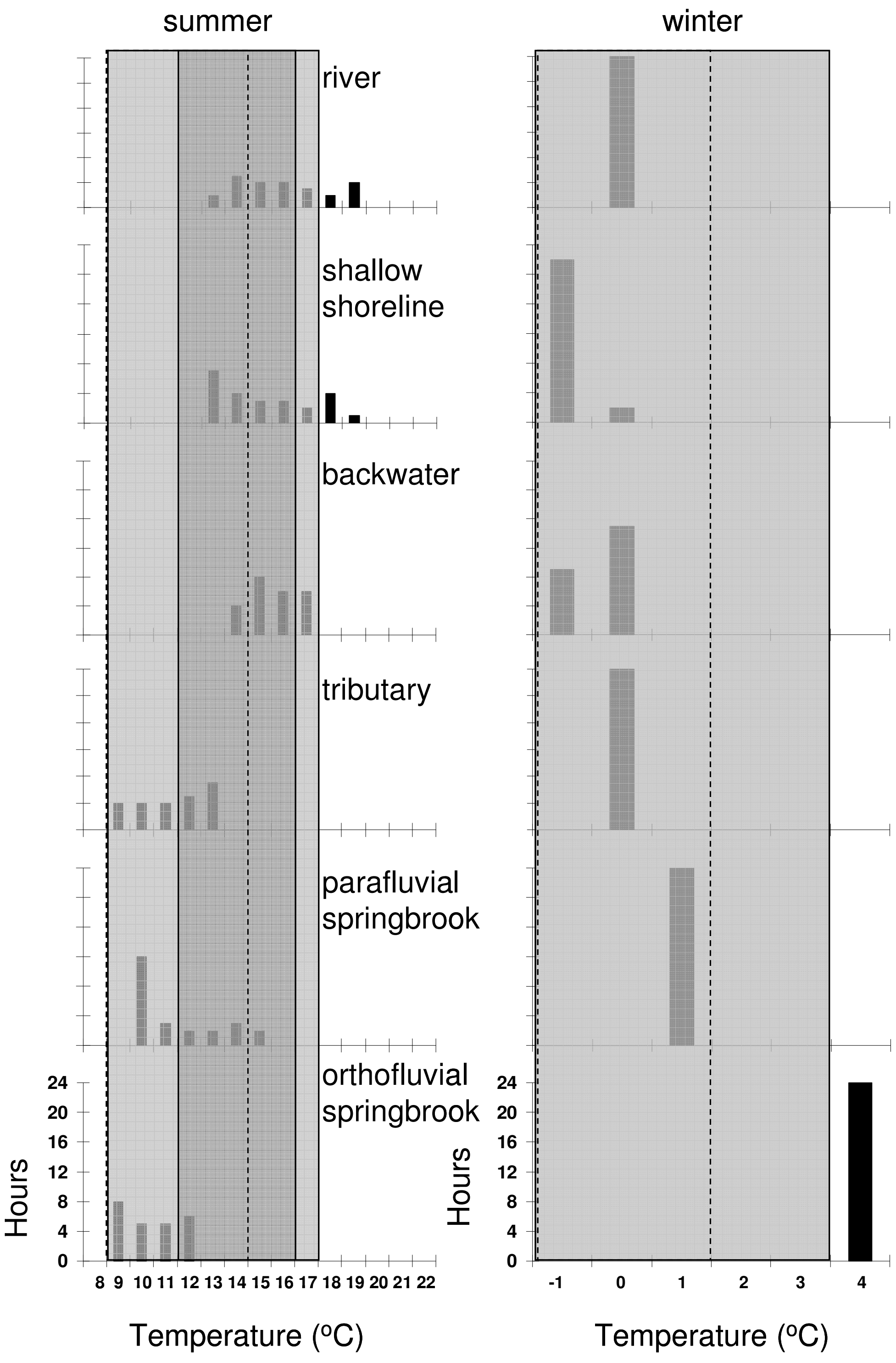

Figure 10. Number of hours at particular temperatures on August 10, 2003 (summer) and January 5, 2004 (winter) in surface water habitats. Shaded bars indicate optimal thermal range for native fish (light gray; dashed outline *S. confluentus*) or non-native fish (dark gray) in summer, or all fish in winter.

CHAPTER 3:

PERIPHYTON RESPONSE TO FLOODING IN LATERAL HABITATS OF AN ALLUVIAL FLOODPLAIN ECOSYSTEM

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ABSTRACT

The influence of flood disturbance on nutrient flux and periphyton development of entire floodplain riverscapes is not well understood. Our study explored nutrient concentrations and periphyton community structure following a large magnitude flood event and a less than bankfull flood event. Research was conducted at the Nyack floodplain, a long-term research site on the Middle Fork of the Flathead River located in Northwest Montana, USA. Study sites were located along a lateral gradient of habitats from main channel shallow shorelines to parafluvial springbrooks to orthofluvial springbrooks. Algal biomass, C:N ratios, and diversity measures were compared with measures of hydrologic disturbance and nutrient availability. The magnitude of disturbance differed considerably by habitat type, with cumulative streamflow energy 2-10 times greater in the main channel than in springbrooks. Surface water chemistry was strongly influenced within and between years by hydrologic change. We observed high resilience in periphyton biomass of all habitats post-flood, with a more rapid recovery following the less than bankfull flood event. Over both years, periphyton biomass changed the least in the orthofluvial springbrooks, habitats characterized by low disturbance and abundant nutrients. Evidence from a nutrient diffusion experiment and measures of algal diversity implicate nutrient co-limitation by N and P in governing periphyton community biomass and composition. This study: 1) highlights the degree of spatial and temporal variability in water chemistry and periphyton populations across floodplain habitats and, 2) provides preliminary evidence for a nutrient-mediated flood disturbance model for periphyton community succession.

INTRODUCTION

In floodplain systems, aquatic primary production is shaped by the annual flood pulse, which governs streambed mobility and architecture (Lorang et al. 2005), delivery of limiting nutrients (Fisher et al. 1982), density of grazers (Arscott et al. 2005), groundwater exchange patterns (Valett et al. 1994), and ultimately riparian vegetation cover (Whited et al. 2007) and light availability. Floodplain landscapes are shifting habitat mosaics in which habitat location governs both the disturbance regimes and nutrient availability to which organisms are exposed. In gravel-bed rivers, nutrients and flow disturbance interact to shape algal community structure (Biggs and Thomsen 1998, Biggs and Smith 2002). Mechanisms governing the response in periphyton community biomass (Bothwell 1988, Coleman and Dahm 1990, Mullholland et al. 1995, Biggs 1996) and diversity (Pringle 1990, Clausen and Biggs 1997, Snyder et al. 2002) to hydrologic change have been examined in streams draining forested (Resh et al. 1988, Power and Stewart 1987) and desert landscapes (Fisher et al. 1982, Marti et al. 1997). Many of these studies have addressed temporal (Grimm and Fisher 1989, Stevenson 1997, Biggs and Smith 2002) or longitudinal (Mullholland 1992, Ortiz-Zayas et al. 2005) succession of periphyton communities in the main river channel in relation to flood disturbance and groundwater exchange (Valett et al. 1994). One drawback of all river research to date has been the attention focused on small, pristine streams of limited habitat complexity rather than large, complex river systems frequently altered by human impacts (Tockner and Stanford 2002). This trend reversed in recent years as scientists began to recognize large river-floodplain ecosystems support tremendous biodiversity, productivity and unique biogeochemical processes (Junk et al. 1989, Stanford et al. 2005). Still, the degree to which flood pulse disturbance structures biotic communities across four-dimensional floodplain landscapes is largely unknown (but see Uehlinger 1991, van der Nat et al 2003, Whited et al. 2007).

We used two ecological hypotheses to build a conceptual floodplain ecosystem model (Fig. 1a) and relate the aquatic subsystem of the model to disturbance, nutrients, and primary production across a habitat successional gradient (Fig. 1b). Our conceptual model illustrates that the aquatic subsystem receives heat inputs from the atmosphere and aquifer, interacts hydrologically with the aquifer via surface water and groundwater exchange (Stanford and Ward 1993), and provides inputs to the soil subsystem through infiltration of surface water. These hydrologic vectors mediate transport of nutrients and organisms between the subsystems, with an additional subsidy of organic matter moving from the terrestrial to aquatic systems through erosion. Periphyton is influenced by subsystem structural complexity through hydrologic variation driven by precipitation and heat, nutrient flux, immigration and emigration of grazers, and physical transport of periphyton into other subsystems.

Within the aquatic subsystem, these same vectors of heat, hydrology, nutrient, and organisms vary spatially across the landscape and through time, creating a “mosaic” of habitats. The Shifting Habitat Mosaic (SHM; Arscott et al. 2002, Hauer et al. 2003, Stanford et al. 2005), a descendent of the “shifting mosaic steady state” terrestrial vegetation model (Cooper 1913, Watt 1947, Bormann and Likens 1979), describes abiotic and biotic features particular to floodplain ecosystems shaped by predictable disturbances. Regular disturbances create a patchwork of habitats in different stages of succession across the landscape. Floods, sediment entrainment and erosion, vegetation structure and surface water-groundwater interactions are the primary drivers in creating the collection of resource patches and distinct communities found in the SHM. The flux of energy, nutrients and biota across floodplain ecotones is expected to create niche diversity and high species richness (Stanford et al. 2005).

As our goal was to study algal production and community dynamics along spatial and temporal disturbance gradients, we chose 3 “lateral” habitat types. Lateral habitats are exposed to a range of hydrologic disturbance intensity and frequency related to their elevation and position on the landscape. Low elevation shallow shoreline areas of the main channel are scoured by annual flooding and subsequently undergo lateral migration in response to flood water recession. These habitats exhibit reduced water velocity and depth with respect to the main channel thalweg. Springbrooks laterally intersect the main channel at different elevations and are influenced by terrestrial-aquatic and groundwater surface water interactions. Mid elevation parafluvial springbrooks sit at the interface between riparian benches and gravel bars. Due to their location these sites are regularly inundated and scoured by flood flows. The short pulses of surface water received by parafluvial springbrooks is complemented by groundwater inputs of variable flowpath length. High elevation orthofluvial springbrooks are infrequently inundated by floodwaters. When flood waters do reach these habitats they most often deposit fine sediments rather than actively scouring out bed material. Groundwater contributes significantly to orthofluvial springbrook streamflows year-round. This helps maintain mature forested stands along the stable banks typical of these habitats.

We modified Huston's (1979) Dynamic Equilibrium Model (DEM) to include effects of flooding, habitat succession and groundwater-surface water dynamics on these 3 lateral habitat types (Fig. 1b). We predicted that gradients in disturbance and nutrient availability would affect temporal and spatial variation in biomass and diversity. In shallow shoreline areas we expected to find high levels of disturbance coupled with low levels of nutrients. We hypothesized this would yield low periphyton biomass and diversity due to intense competition for limiting resources and high mortality from the frequent disturbances. Parafluvial springbrooks were expected to receive intermediate levels of disturbance due to their location and intermediate levels of nutrients from groundwater interactions. We anticipated this combination would yield the highest periphyton biomass and diversity by creating a complex niche space. Abundant resources should allow some periphyton to achieve high biomass but not reach the point of competitive exclusion due to the levels of disturbance. In orthofluvial springbrooks, low levels of disturbance are expected to coincide with high nutrient availability. Again, some periphyton species should achieve a high, steady-state level of biomass due to low disturbance but in this case competitive exclusion will likely reduce diversity.

We examined multiple lines of evidence that these lateral habitats are: 1) influenced by different frequency and intensity of disturbance and 2) variable over space or time in relation to water chemistry and periphyton community metrics. We predicted that the annual flood pulse disturbance was the major force controlling periphyton community biomass, nutrient status and species composition, with secondary control by surface and groundwater mediated water chemistry fluctuations during lower flow periods.

STUDY AREA

Our study was conducted on the Nyack flood plain of the Middle Fork of the Flathead River in northwestern Montana (Figure 2). A fifth order, anastomosed floodplain, the Nyack drainage basin encompasses portions of Glacier National Park and the Great Bear Wilderness Area (United States Forest Service) on opposite sides of the river. Minor anthropogenic disturbances exist in the watershed and are restricted to a two-lane highway, a single rail train line, and small-scale hay and cattle grazing operations. These minimal land use impacts occur outside of our study sites on higher mid-elevation benches less prone to flooding. The floodplain is approximately 10 km long by 2 km wide and bounded upstream and downstream by bedrock canyons forming knickpoints. Floodplain sediments consist of a heterogeneous mix of aggraded alluvial cobble, pebble, and sand fill overlaying layers of sand and clay. The annual hydrograph of the Middle Fork of the Flathead River is a dominated by spring snowmelt with discharge ranging from to 541 $m^3 s^{-1}$ (mean peak annual discharge; May-June) to 17 $m^3 s^{-1}$ (mean annual baseflow; December-January). During the 3 years of sampling in this study (Figure 2), 1997 produced a 10-year recurrence interval flood (850 $m^3 s^{-1}$; Whited et al 2007), while 2004-2005 produced floods of 1 year recurrence to near bankfulll conditions (1 year recurrence at 105 $m^3 s^{-1}$; bankfull at 465 $m^3 s^{-1}$; recurrence interval of 1.4 years; Whited et al 2007). Hydraulic conductivities average 13 m day^{-1} (Johnson 2003, Diehl 2004) through porous bed materials, facilitating surface water-groundwater interactions that support biogeochemical complexity and a distinctive groundwater food web (Ward et al. 1994, Ellis et al. 1998, Craft 2002). Hydrologic variability is a known driver of nutrient variation in the Flathead River system (Hauer et al. 2002). The main channel is dominated by surface flow with localized groundwater interactions on the order of centimeters to meters (Pepin and Hauer 2002). Hyporheic flow appears largely responsible for maintenance of springbrook habitats in both actively scoured (parafluvial) and infrequently flooded depositional zones (orthofluvial) of the flood plain. Main channel edges are open gravel surfaces nearly devoid of vegetation. Vegetation along parafluvial springbrook banks is comprised of a mixed forb community with newly colonizing cottonwood (*Populus trichocarpa*), and willow (*Salix spp*.). Orthofluvial springbrook streamside vegetation consists of mature forest with gallery cottonwood, red alder (*Alnus incana*), spruce (*Picea spp*.), and Douglas fir (*Pseudotsuga menziesii)* (Mouw and Alaback 2003). Minimal canopy cover exists at main channel and parafluvial springbrook sites (0-5%) while orthofluvial springbrook canopy cover is between 20-60% (Bansak 1998, Fig. 1b).

METHODS

Site Selection

In 1997, main channel shallow shoreline sites were chosen near the upstream and downstream knickpoints of the Nyack floodplain. Sites were located within regional upwelling, downwelling and neutral zones to represent the full range of natural variation in main channel surface water-groundwater interactions. We used approximately the same main channel study sites again in 2005, with the understanding that channel change over the seven years precluded sampling of exact study locations. We excluded a downsteam upwelling reach entirely in 2005 due to dramatic channel alterations since

1997. The 1997 work also included 4 springbrook sites but did not differentiate in design between parafluvial (n=1) and orthofluvial (n=3) types. In 2005 we used a more balanced design that separated springbrook types. We chose 3 new orthofluvial springbrook sites that were similar in size, retained one overlapping orthofluvial springbrook site from 1997, and selected 4 new parafluvial springbrook sites. We were unable to sample the 1 parafluvial springbrook site from 1997 as it had filled in with a large deposit of fine sediments which blocked most surface flows by 2005. The 1997 sites each covered an area 15 m long by 5 m wide; 2005 site area varied from 2-3 m long and 1-5 m wide.

Data Sources and Processing

Hydrologic Disturbance –Temporal measures of flood disturbance duration, frequency and predictability were constructed for the entire floodplain using USGS gauging station records. We assembled a continuous 10-year hydrograph and calculated number of days per year above 1-year recurrence (105 m^3/sec) and 2-3 year recurrence bankfull flood flows (405 m^3/sec) (Figure 3). Peak flow discharge for the season and time in weeks past the bankfull disturbance threshold were obtained from mean daily average discharge records for USGS gauging station #12358500 located 11 km downstream at West Glacier.

It is less straightforward to measure cumulative disturbance effects across a range of floodplain habitats. Minimum critical flows for disturbance of periphyton located in parafluvial zones are expected to be found when local shear stress becomes elevated (Biggs and Thomsen 1995) and fine sediments are in transport (Fisher et al. 1982, Grimm and Fisher 1989), producing physical abrasion and sediment deposition on existing biofilms. Physiological stress in aquatic organisms is known to increase with both concentration and duration of sediment exposure (Newcombe and MacDonald 1991). Transport of fine-grained material is expected to occur at and above the bankfull flows which produce sustained transport of gravel and cobble bedload (Lorang and Hauer 2003).

We developed a quantitative approach to modeling hydrologic disturbance across different floodplain habitats based on boundary shear stress equations. Boundary shear stress (a measure of disturbance potential) is calculated using depth and velocity derived from hyperspectral imagery. Boundary shear stress was used to calculate daily stream power, and from that energy. This allows us to create a cumulative energy curve for each site, a visual representation of disturbance potential over time. An equation used to calculate boundary shear stress (ζ_b) was obtained from M. Lorang (personal communication):

$$\zeta_b = 1000 * \frac{V}{(8.84 * (5.76 *(\log_{10}*((0.6 * D)/0.4)))^2}$$

where V is the water velocity (m sec^{-2}) and D is the water depth (meters). Stream power was then calculated as:

$$P=\zeta*V$$

Energy is power multiplied by time from which we estimated total energy per day over the time period of this study. Estimates of stream depth and velocity were derived from classified airborne hyperspectral imagery, high resolution satellite imagery, and a LiDAR based digital elevation model in conjunction with ground-truth water depth and velocity data collected in 2002-2005. Image processing and hydrologic and habitat classification methods are described in Lorang et al. (2005). In situ ground-truth measurements of site water depth and mean current velocity were collected using either a Gurly model 1210 (Price-type) mini current meter attached to a CMD 9000 (Digimeter-type) digitizer or handheld acoustic doppler velocity meter (ADV) at 60% total water depth. Using the imagery classification for the peak annual discharge flow, we selected a random sample of 10 pixels (1 m resolution) per sites, recorded the stream depth and velocity values for each pixel and averaged the 10 values to achieve a site average.

We obtained D_{mean} and D_{max} estimates at sites using either a modified Wolman pebble count (n=100 rocks/site, Wolman and Miller 1960) in 1997 or a photo-seive technique modified from Gee (1979) and Ibbeken and Schleyer (1986) in 2005. The photo-seive technique involves using 0.25 m^2 quadrat substrate photos taken in the field and processed in the lab with ImagePro Plus 4.5 program. Photo-seive methods of quantifying grain size work well for sediment > 0.001 m, provide more of a qualitative information on grain sizes < 10mm. At our site all substrate smaller than 0.001 m are generally silt/ sand and were assigned a d_{mean} = 0.0003 m and d_{max} = 0.001 m.

Water Chemistry – Surface water chemistry measurements were collected in study years to assess variation in vertical hydraulic gradient and nutrient availability in the 3 habitat types during pre- and post-flood periods. Temperature was continuously recorded at all sites using temp loggers (Vemco, Hobo®, Onset Computer Corporation, data loggers) from June-December 1997 and January-December 2005. A Hydrolab^{TM} Surveyor III, YSI^{TM} 55 DO, and Oakton^{TM} pH/Con 10 series meters were used to collect *in situ* measures of dissolved oxygen (DO, mg/L), temperature (^{o}C), pH, and specific conductance (SpCond, µS) during each sampling event. Surface water grab samples were collected every 3-6 weeks from July-November 1997 and Feb-August 2005. Water samples were collected in 1-L polyethylene bottles for overall water chemistry analysis and 500 ml borosilicate glass bottles preserved with 1 mL phosphoric acid for carbon analysis. An additional set of shallow hyporheic water samples were collected using either a drill-mounted peristaltic pump or a hand-operated bilge pump and stainless steel piezometers (Lee and Cherry 1978) at all sites in August of 1998 and at the headwater regions of springbrook sites in August of 2005. All water samples were transported on ice to for analysis at the Flathead Lake Biological Station Freshwater Research Laboratory (FLBS-FRL). Water samples were analyzed for soluble phosphorous (SP, ± 0.5-2.0 μg/L) and total phosphorous (TP, ± 0.5-2.0 μg/L) using an ammonium persulfate digestion (APHA 4500-P F 1998), soluble reactive phosphorous (SRP, ± 0.5-1.4 μg/L) using a molybdate SRP method (Murphy and Riley 1962), nitrate-nitrite (NO2+3-N, ± 0.4-0.8 μg/L) using a cadmium reduction method (Wood et al 1967), ammonia ($NH4^+$,± 0.5-2.0 μg/L) using an automated phenate method (Priscu and Carlton 1980), total persulfate nitrogen (TPN, ± 5-20 μg/L) using a potassium persulfate digestion (APHA 4500-N C 1998), and dissolved organic carbon (DOC, ± 0.4-1.0 mg/L) and particulate organic carbon (POC, ± 0.4-1.0 mg/L) using a heated persulfate digestion with acid liberation (1997) or heated persulfate oxidation (2005) both followed by infrared CO_2 detection (APHA 5310-C). Carbonate alkalinity (Alk, ± 0.4-0.8 mg/L) was assessed by colorometric titration (Dye 1958). Bioavailable atomic N:P was calculated using nitrate and SRP, parameters collected in both 1997 and 2005 (but see Dodds 2003b as to why SP might be preferable). Precision of the laboratory analyses was evaluated using duplicate samples. Overall QA/QC of FLBS-FRL performance was tested by running standard samples provided by the EPA every 6 months.

Groundwater Exchange – Vertical hydraulic gradient (VHG) was measured during sampling events as an index of a site's potential for surface-water-groundwater interactions. Methods of obtaining VHG are described in detail in Baxter et al (2003). We employed 2 types of mini-piezometers: 3-cm internal diameter steel and 1.59-cm internal diameter chlorinated polyvinyl chloride (CPVC). Each was constructed with 20-30 evenly spaced holes (0.7-cm or 0.238-cm diameter for steel and CPVC respectively) over the bottom 16-cm of the mini-piezometers' length. We used a sledge hammer to drive mini-piezometers 10-40 cm deep into the stream bed and allowed the water level to equilibrate for ~5 minutes (Baxter et al. 2003) before calculating VHG using the equation described in Dahm et al. (2006) as $VHG = (h_s - h_p) / L$, where h_s represents the height of the top of the mini-piezometer above stream surface; h_p is height from the top of the mini-piezometer to the water level inside the mini-piezometer; L is the depth the mini-piezometer was driven into the sediment from the substratum surface (Baxter and Hauer 2000). Positive VHG readings indicate the groundwater pressure head is greater than surface water pressure head while the situation is reversed for negative VHG readings. VHG indicates the potential for groundwater discharge into surface water ($^{+}$ VHG) or surface water recharge into the groundwater province ($^{-}$ VHG).

Periphyton - We quantified chlorophyll *a*, ash free dry mass (AFDM), carbon (C) and nitrogen (N) content of periphyton at sites in August-November 1997 and April, June, August and October 2005 for a total of over 500 samples. At each site, we randomly selected 9-10 cobbles from the stream and used a razor blade to scrape off all organic matter found on the top of each cobble within 4- cm^2 sample grids. One sample per rock was collected for chlorophyll *a* analysis, filtered onto glass fiber filters (Gelman and Whatman type GF/F, 47 mm diameter, 1 um pore size), placed inside a glass vial wrapped in aluminum foil, and frozen with dry ice in the field (Steinman and Lamberti 1996). A 2rd and 3rd scrape in 1997 or a separate rock scrape entirely in 2005 was collected and filtered onto pre-weighed glass fiber filter and frozen for AFDM and C:N content. In 2005 a subset of additional samples was collected in August for species identification. These samples were preserved in the field with either a 4% formaldehyde solution or Lugol's iodine. These samples complemented an existing study of algal diversity in main channels upwelling and downwelling habitats (Wyatt et al. 2008).

Samples were taken back to FLBS-FRL for analysis. Chlorophyll *a* and phaeophyton samples were processed using a 90% acetone extraction (Marker et al 1980) and analyzed with a Perkin Elmer 559 Uv-Vis Spectrophotometer (Tett 1975). AFDM and C, N content samples were oven dried at 80 ^{o}C for 24-48 hours, then cooled in a dessicator for at least 1 hour and subsequently weighed to 0.0001 g. Samples were then ashed at 500 ^{o}C for 4 hours, rewet, redried, and reweighed (Valettt et al 1994, Steinman and Lamberti 1996). C and N content was quantified at FLBS-FRL in 1997 using a Fissons Instruments NA 1500 and in 2005 analysis by D. Harris at the University of California-Davis Stable Isotope Lab.

Preserved algal species composition samples were homogenized with a blender and a 0.1-mL aliquot of the homogenized sample was pipetted into a Palmer-Maloney nanoplankton-counting chamber from which Whipple grid fields were identified using Wehr and Sheath (2003) and counted until 300 cells were enumerated (Lowe and Laliberte 1996, Biggs and Kilroy 2000). In the instances where filaments had very fine cells that were difficult to discern, the number of 10-μm long units was counted (Biggs and Kilroy 2000). Benthic algae were enumerated as cells/cm^2 of substrata using the formula provided in Lowe and Laliberte (1996) and relative biovolume of taxa per sample was assessed.

Nutrient diffusion experiments – Using methods similar to Bernhardt and Likens (2004), nutrient diffusion substrates (NDS, Fairchild et al 1985) were used to test the effects of different nutrient amendments on algal biomass across habitats in July-August 2005. Sites included one main channel site, two parafluvial springbrook sites and one orthofluvial springbrook site. 80 clay pots were assigned in blocks of 30 to one of the following four treatments: N (1 M NO_{3-} in purified agar), P (0.1 M PO_4^{3-} in purified agar), N+P (1 M NO_{3-} and 0.1 M PO_4^{3-} in purified agar), and a control (purified agar). Each pot was filled with agar treatment, allowed to cool and sealed with a 4x4- inch^2 plexiglass tile sealed to the top of the pot with aquarium sealant. All four treatments were deployed on July 15th, 2005 in 5 replicate blocks at each site for a total of five NDS per treatment per site at 4 sites. NDS were retrieved from all sites on August 3rd, 2005, placed in individually labeled Ziploc bags and transported back to FLBS-FRL on ice. The NDS surface was scrubbed and washed to obtain a chlorophyll *a* sample which was subsequently processed using a 90% acetone (Marker et al 1980) extraction and analyzed with a Perkin Elmer 559 Uv-Vis Spectrophotometer as outlined above. In order to assess the degree to which periphyton growing on NDS treatments were N limited without regard to the confounding effects of P, and vice versa, nutrient deficiency was calculated for each site as modified after Dodds et al (2004), given by N deficiency = $(B_{n+p} – B_p)/B_{control}$ and, P deficiency = $(B_{n+p} – B_n)/B_{control}$, where B_{n+p} =mean biomass in N+P diffusion treatments, B_p =mean biomass in P diffusion treatments, B_n =mean biomass in N diffusion treatments and $B_{control}$ =biomass in control treatments.

Data Analysis

Due to variation in data collection across sample events and years, a statistical comparisons of year to year or habitat specific comparisons within the 1997 data proved difficult. Instead we focused on the balanced data from 2005 (n=4 for all site types and variables) for all parametric analyses. We used a combination of one-way ANOVA with Tukey's HSD post-hoc tests, Kruskall-Wallis (Kruskall and Wallace 1952) and Wilcoxon Mann-Whitney tests to compare water chemistry and periphyton variables between site types in August 2005. We focused the analyses on data collected in August during the 2nd post-flood sampling period as this coincided with the peak growing season for algae and the period in which stress from temperature and dissolved oxygen variation coupled with nutrient limitation are suspected to be most severe for periphyton. The variables TP, chlorophyll *a* and C:N were $\log_{10}$ transformed to meet assumptions of parametric tests. Temperature, dissolved organic carbon (DOC), nitrate-nitrite (NO2/3) and vertical hydraulic gradient all had significant departures from parametric test assumptions of normality or equality of variance that could not be corrected using transformations. We analyzed these variables using the Kruskall-Wallis test. Variables judged to be significant ($P < 0.05$) in the Kruskall-Wallis test were then compared pairwise using Wilcoxon Mann-Whitney tests to produce p-values for habitat type differences.

In order to address changes in periphyton over days post-flood (DPF) in different habitat types, we used a full factorial repeated measures ANOVA on all chlorophyll *a* data from 2005. Chlorophyll *a* was the only periphyton metric which met ANOVA assumptions of normality and equality of variance, following an *ln* (x+1) transformation of the data. An interaction term was added for type and DPF.

Exploration of the relationship between periphyton metrics and environmental variables was initiated using separate principal components analyses of data from August 1997 and 2005. Based in part on the results of this analysis, the non-parametric Mann-Whitney test was used to evaluate the relationship between chlorophyll *a* and VHG by habitat type in 2005. All statistical analyses were performed in SPSS vs. 12.02 except for the principal component analysis which was performed in S-PLUS 4.5.

RESULTS

Hydrologic Disturbance

Timing, magnitude and duration of disturbance differed greatly between 1997 and 2005 (Fig. 3). Bankfull flooding commenced at both sites in late April, coinciding with the beginning of spring snowmelt. Flooding peaked at 343 $m^3 s^{-1}$ and receded below bankfull in early July of 2005 while flood flows in 1997 peaked at 886 $m^3 s^{-1}$ and recession below bankfull did not occur until late July. In 1997 the floodplain experienced over 20 days of bankfull flooding while there was no bankfull flood event in 2005. A nearly equal number of days above the annual flood recurrence stage occurred in 1997 and 2005.

Modeled streamflow cumulative energy in 2005 revealed a similar curve of energy accumulation across habitats over the year, with all habitats accumulating most of their energy from May 1-September 1 (Fig. 4). Very different ranges of energy values were observed for different habitat types. Total energy accumulation in main channel sites ranged from 75 x 10^5 to 225 x 10^5 Joules, 2 to 20 times higher than cumulative energy values for either springbrook habitat type. Within springbrooks, total cumulative energy varied as much between sites as among the two springbrook types.

Spatial and Temporal Variation in Water Chemistry

Water chemistry varied across years, seasons, and habitat types during this study (Table 1). Specific conductivity, alkalinity, NO 2/3, TPN and N:P values were elevated across seasons and habitats in 2005 in comparison with 1997. Seasonal variation across habitats in both years revealed high temperatures in August coupled with low dissolved oxygen, while conductivity, alkalinity, DOC, SRP and TP all reached peak values in April through June, coinciding with the onset and duration of annual flooding. These trends were somewhat muted in the orthofluvial springbrooks. Annual variation in NO 2/3 and TPN cycled from a summer low to peak sometime between late fall and early spring.

In comparing habitat types, a gradient of high to low temperatures, dissolved oxygen values and DOC and low to high conductivity and alkalinity existed from the main channel to orthofluvial springbrooks. Parafluvial springbrook values for most variables fell between the extremes except for nitrogen and phosphorous related measures. NO 2/3, TPN and N:P were similarly low and SRP values similarly high in both springbrook types.

Periphyton Production

In both years periphyton biomass measures of chlorophyll *a* and AFDM were at their lowest across habitats 9-16 days post-flood (DPF), with the most pronounced decreases at parafluvial springbrook and main channel sites in 1997 (Fig. 5, 6). Biomass in general was lower across habitats in 1997 than in 2005. In 2005 biomass returning or exceeded pre-disturbance levels by 99 to 123 DPF. Across habitat types in both years, periphyton biomass was maximum across DPF at orthofluvial sites and similar between main channel and parafluvial springbrook sites until 3-4 months after flooding. Chlorophyll *a* in parafluvial springbrooks at this point overtook shallow shoreline biomass, peaking at 99 to 123 DPF in both years while main channel values peaked in 51 to 57 DPF in 2005 and 101 to 103 DPF in 1997. AFDM patterns were similar except for 99 to 123 DPF in 2005, when shallow shoreline AFDM was higher than in the parafluvial springbrook. C:N values for shallow shorelines and parafluvial springbrooks were similar across DPF and years (Fig. 7). It appears that the increased flood flows in 1997 may have had an effect on orthofluvial springbrook C:N as evidenced by higher values across DPF in 2005.

Results of the ANOVA indicated that type ($p = 0.001$), DPF ($p < 0.001$) and the type x DPF interaction ($p < 0.001$) were all highly significant in relation to chlorophyll *a* values (Table 2). Post-hoc tests indicated that contrasts between site types were all significant, with main channel versus parafluvial springbrooks ($p = 0.001$) and main channel versus orthofluvial springbrooks ($p = 0.018$) being a more significant differences than between the two springbrook types ($p = 0.11$).

We explored the relationship between VHG and algal biomass in greater depth across years and using just the 2005 data (Fig. 8). A large degree of scatter in the VHG to chlorophyll *a* relationship at springbrook sites made the role of VHG in these environments unclear. We were able to show a significant correlation between $^+$VHG and chlorophyll *a* at main channel sites (Mann Whitney test, P=0.01).

Nutrients and Periphyton

Chlorophyll *a* concentrations on the control nutrient diffusion substates were not different than ambient chlorophyll *a* found on instream rocks. The N+P treatment had the greatest effect on chlorophyll *a* across habitats, with the largest increase over the control occurring at the orthofluvial site (Figure 9). The P treatment appeared to have a greater effect on chlorophyll *a* than N alone. Deficiency in N and P were highest in the main channel and lowest in parafluvial springbrooks.

Periphyton and Environmental Covariates

One-way ANOVA and Wilcoxon-Mann-Whitney tests indicated differences existed between main channel sites and springbrooks while no such differences existed between springbrooks (Table 3). Main channel sites had higher temperatures, dissolved oxygen, and ph as well as lower specific conductivity, and alkalinity than parafluvial springbrooks. The contrast between main channel and orthofluvial springbrook sites revealed the same pattern with an additional difference in mean negative VHG values in the main channel versus positive VHG values ($p = 0.057$) and higher C: N values in the orthofluvial springbrook ($p = 0.031$).

The PCA analysis revealed distinct patterns of association for August 1997 and 2005, although both held only weak associations across the data set (Table 4, Figure 10). In 1997 the first 4 principle components explained a large degree of variation inherent in the data (92%), with most being explained by the 1st (47%) and 2nd (25%) principle components. We interpret principle component 1 to represent springbrook sites due to the positive values for specific conductivity, alkalinity, DOC, SRP, VHG and periphyton metrics and negative values for velocity, depth, mean course sediment grain size (D_{50}), temperature, pH, TP, TPN and N: P. This is consist with general trends in water chemistry, periphyton metrics, and disturbance in springbrook environments previously mentioned. We interpreted component 2 to be the algal response to the main channel environment, with a positive association between algal metrics and the higher water velocities, dissolved oxygen, NO 2/3, TPN, D_{50}, and DOC found in the main channel and negatively associated with the higher SRP values, lower temperatures and less depth found in springbrook environments.

In 2005 the PCA analysis revealed similar patterns to 1997, but weaker trends as it took 5 principle components to explain 87% of the total variation. Principle component 1 comprised 29% of total variation and is again seen to represent springbrook sites, with positive values for C: N, VHG, alkalinity and specific conductivity opposed by negative values for depth, temperature, dissolved oxygen, pH and N: P. This also remained consist with general trends in water chemistry, periphyton metrics, and disturbance previously mentioned. We interpreted principle component 2, with 22% of the variation, to be environmental variables we suspect are correlated with periphyton chlorophyll *a* and AFDM across site types, including positive associations with the NO2/3, N: P and SRP and a negative relationship to TP, DOC, water velocity, D_{50} and temperature. Component 3 mainly shows the strong association between nitrogen (TPN) and periphyton C: N ratios. Components 4 and 5 respectively associate sediment grain size positively with N: P or DOC and negatively with SRP values, the importance of which remains unclear.

Algal Community Composition

We identified 39 genera of algae from samples taken in 2004-2005 (Figure 11, Appendix 1). Average sample taxa richness was high at parafluvial springbrook (9.5±3.4), main channel $^-$ VHG (9.3±2.6), and orthofluvial springbrook (8.5±4.0) sites while main channel $^+$ VHG sites (6.5±3.2) average sample richness was much lower. In contrast, $^+$VHG main channel sites had the highest overall taxa species richness observed (24), followed by $^-$VHG main channel (23), parafluvial springbrook (21) and orthofluvial springbrook (17) sites.

Samples were characterized primarily by diatoms (Bacillariophyceae), which comprised 58% of algal biovolume at shallow shoreline sites, 86% at parafluvial springbrook sites and 67% at orthofluvial sites. Diatom relative abundance varied greatly in relation to VHG at shallow shoreline sites, composing 93% of algal biovolume at $^-$ VHG sites as opposed to only 22% at $^+$VHG sites. *Hydrurus foetidus* (Vauch.) Kirchn. (Chrysophyceae) represented more than 8% of the relative abundance of algal cells collected at $^+$VHG sites while representing only a minor or missing component of assemblages in the other habitat types.

Chlorophyceae (*Mougeotia* sp., *Pediastrum* sp., *Scenedesmus* sp., *Spirogyra* sp., *Stigeoclonium* sp., *Zygnema* sp.) comprised 70% of the relative abundance of algal cells at $^{+}$VHG main channel sites and 6%, 11% and 16% at $^{-}$VHG main channel, parafluvial springbrook and orthofluvial springbrook sites respectfully. Cyanophyceae (*Lyngbya* sp., *Merismopedia* sp., *Plectonema* sp., *Phormidium* sp.) represent a minor component of the total assemblage at $^{-}$VHG main channel (<1%), $^{+}$VHG main channel (<1%) and parafluvial springbrook (3%) sites, but were more common at orthofluvial springbrook sites (14%).

Sites varied in the architecture of algal development on substrate. Main channel samples and parafluvial springbrook samples were structurally simple and most often occurred as thin biofilms on the surface of rocks. Orthofluvial springbrook samples in contrast were structurally diverse, with samples varying from patches of algal filaments to diatom films to “old growth” cructose accumulations.

DISCUSSION

Periphyton and disturbance

Annual periphyton biomass peaked in all habitats and years at 3 to 4 months post-flood, followed by a late season decline. Across the successional landscape biomass was minimal throughout the season in higher disturbance main channel habitats while biomass was greatest in lower disturbance orthofluvial springbrook habitats. Biomass reached a similar high level for both springbrook types by late season in 2005 following a small flood, but values remained disparate during 1997 after higher flows. These results matched model expectations generally but it is apparent that disturbance may have a greater impact on parafluvial springbrook habitats than previously considered or than we measured. What is curious is the cumulative energy model indicates little variation in disturbance for parafluvial versus orthofluvial springbrooks. We suggest the disparity may be in part due to the models ability to detect gross differences like those between the main channel and springbrook sites but poor model performance across finer scale variation. The data is also based on passive remote sensing tools that have less ability to accurately model tree-covered habitats due to the effects of shadows.

In 2005 we were able to compare pre-flood and post-flood recovery of periphyton biomass. All habitat types exhibited resilience, recovering or exceeding pre-flood biomass within 2-4 months after flood recession. This was not surprising as floodplain biotic communities are expected to follow a homeorhesis pattern and return to a pre-disturbance trajectory following flood perturbation (O'Neill et al. 1986, Arscott et al. 2002). Habitats were unequally resistant to flood scour, with lower resistance to periphyton biomass loss in the parafluvial springbrooks than orthofluvial springbrooks. Shallow shoreline values were already low before the flood period. Main channel algal communities presumably go into the flood season having been covered over the winter by ice (Anderson et al. in prep), which may cause the low main channel biomass values observed prior to flooding.

This raises the point that temperature as a disturbance factor may play an important role in structuring periphyton communities (Phinney and McIntire 1965, Power et al. 1988, Tockner et al. 2000) that was beyond the scope of this study to consider. Temperature mean and variation together can influence periphyton production in dynamic ways (Beyers and Odum 1993). Springbrook temperatures during most of the years were below the optimal range for photosynthesis of many common algal species

(Mosser and Brock 1976, Anderson in prep), yet production remained high. In the winter springbrooks remained stable at the low end of photosynthetic capacity while the habitat remained ice free. This may have allowed algae to support low levels of overwinter production or achieve a state of dormancy without full senescence that provides a competitive advantage come spring. During the same period main channel habitats are alternately much warmer in the summer and ice covered in winter, reducing light available to algae and creating physical disturbance with anchor ice formation and ice break-up in the spring.

Periphyton and nutrients

We established landscape level patterns of variation in inorganic chemical constituents of the water but less conclusive results for limiting nutrient spatial distribution. Nutrient concentrations were lower in the main channel and higher in springbrook habitat types in the high flow year, but this trend persisted only for SRP and DIC in the low flow year. There was no distinct pattern of difference in nutrients between the parafluvial and orthofluvial springbrooks, undercutting any clear understanding of mechanisms of algal-nutrient interactions. The higher nitrogen concentrations observed across habitats in 2005 may be indicative of long term trends of nitrogen increase in basin (Ellis 2006), or could simply be “noise” attributable to limited sampling. Either source of variation could be confounding our analysis of flood disturbance in relation to nutrient dynamics.

We expected minimal variation in the spatial distribution of algal nutrient concentrations and life history characteristics related to nutrient preference due to the lack of clear spatial differences in ambient water nutrient availability. N and P are low at Nyack in comparison to other well studied sites such as Sycamore Creek in Arizona (Coleman and Dahm 1990, Grimm and Fisher 1986) and Walker Branch in Oak Ridge, Tennessee (Hill et al. 1998), particular in relation to P concentrations (Fisher et al. 1982). We anticipated system wide low nutrient availability to induce chronic stress on algal communities. We did find evidence that P could be limiting at all sites in the widespread distribution of algae well-adapted to uptake of phosphorous such as *Stigeoclonium* sp., (Chessman at al. 1992) and *Acnanthidium* sp. (Fairchild et al. 1985) or algae typically exhibiting high N:P ratios such as *Navicula*, *Cocconeis*, and *Gomphonema* (Bradbury and Winter 1976, Rhee and Gotham 1980, Pringle 1990). The strength of the response to P and N+P additions in the NDS treatments further demonstrated nutrient limitation across habitats at Nyack.

Instead of low variation in algal nutrients we observed high C:N and responsiveness to nutrient amendment treatments in orthofluvial springbrook environments, low N and P nutrient deficiency of algae in parafluvial springbrook sites and a strong association between chlorophyll *a* and $^+$ VHG in the main channel. We also found green and blue-green algal species more frequently, and in greater abundance, at sites with $^+$ VHG. *Stigeoclonium*, a disturbance (Biggs 1996) and nutrient specialist (Kingston 2003), comprised over 50% of the biovolume at $^+$ VHG main channel sites. Many blue-green algae such as *Plectonema* sp. are capable of nitrogen fixation (Misra and Tuli 2000).

It appears that the response of algae to ambient nutrient availability in disturbed environments is more complex than we originally envisioned as has been the case in other systems (Dodds et al. 2002). Localized differences in water chemistry may well exist and we expect these differences to be driven by interactions between hyporheic and surface waters at the bed sediment-stream water interface on the scale of centimeters to meters. We agree with Pringle (1987, 1990) assessment that low nutrient systems exhibit a strong relationship between algal community composition and spatial heterogeneity of nutrients. Nutrient enrichment of hyporheic waters has been well documented in the literature (Grimm and Fisher 1984, Valett et al. 1993, 1994, Holmes et al. 1994, 1996, Dahm et al. 1998). In addition VHG seems to exhibit strong seasonal variation in the magnitude and direction of exchange (Valett et al. 1994, Bansak 1998) which may control the timing and rate of delivery of nutrients to algae at localized scales. The major interface for nutrient flux may be over very small spatial scales at the sediment-water interface (Triska et al 1989, Coleman and Dahm 1990, Jones and Holmes 1996, Dodds et al. 2003a, Hagerthy and Kerfoot 2005). In order to determine more precisely the response of algae to nutrient concentrations, a more spatial explicit sampling design at much smaller spatial scales may be necessary.

There is a need for greater understanding of hyporheic and streambed surface bacterial community structure and function in relation to nutrient conversion and delivery to surface waters (Romani and Sabater 2001, Kreutzweiser and Capell 2003). This should include whole stream metabolism studies that account for groundwater inputs (Hall and Tank 2005). Novel approaches to investigating flux and establishment of algal propagules moving between habitat patches would enhance our understanding of disturbance effects on dispersal and recruitment (Dial and Roughgarden 1998). Finally, we need to look across river systems at a broad range of N, P availability and flood regimes to look for divergence from model predictions as the interaction between nutrients, disturbance, biomass and diversity is almost certainly non-linear and multi-modal (Roxburgh et al. 2004, Biggs and Smith 2002).

Periphyton diversity

Habitat specific average species richness corresponded to model predictions of higher diversity in intermediate disturbance springbrook habitats if main channel sites are considered as a single group (S' = 7.9). However, average sample species richness was high in –VHG main channel sites when considered separately from +VHG sites. These –VHG sites also had a higher abundance of flood resistant diatoms (Peterson 1987) and far less dominance by green and blue-green algae than +VHG sites. We attribute this difference to competitive exclusion of taxa at the +VHG sites, likely through dominance by strong competitors for space and nutrient resources.

Total taxa richness showed an unexpected response, peaking in the high disturbance habitats and displaying lowest taxa richness in low disturbance habitats. This however was most likely an artifact of sample design as we analyzed more samples from high disturbance habitats and subsequently were more likely to pick up rare or unevenly distributed species.

CONCLUSIONS

This study 1) highlights the degree of spatial and temporal variability in water chemistry and periphyton communities across floodplain habitats in relation to flood disturbance and 2) provides preliminary evidence for a model of periphyton biomass and diversity in alluvial floodplain ecosystems. We conclude that in low nutrient, high disturbance floodplain ecosystems periphyton community structure is continually reshaped by spatial and temporal variation in the annual flood disturbance cycle.

We hypothesize that periphyton populations are secondarily shaped by nutrient interactions at localized spatial scales which may persist over long time periods in more stable habitats. This pattern fits existing work illustrating an interaction between disturbance and nutrients in which more nutrient enriched sites lose less chlorophyll *a* and AFDM following spates (Biggs and Thomsen 1998). P limitation in the disturbed main channel areas may be exacerbated by decreased P uptake due to higher water velocities (Borchardt et al. 1994). The high ratios of C:N found in orthofluvial springbrooks indicates buildup of a thick, older biofilm and detritus (Dodds et al. 2002). Dense cructose algal layers were commonly observed at these sites in the field. In turn these developed biofilms are more proficient at internal cycling of nutrients (Hansonn 1989, Petersen and Grimm 1992) and are more photosynthetically efficient in low velocity habitats (Biggs and Thomsen 1995). Recycling can compensate for low nutrient levels when enough biomass has accrued (Mullholland et al. 1991 a, b, Steinman 1995), especially in the case of cructose algal forms which favor uptake of CO_2 and inorganic P (Raven 1992). Fungal activity in springbrook systems has also been associated with high N, P concentrations in the biofilm community, especially in connection with detritus (Elwood et al. 1991, Newbold et al. 1983, Mulholland et al. 1995, Robinson et al. 2000).

Whether we understand the mechanisms driving algal community structure or not, we can readily observe that the variety of habitats found in an unmodified flood plain adds to overall system aquatic primary productivity, diversity, and stability. Stevenson

(1997) proposed this same pattern as an emergent property of aquatic habitat heterogeneity. Loss of lateral habitats, as we often see in regulated river systems, could in this system result in a 25% reduction in total algal taxa richness and a 60-75% loss of total system algal biomass if response to habitat loss was linear (based on an estimate of 20% of total aquatic area classified as springbrook at baseflow, D. Whited personal communication). Studies that build on existing work such as this are critical to our understanding of disturbance and nutrient cycling in floodplain river regulation and restoration (Tockner and Stanford 2002, Lefebvre et al 2004).

LITERATURE CITED

APHA. 1998. Standard Methods for the Examination of Water and Wastewater, 20th Edition. American Public Health Association, Washington, D.C.

Anderson, M. A. 2008. Chapter 2: Thermal variability and the phenology of aquatic organisms on an alluvial flood plain.

Arscott, D. B., K. Tockner, and J. V. Ward. 2002. Aquatic habitat dynamics along a braided Alpine river ecosystem (Tagliamento River, N.E. Italy). Ecosystems **5**: 802–814.

Arscott, D. B., K. Tockner, and J. V. Ward. 2005. Lateral organization of aquatic invertebrates along the cooridor of a braided floodplain river. Journal of the North American Benthological Society **24**: 934-954.

Bansak, T. S. 1998. The influence of vertical hydraulic exchange on habitat heterogeneity and surficial primary production on a large alluvial flood plain of the Middle Fork Flathead River. M. S. Thesis. University of Montana, Missoula, Montana.

Baxter, C. V., F. R. Hauer, and W. W. Woessner. 2003. New techniques for installing piezometers, estimating hydraulic conductivity and detecting patterns in groundwater-stream water exchange. Transactions of the American Fisheries Society **132**: 493-502.

Bernhardt, E. S. and G. E. Likens. 2004. Controls on periphyton biomass in heterotophic streams. Freshwater Biology **49**: 14-27.

Biggs, B. J. F. 1996. Patterns in benthic algae of streams. Pages 31-56 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). Algal ecology- freshwater benthic ecosystems. Academic Press, San Diego, California.

Biggs, B. J. F. and H. A. Thomsen. 1995. Disturbance of stream periphyton by perturbations in shear stress: time to structural failure and differences in community resistance. Journal of Phycology **31**: 233-241.

Biggs, B. J. F., and C. Kilroy. 2000. Stream periphyton monitoring manual. NIWA, Christchurch, New Zealand.

Biggs, B. J. F., and R. A. Smith. 2002. Taxonomic richness of steam benthic algae: Effects of flood disturbance and nutrients. Limnology and Oceanography **47**: 1175-1186.

Bormann, F. H. and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Borchardt, M. A., J. P. Hoffman, and P. W. Cook. 1994. Phosphorous uptake kinetics of *Spirogyra fluviatilis* (Charophyceae) in flowing water. Journal of Phycology **30**: 403-417.

Bothwell, M. L. 1988. Growth rate responses of lotic periphytic diatoms to experimental phosphorus enrichment. Candian Journal of Fisheries and Aquatic Sciences **45**: 261-270.

Bradbury, J. P., and T. C. Winter. 1976. Areal distribution and stratigraphy of diatoms in the sediments of Lake Sallie, Minnesota. Ecology **57**: 1005-1014.

Beyers, R. J. and H. T. Odum. 1993. Ecological Microcosms. Springer-Verlag, New York.

Chessman, B., I. Growns, J. Curreys, and N. Plunkett-Cole. 1999. Predicting diatom communities at the genus level for the rapid biological assessment of rivers. Freshwater Biology **41**: 317-331.

Clausen, B., and B. J. F. Biggs. 1997. Relationships between benthic biota and hydrological indices in New Zealand streams. Freshwater Biology **38**: 327-342.

Coleman, R. L. and C. N. Dahm. 1990. Stream geomorphology: effects on periphyton standing crop and primary production. Journal of the North American Benthological Society **9**: 293-302.

Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior and its development. Botanical Gazette, **15**: 1-44, 115-40, 189-235.

Craft, J. A., J. A. Stanford, and M. Pusch. 2002. Microbial respiration within a floodplain aquifer of a large gravel-bed river. Freshwater Biology **47**: 251-261.

Dahm, C. N., N. B. Grimm, P. Marmonier, H. M. Valett and P. Vervier. 1998. Nutrient dynamics at interface between surface water and groundwaters. Freshwater Biology **40**: 427-452.

Dahm, C. N., H. M. Valett, C. V. Baxter, and W. W. Woessner. 2006. Hyporheic zones. Pages 000-000. in F. R. Hauer and G. A. Lamberti (editors) 2nd edition. Methods in stream ecology. Academic Press. San Diego, California.

Dial, R. and J. Roughgarden. 1998. Theory of marine communities: The intermediate disturbance hypothesis. Ecology **79**: 1412-1424.

Dodds, W. K. 2003a. The role of periphyton in phosphorous retention in shallow freshwater aquatic systems. Journal of Phycology **39**: 840-849.

Diehl, J. C. 2004. Controls on the magnitude and location of groundwater / surface water exchange in a gravel dominated alluvial floodplain system, northwestern Montana. Master's Thesis. University of Montana, Missoula, 52 p.

Dodds, W. K. 2003b. Misuse of inorganic N and soluble reactive P concentrations to indicate nutrient status of surface waters. Journal of the North American Benthological Society **22**: 171-181.

Dodds, W.K., V. H. Smith, and K. Lohman. 2002. Nitrogen and phosphorous relationships to benthic algal biomass in temperate streams. Canadian Journal of Fisheries and Aquatic Sciences **59**: 865-874.

Dye, J. F. 1958. Correlation of two principle methods of calculating the three forms of alkalinity. Journal of the American Water Works Association **50**: 812.

Ellis, B. K., J. A. Stanford, and J. V. Ward. 1998. Microbial assemblages and production in alluvial aquifers of the Flathead River, Montana, USA. Journal of the North American Benthological Society **17**: 382-402.

Ellis, B. K. 2006. Alternate states in a large oligotrophic lake: A restrospective analysis of nutrient loading and food web change. Dissertation, University of Montana, Missoula, Montana.

Elwood, J. W., J. D. Newbold, A. F. Trimble and R. W. Stark. 1991. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. Ecology **62**: 146-158.

Fairchild, G. W., R. L. Lowe, and W. T. Richardson. 1985. Algal periphyton growth on nutrient-diffusing substrates: an in situ bioassay. Ecology **66**: 465-472.

Fisher, S. G., L. J. Gray, N. B. Grimm, D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecological Monographs **52**: 93-110.

Gee, J. H. R. 1979. A comparison of gravimetric and photographic methods of stream substrate analysis in a study of benthos microdistribution. Oikos **33**: 74-79.

Grimm, N. B. and S. G. Fisher. 1984. Exchange between surface and interstitial water: Implications for stream metabolism and nutrient cycling. Hydrobiologia **111**: 219-228.

Grimm, N. B. and S. G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. Journal of the North American Benthological Society **8**: 293-307.

Grimm, N. B. and S. G. Fisher. 1986. Nitrogen limitation in a Sonoran Desert stream. Journal of the North American Benthological Society **5**: 2-15.

Hagerthy, S. E. and W. C. Kerfoot. 2005. Spatial variation in groundwater-related supply influences freshwater benthic algal assemblage composition. Journal of the North American Benthological Society **24**: 807-819.

Hall, R. O. and J. L. Tank. 2005. Correcting whole-stream estimates of metabolism for groundwater input. Limnology and Oceanography Methods **3**: 222-229.

Hansson, L. 1989. The influence of a periphytic biolayer on phosphorus exchange between substrate and water. Archiv fur Hydrobiologie **115**: 21-26.

Hauer, F. R., D. B. Fagre, and J. A. Stanford. 2002. Hydrologic processes and nutrient dynamics in a pristine mountain catchment. Verhandlungen der Internationalen Vereingung fur theoretische und angewandte Limnologie **28**: 1490-1493.

Hauer, F. R., C. N. Dahm, G. A. Lamberti and J. A. Stanford. 2003. Landscape and ecological variability of rivers in North America: Factors affecting restoration strategies, Chapter 4 in Strategies for restoring river ecosystems: sources of variability and uncertainty in natural and managed systems, pp. 81-105.

Hill, A.R., Labadia, C.F., and Sanmugadas, K. 1998. Hyporheic zone hydrology and nitrate dynamics in relation to the streambed topography of a N-rich stream. Biogeochemistry **42**: 285–310.

Holmes, R. M., S. G. Fisher and N. B. Grimm. 1994. Parafluvial nitrogen dynamics in a desert stream ecosystem. Journal of the North American Benthological Society **13**: 468-478.

Ibbeken, H. and R. Schleyer. 1986. Photo-seiving: a method for grain-size analysis of course grained, unconsolidated bedding surface. Earth Surface Processes and Landforms **11**: 59-77.

Johnson, A.N. 2003. Preliminary hydrogeological and ground penetrating radar investigation of preferential flow zones in a gravel-dominated floodplain, northwest Montana. Master's Thesis. University of Montana, Missoula, 131p.

Jones, J.B., and Holmes, R.M. 1996. Surface–subsurface interactions in stream ecosystems. Trends in Ecology and Evolution **11**: 239–242.

Junk, W. J., P. B. Bayley and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Pages 110-127 in D. P. Dodge (editor). Proceedings of the International Large River Symposium. Canadian Special Publications in Fisheries and Aquatic Sciences **106**: 110-127.

Kingston, J. C. 2003. Araphid and monoraphid diatoms. Pages 595-636 in J. D. Wehr and R. G. Sheath (editors). Freshwater algae of North America: ecology and classification. Academic Press, New York, New York.

Kreutzweizer, D. P. and S. S. Capell. 2003. Benthic microbial utilization of different organic matter sources in a forest headwater steam. Canadian Journal of Forest Research. **33**: 1444-1451.

Kruskal, W. H., and W. A. Wallis. 1952. Use of ranks in one-criterion analysis of variance. Journal of the American Statistical Association **47**: 583-621.

Lee, D. R., and J. A. Cherry. 1978. A field exercise on groundwater flow using seepage meters and minipiezometers. Journal of Geological Education **27**: 6-10.

Lefebvre, S., P. Marmonier, and G. Pinay. 2004. Stream regulation and nitrogen dynamics in sediment interstices: comparison of natural and straightened sectors of a third-order stream. River Research and Applications **20**: 499–512.

Lorang, M. S., and F. R. Hauer. 2003. Flow competence and streambed stability: an evaluation of technique and application. Journal of the North American Benthological Society **22**: 475–491.

Lorang, M. S., D. C. Whited, F. R. Hauer, J. S. Kimball, and J. A. Stanford. 2005. Using airborne multispectral imagery to evaluate geomorphic work across floodplains of gravel-bed rivers. Ecological Applications **15**: 1209-1222.

Lowe, R. L., and G. D. Laliberte. 1996. Benthic stream algae: distribution and structure. Pages 269-293 in F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. Academic Press, San Diego, California.

Marker, A. F. H., C. A. Crowth, and R. J. M. Gunn. 1980. Methanol and acetone as solvents for estimating chlorophyll phaeopigments by spectrphotometry. Ergeb. Limno. **14**: 52-69.

Marti, E., N. B. Grimm, S. G. Fisher. 1997. Pre- and postflood efficiency of nitrogen in a Sonoran Desert stream. Journal of the North American Benthological Society **16**: 805-819.

Mosser, J. L. and T. D. Brock. 1976. Temperature optima for algae inhabiting cold mountain streams. Arctic and Alpine Research **8**: 111-14.

Mulholland, P. J. 1992. Regulation of nutrient concentrations in a temperate forest stream: roles of upland, riparian, and instream processes. Limnology and Oceanography **37**: 1512-1526.

Mulholland, P. J., E. R. Marzolf, S. P. Hendricks, and R. V. Wilkerson. 1995. Longitudinal patterns of nutrient cycling and periphyton characteristics in streams: a test of upstream-downstream linkage. Journal of the North American Benthological Society **14**: 357-370.

Mulholland, P. J., A. J. Steinman, A. V. Palumbo, J. W. Elwood, and D. B. Kirschtel. 1991a. Role of nutrient cycling and herbivory in regulating periphyton communities in laboratory streams. Ecology **72**: 966-982.

Mulholland, P. J., A. J. Steinman, A. V. Palumbo, D. L. DeAngelis, and T. E. Flum. 1991b. Influence of nutrients and grazing on the response of stream periphyton communities to a scour disturbance. Journal of the North American Benthological Society **10**: 127-142.

Murphey, J. and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta **27**: 31-36.

Newbold, J. D., J. W. Elwood, R. V. O’Neill and A. L. Sheldon. 1983. Phosphorous dynamics in a woodland: a study of nutrient spiraling. Ecology **64**: 1249-1265.

Newcombe, C. P. and D. D. MacDonald. 1991. Effects of suspended sediments on aquatic ecosystems. North American Journal of Fisheries Management. **11**: 72-82.

O'Neill, R.V. D. L. DeAngelis, J. B. Waide, and T. F. S. Allen. 1986. A hierarchical concept of ecosystems. Princeton (NJ): Princeton University Press. 154 p.

Ortiz-Zayas, J. R., W. H. Lewis, Jr., J. F. Saunders, III, and J. H. McCutchan, Jr. 2005. Metabolism of a tropical rainforest stream. Journal of the North American Benthological Society **24**: 769-783.

Pepin, D. M. and F. R. Hauer. 2002. Benthic responses to groundwater-surface water exchange in 2 alluvial rivers in northwestern Montana. Journal of the North American Benthological Society **21**: 370-383.

Peterson, C. G. 1987. Influences of flow regime on the development and dessication response of lotic diatoms. Ecology **68**: 946-954.

Petersen, C. G. and N. B. Grimm. 1992. Temporal variation in enrichment effects during periphyton succession in a nitrogen-limited desert stream ecosystem. Journal of the North American Benthological Society **11**: 20-36.

Phinney, H. K. and C. D. McIntire. 1965. Effect of temperature on metabolism of periphyton communities developed in laboratory streams. Limnology and Oceanography **10**: 341-344.

Power, M. E, and A. J. Stewart. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma Stream. American Midland Naturalist. **117**: 333-345.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner, and I. R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society **7**: 456–479.

Pringle, C. M. 1987. Effects of water and substratum nutrient supplies on lotic periphyton growth: an integrated bioassay. Canadien Journal of Fisheries and Aquatic Sciences **44**: 619-629.

Pringle, C. M. 1990. Nutrient spatial heterogeneity: effects on community structure, physiognomy, and diversity of stream algae. Ecology **71**: 905-920.

Priscu, J. and R. Carlton. 1980. A modified method for the determination of low levels of ammonia using a 10 mL sample size.

Raven, J. A. 1992. How benthic macroalgae cope with flowing freshwater: resource acquisition and retention. Journal of Phycology **28**: 133-146.

Rhee, G. Y., and I. J. Gotham. 1980. Optimum N:P ratios and the coexistence of planktonic algae. Journal of Phycology **16**: 486-489.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society **7**: 433–455.

Robinson, C. T., M. O. Gessner and J. V. Ward. 2000. Leaf breakdown and associated macroinvertebrates in alpine glacial streams. Freshwater Biology **40**: 215-228.

Romani, A. M. and S. Sabater. 2001. Structure and activity of rock and sand biofilms in a Mediterranean stream. Ecology **82**: 3232-3245.

Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. Ecology **85**: 359-371.

Snyder, E. B., C. T. Robinson, G. W. Minshall and S. R. Rushforth. 2002. Regional patterns of diatom assemblage structure in a heterogenous nutrient landscape. Canadian Journal of Fisheries and Aquatic Sciences **59**: 564-577.

S-PLUS 4.5. 1999. MathSoft, Inc., Cambridge, MA, USA.

SPSS for Windows, version 12.0.2. 2003. SPSS Inc., Chicago, IL, USA

Stanford, J. A. and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society **12**: 48-60.

Stanford, J. A., M. S. Lorang, and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. Verh. Internat. Verein. Limnol. **29**: 123–136.

Steinman, A. D., P. J. Mulholland and J. J. Beauchamp. 1995. Effects of biomass, light and grazing on phosphorous cycling in stream periphyton communities. Journal of the North American Benthological Society **14**: 371-381.

Steinman, A. D., and G. A. Lamberti. 1996. Biomass and pigments of benthic algae. Pages 295-313 in F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. Academic Press, San Diego, California.

Stevenson, J. R. 1997. Benthic algal community dynamics in a stream during and after a spate. Journal of the North American Benthological Society **9**: 277-288.

Tett, P., M. G. Kelly, and G. M. Hornberger. 1975. A method for the spectrophotometric measurement of chlorophyll *a* and pheophytin *a* in benthic microalgae. Journal of Limnology and Oceanography **20**: 887-896.

Tockner, K., M. Florian, and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes **14**: 2861–2883.

Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: present state and future trends. Environmental Conservation **29**: 308–330.

Triska, F. J., V. C. Kennedy, R. J. Avanzino, G. W. Zellweger and K. E. Bencala. 1989. Retention and transport of nutrients in a third-order stream in northwestern California: hyporheic processes. Ecology **70**: 1893-1905.

Uehlinger, U. 1991. Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). Archiv fur Hydrobiologie **123**: 219-237.

Valett, H. M., S. G. Fisher, N. B. Grimm, E. H. Stanley, and A. J. Boulton. 1993. Surface-hyporheic interactions in a Sonoran Desert stream: hydrologic exchange and diel periodicity. Hydrobiologia **259**: 133-144.

Valett, H. M., S. G. Fisher, N. B. Grimm, and P. Camill. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. Ecology 75:548-560.
van der Nat, D., K. Tockner, P. J. Edwards, J. V. Ward, and A. M. Gurnell. 2003. Habitat change in braided flood plains (Tagliamento, NE-Italy). Freshwater Biology **48**: 1799–1812.

Van der Nat, D., K. Tockner, P. J. Edwards, J. V. Ward, and A. M. Gurnell. 2003. Habitat change in the braided flood plains (Tagliemento, NE-Italy). Freshwater Biology **48**: 1799-1812.

Ward, J. V. and Palmer, M. A. 1994. Distribution patterns of interstitial freshwater meiofauna over a range of spatial scales, with emphasis on alluvial river-aquifer systems. Hydrobiologia **287**: 147-156.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology, **35**: 1-12.

Wellnitz, T., and R. B. Rader. 2003. Mechanisms influencing community composition and succession in mountain stream periphyton: interactions between scouring history, grazing, and irradiance. Journal of the North American Benthological Society **22**: 528-541.

Wehr, J. D., and R. G. Sheath (editors). 2003. Freshwater algae of North America: ecology and classification. Academic Press, New York, New York.

Whited, D. C., M. S. Lorang, M. J. Harner, F. R. Hauer, J. S. Kimball and J. A. Stanford. 2007. Climate, hydrologic disturbance and succession: drivers of floodplain pattern. Ecology (in press).

Wolman, M. G., and J. P. Miller. 1960. Magnitude and frequency of forces in geomorphic processes. J. Geology **68**: 54–74.

Wyatt, K. H., F. R. Hauer and G. F. Pessoney. 2008. Benthic algal response to hyporheic-surface water exchange in an alluvial river. Hydrobiologia **607**: 151-161

Table 1. Water chemistry variation among habitats in 1997 and 2005. Values are means (± SD) for main channel (n=5 in 1997, n=4 in 2005), parafluvial springbrook (n=1 in 1997, n=4 in 2005) and orthofluvial springbrook (n=3 in 1997, n=4 in 2005) sites.

				Main Channel			
Variable	Year	April	June	Aug.	Sept.	Oct.	Nov.
Temp	1997	-	8.32±0.21	12.79 ±0.35	10.50 ±0.18	6.36 ±0.15	2.25 ±0.16
(°C)	2005	5.98 ±0.98	7.20 ±0.26	16.16 ±2.07	-	7.22 ±0.93	-
DO	1997	-	-	9.22 ±0.12	10.09 ±0.17	11.41 ±0.33	11.91 ±0.16
(mg/L)	2005	11.42 ±0.21	10.71 ±0.03	9.15 ±0.25	-	11.58 ±0.34	-
pH	1997	-	-	8.35 ±0.02	8.30 ±0.02	8.35 ±0.01	8.32 ±0.03
(units)	2005	7.87 ±0.32	8.38 ±0.02	8.62 ±0.22	-	8.43 ±0.02	-
Sp. Cond.	1997	175 ±8	113 ±5	159 ±7	169 ±7	176 ±4	179 ±2
(μS)	2005	147 ±2	133.78 ±0.95	177 ±7	-	174 ±3	-
Alkalinity	1997	96.35 ±1.19	68.35 ±15.23	86.80 ±1.94	95.20 ±5.07	98.11 ±3.68	100.35 ±2.18
(mg/L-CaCO3)	2005	89.76 ±1.16	69.79 ±0.46	92.89 ±2.20	-	-	-
DOC	1997	1.12 ±0.56	2.21 ±0.71	1.64 ±1.29	1.45 ±095	1.89 ±0.93	0.70 ±0.11
(mg/L-C)	2005	1.11 ±0.34	1.41 ±0.02	1.00 ±1.00	-	-	-
SRP	1997	0.67 ±0.17	2.12 ±0.16	0.64 ±0.19	0.83 ±0.14	0.74 ±0.32	0.60 ±0.07
(μg/L-P)	2005	0.85 ±0.31	1.23 ±0.16	0.60 ±0.14	-	-	-
TP	1997	5.26 ±0.90	31.70 ±5.59	5.86 ±1.52	2.62 ±0.26	3.34 ±1.80	2.48 ±0.46
(μg/L-P)	2005	4.88 ±1.15	33.02 ±3.23	4.05 ±3.00	-	-	-
NO 2/3-N	1997	99.50 ±4.09	61.10 ±2.49	35.41 ±1.93	45.74 ±2.05	50.23 ±2.75	77.19 ±1.26
(μg/L-N)	2005	178.07 ±6.82	124.09 ±2.10	57.29 ±4.64	-	-	-
TPN	1997	135.52 ±5.84	102.63 ±6.47	43.40 ±2.05	55.97 ±6.36	70.10 ±8.00	100.44 ±9.90
(μg/L-P)	2005	216.31 ±2.90	212.79 ±8.55	80.90 ±4.33	-	-	-
N : P	1997	104 ±7	63 ±7	52 ±7	131 ±38	125 ±20	166 ±45
(molar)	2005	504 ±154	226 ±30	223 ±68	-	-	-

Table 1. (cont.)

				Parafluvial Springbrook			
Variable	Year	April	June	Aug.	Sept.	Oct.	Nov.
Temp	1997	-	-	12.13	12.31	10.28	6.07
(^{o}C)	2005	5.30 ±0.53	7.48 ±0.44	12.6 ±4.46	-	8.01 ±1.12	-
DO	1997	-	-	4.72	7.63	8.18	7.35
(mg/L)	2005	9.70 ±1.00	9.35 ±1.26	5.79 ±0.90	-	7.08 ±0.77	-
pH	1997	-	-	8.09	8.65	8.41	8.19
(units)	2005	7.92 ±0.43	8.28 ±0.12	8.09 ±0.10	-	7.98 ±0.08	-
Sp. Cond.	1997	-	-	200	206	212	207
(µS)	2005	172 ±16	172 ±40	251 ±29	-	244 ±14	-
Alkalinity	1997	-	-	112	117.6	116.48	115.36
(mg/L-CaCO3)	2005	105.17 ±11.96	81.85 ±21.39	135.72 ±20.65	-	-	-
DOC	1997	-	-	1.35	0.95	0.77	0.51
(mg/L-C)	2005	0.75 ±0.26	1.20 ±0.51	0.88 ±0.70	-	-	-
SRP	1997	-	-	1.82	1.86	1.33	1.51
(µg/L-P)	2005	1.26 ±0.52	1.36 ±0.53	0.83 ±0.51	-	-	-
TP	1997	-	-	2.55	3.54	3.28	3.21
(µg/L-P)	2005	3.46 ±1.51	13.40 ±7.15	8.20 ±5.36	-	-	-
NO 2/3-N	1997	-	-	39.6	39.4	47.4	65.3
(µg/L-N)	2005	106.72 ±67.37	124.23 ±28.40	39.83 ±30.45	-	-	-
TPN	1997	-	-	39.33	44.03	70.1	101.14
(µg/L-P)	2005	131.33 ±53.69	169.22 ±46.31	74.88 ±18.62	-	-	-
N : P	1997	-	-	-	47	47	79
(molar)	2005	270 ±208	216 ±45	114 ±79	-	-	-

Table 1. (cont.)

				Orthofluvial Springbrook			
Variable	Year	April	June	Aug.	Sept.	Oct.	Nov.
Temp	1997	-	5.70 ±0.92	7.03 ±0.87	7.72 ±0.87	6.89 ±1.54	4.21 ±3.80
(^{o}C)	2005	5.51 ±1.60	7.08 ±0.67	8.24 ±0.46	-	8.19 ±1.29	-
DO	1997	-	-	6.85 ±1.74	5.96 ±2.68	6.35 ±1.94	7.33 ±2.16
(mg/L)	2005	8.71 ±0.68	8.28 ±1.83	5.80 ±1.55	-	6.64 ±1.56	-
pH	1997	-	-	8.10 ±0.14	7.97 ±0.22	8.05 ±0.16	8.13 ±0.01
(units)	2005	7.28 ±0.30	8.18 ±0.16	8.20 ±0.13	-	-	-
Sp. Cond.	1997	212 ±60	156 ±57	206 ±31	213 ±3	221 ±42	199 ±11
(µS)	2005	203 ±15	188.23 ±31.73	242 ±12	-	245 ±9	-
Alkalinity	1997	119.90 ±26.85	84.27 ±26.67	116.11 ±18.55	122.45 ±23.29	126.56 ±25.32	109.76 ±9.50
(mg/L-CaCO3)	2005	120.70 ±9.25	120.41 ±11.94	123.68 ±5.79	-	-	-
DOC	1997	2.35±1.11	2.11 ±1.07	1.70 ±0.77	1.42 ±1.07	0.76 ±0.12	0.47 ±0.01
(mg/L-C)	2005	0.51 ±0.15	0.61 ±0.12	0.53 ±0.27	-	-	-
SRP	1997	0.51±0.23	2.11 ±0.41	1.14 ±0.43	1.76 ±0.33	1.08 ±0.44	1.91 ±0.06
(µg/L-P)	2005	1.26 ±0.26	0.96 ±0.12	0.85 ±0.33	-	-	-
TP	1997	4.07±0.31	15.62 ±9.42	2.54 ±0.37	4.90 ±1.44	3.55 ±0.42	2.88 ±0.06
(µg/L-P)	2005	7.01 ±2.82	4.92 ±1.60	3.82 ±1.02	-	-	-
NO 2/3-N	1997	76.16 ±32.40	51.01 ±10.41	29.89 ±17.96	31.26 ±24.64	34.90 ±28.16	68.47 ±11.82
(µg/L-N)	2005	112.62 ±7.00	79.88 ±8.13	65.50 ±16.55	-	-	-
TPN	1997	112.28 ±25.46	70.46 ±15.19	36.95 ±11.01	45.51 ±1.96	54.18 ±8.96	89.39 ±27.47
(µg/L-P)	2005	139.88 ±13.18	99.46 ±8.36	77.83 ±28.21	-	-	-
N : P	1997	98 ±8	54 ±5	31 ±4	54 ±24	43 ±37	62 ±47
(molar)	2005	212 ±26	186 ±45	205 ±98	-	-	-

Table 2. Repeated-measures ANOVA results for chlorophyll *a* over the post-flood period in 2005. Habitat type (main channel, parafluvial springbrook, orthofluvial springbrook) is the independent variable and DPF (days post-flood) is the repeated variable. Within type main channel site contrasts are designated "a", parafluvial sites are designated "b", and orthofluvial sites are designated "c". These coupled letters indicate Tukey's b (α = 0.05) post-hoc significantly different pairs while all other significance levels were assessed using Huynh-Feldt correction for non-sphericity.

			Independent Variables		
Dependent variable		Mean square error	Type	DPF	Type x DPF
			F statistic†		
Chlorophyll *a*	between	11.08	16.81****, ab**, ac****, bc*	-	-
	(error)	0.66	-	-	-
	within	4.21	-	11.69****	-
			-	-	10.56****
	(error)	0.36	-	-	-

*P ≤ 0.1, **P ≤ 0.05, *** P ≤ 0.01, **** P ≤ 0.001

† Degrees of freedom for between-subjects effects for habitat type: 2; error: 9

Degrees of freedom for within-subjects effects for time: 3; habitat type x DPF: 6; error: 27

Table 3. One-way ANOVA and Wilcoxon-Mann-Whitney test results comparing water chemistry and periphyton by site type in August 2005. †Designates variables which did not meet normality and/or equality of variance assumptions and whose p-values are exact significance reported from Wilcoxon-Mann-Whitney non-parametric tests. All other p-values are from Tukey's HSD post-hoc tests.

	Site Type Comparisons		
Variable	main channel vs. parafluvial springbrook	main channel vs. orthofluvial springbrook	parafluvial springbrook vs. orthofluvial springbrook
Temperature †	n.s.	0.029	n.s.
DO	0.004	0.004	n.s.
pH	0.001	0.002	n.s.
Sp. Cond.	>0.000	>0.000	n.s.
Alkalinity	0.002	0.017	n.s.
DOC†	n.s.	n.s.	n.s.
SRP	n.s.	n.s.	n.s.
Log_{10} TP	n.s.	n.s.	n.s.
NO2/3†	n.s.	n.s.	n.s.
TPN	n.s.	n.s.	n.s.
N: P	n.s.	n.s.	n.s.
VHG†	n.s.	0.057	n.s.
Log_{10} Chl a	n.s.	n.s.	n.s.
AFDM	n.s.	n.s.	n.s.
Log_{10} C: N	n.s.	0.031	n.s.

Table 4. Principal component loadings for periphyton metrics and environmental variables analyzed for the 2nd post-flood period in 1997 (top) and 2005 (bottom).

Variables	Comp. 1	Comp. 2	Comp. 3	Comp. 4	Comp. 5
1997					
velocity	-0.172	0.358		0.237	
depth	-0.113	-0.265		-0.627	
D50	-0.278	0.221			
Dmax		0.181	0.484	-0.118	
temperature	-0.263	-0.242		0.189	
DO	-0.276	0.189	0.155		
pH	-0.323				
sp. cond.	0.307		0.152	-0.122	
alkalinity	0.311		0.154	-0.129	
DOC	0.138	0.283	0.271	-0.209	
SRP	0.142		-0.505	-0.189	
TP	-0.288	-0.117	0.226	-0.198	
NO23	-0.157	0.287	-0.273	-0.219	
TPN	-0.243	0.223	-0.275	-0.153	
NtoP	-0.280		0.210		
VHG	0.190	0.251	-0.208	0.428	
Chl a	0.139	0.385		-0.262	
AFDM	0.150	0.364		-0.145	
CN	0.275	0.151	0.239		
% of variation	47%	25%	14%	6%	
2005					
velocity		-0.330	0.229	-0.266	
depth	-0.354			0.220	0.290
D50		-0.223	0.178	-0.234	0.491
Dmax				0.544	0.273
Temp	-0.241	-0.367			-0.113
DO	-0.382		0.225		
pH	-0.404				
Scond	0.384		0.164	0.162	
Alk	0.358	-0.120		0.280	
DOC		-0.287	0.161		0.509
SRP	0.140	0.170	-0.291	-0.427	0.111
TP	0.138	-0.372	0.205		-0.245
NO23	-0.110	0.404	0.200		
TPN			0.553		-0.173
NtoP	-0.204	0.236	0.271	0.326	
VHG	0.278		0.113	-0.124	0.216
Chla		0.293	0.204	-0.210	
AFDM		0.309		0.125	0.378
CN	0.1371	0.153	0.434	-0.201	
% of variation	29%	22%	13%	10%	9%

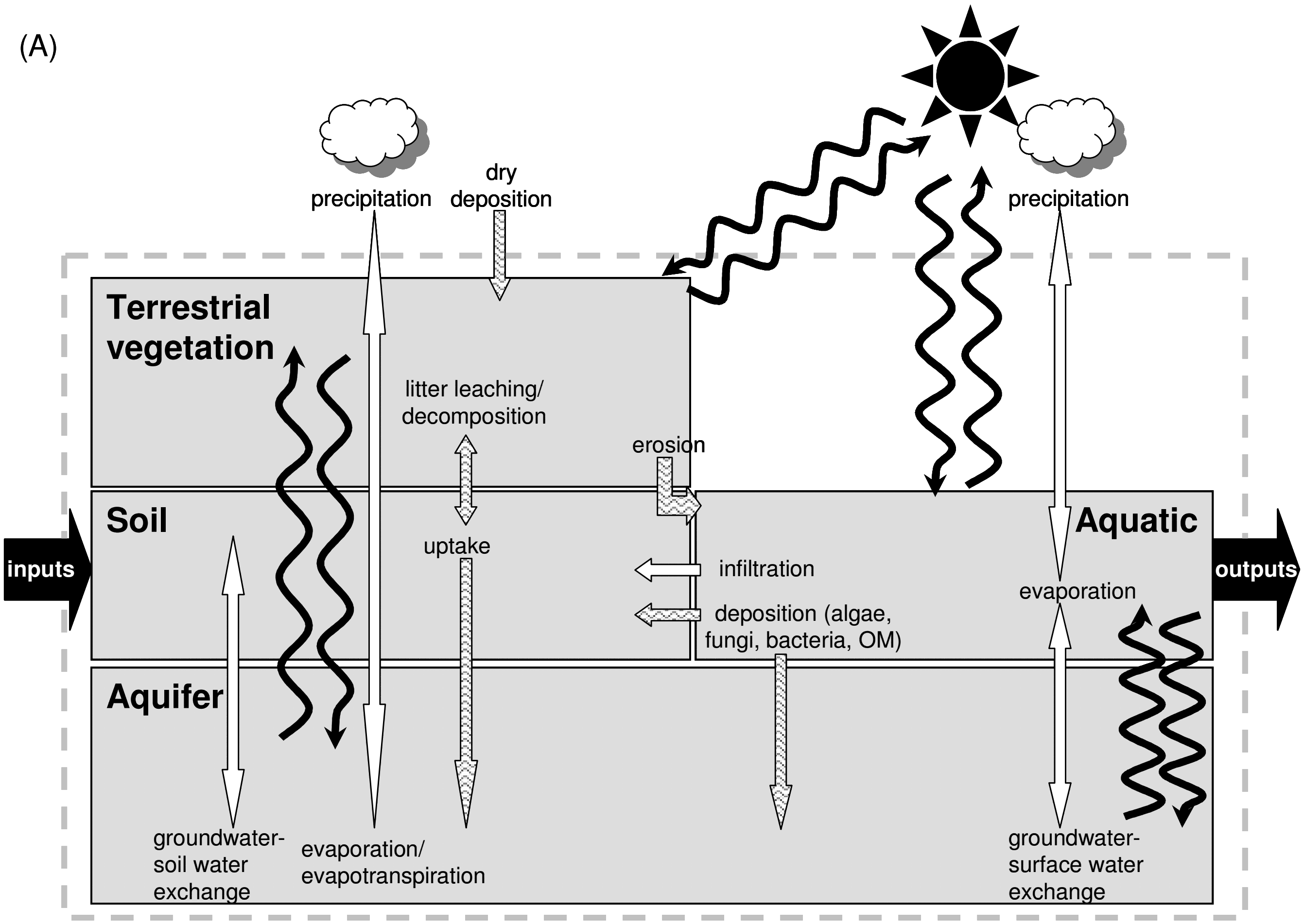


Figure 1. (A) Conceptual process model of the floodplain ecosystem in the context of periphyton dynamics. Arrows indicate pathways of exchange for water (open arrows), heat (solid wavy arrows) and organic matter (hatch marked arrows). Large boxes are subsystems of the flood plain interacting via the pathways of exchange.

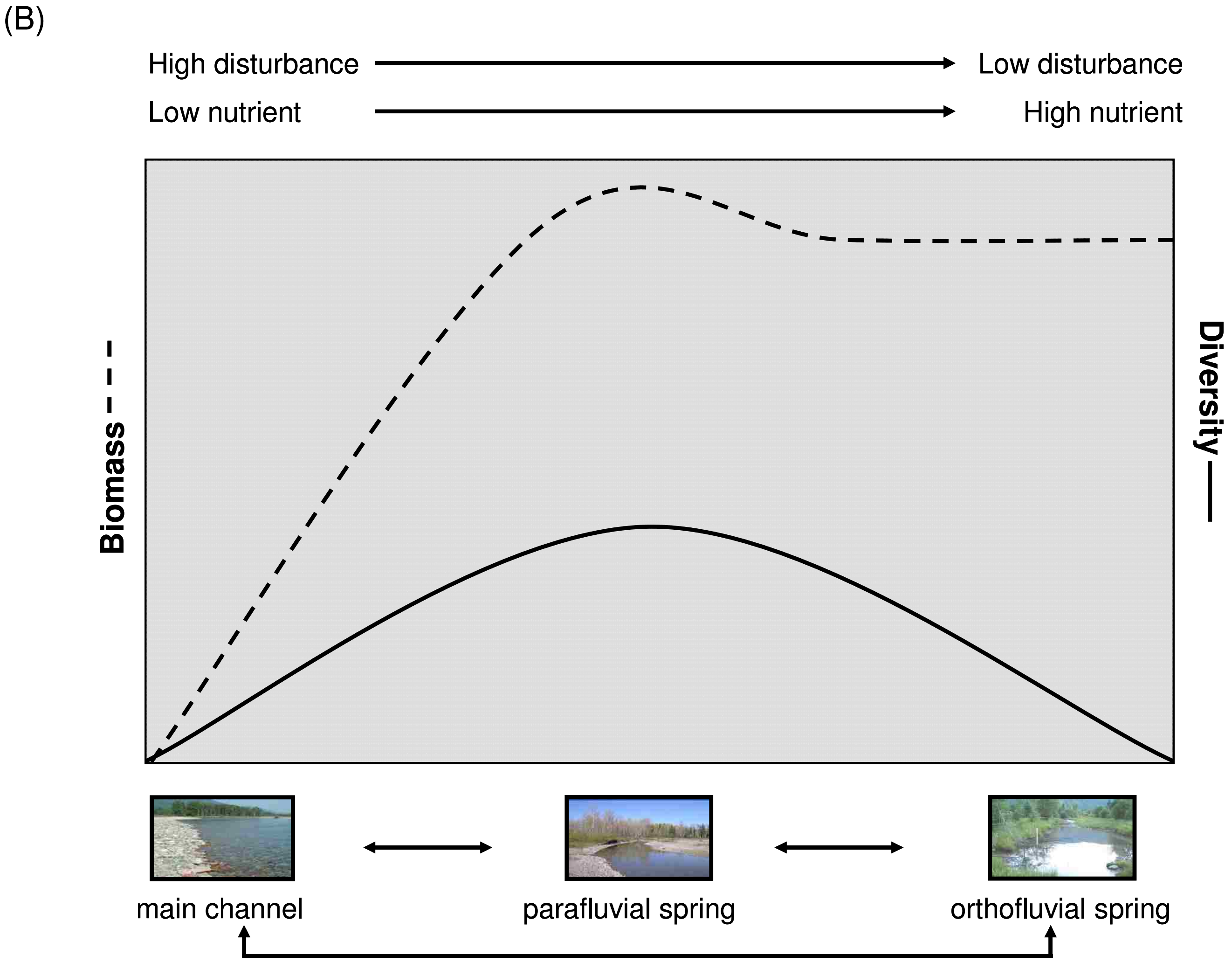


Figure 1. (cont.) (B) Model of variation in disturbance and nutrients in lateral habitats showing the impacts on periphyton biomass and diversity in the aquatic subsystem.

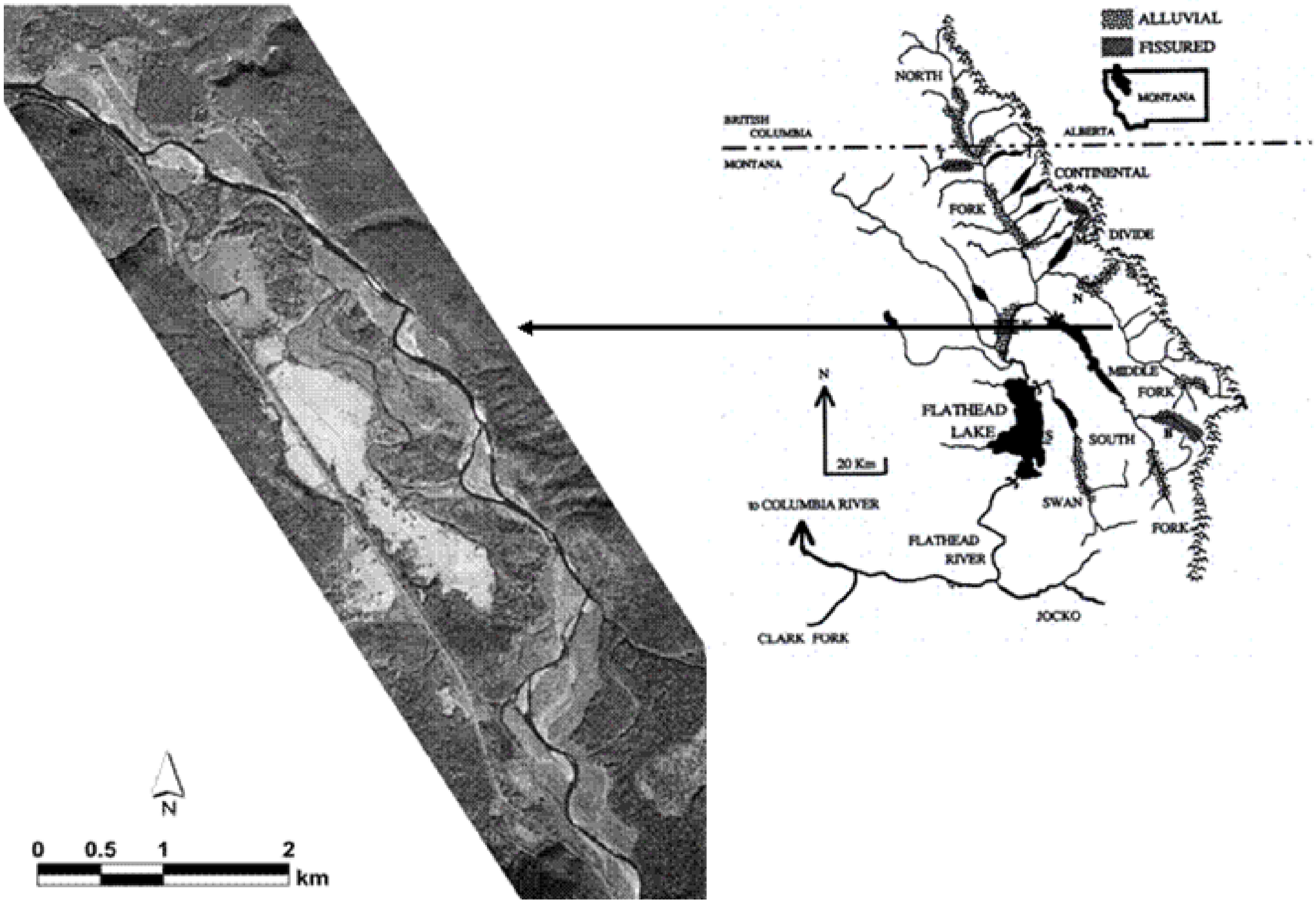


Figure 2. Nyack floodplain study site.

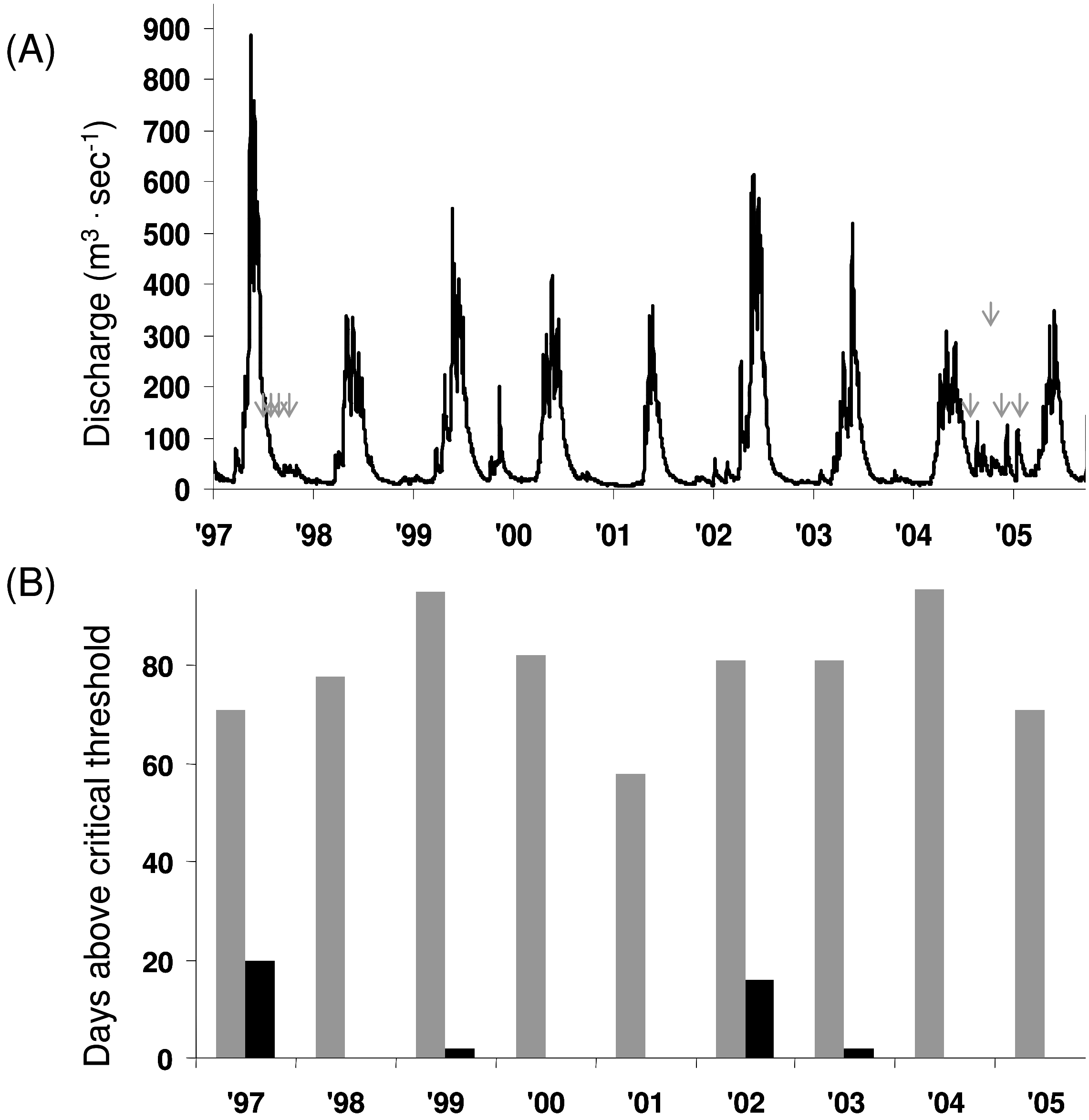


Figure 3. Annual flood disturbance frequency across years at Nyack. (A) The annual hydrograph of daily mean discharge on the Middle Fork of the Flathead River between 1997 and 2005 (arrows indicate sampling events) and (B) days above the 1-year flood recurrence interval (105 m^3/s; gray bars) and the bankfull flood recurrence interval (465 m^3/s; black bars). Recurrence interval discharge values from Whited et al. 2007.

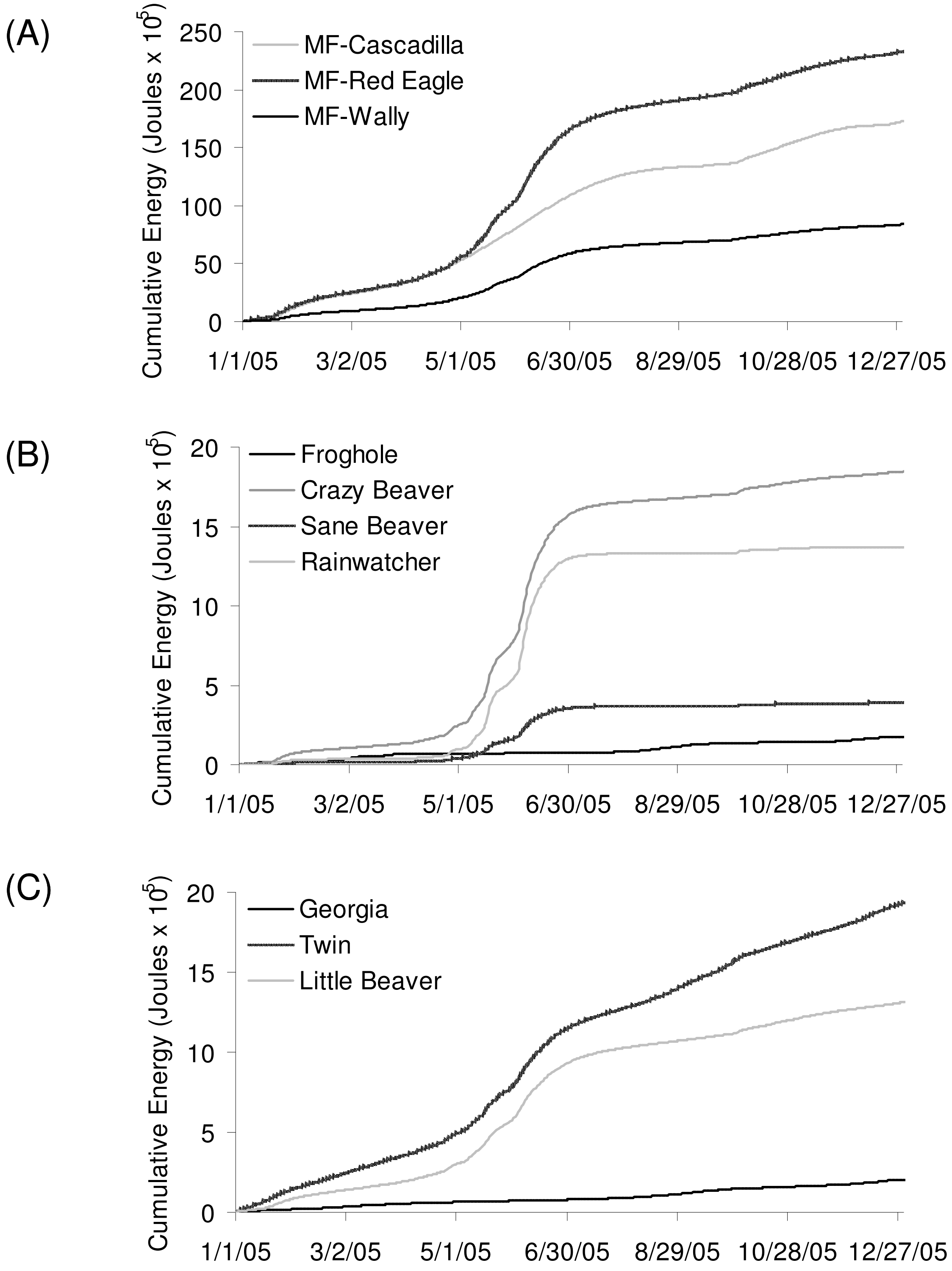
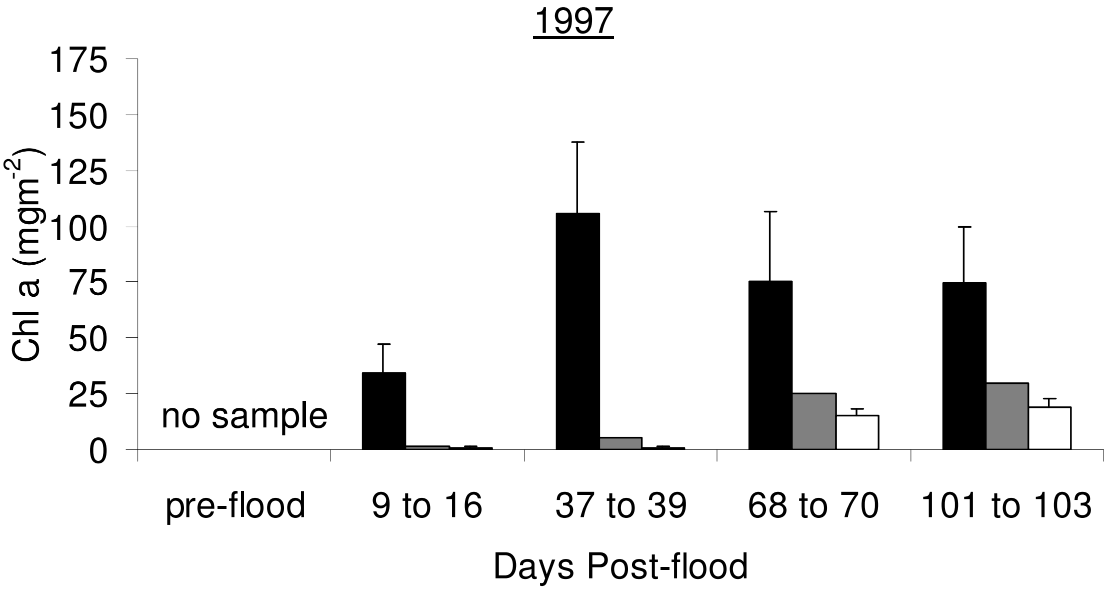


Figure 4. Streamflow cumulative energy curves for (A) main channel, (B) parafluvial springbrook and (C) orthofluvial springbrook sites in 2005.



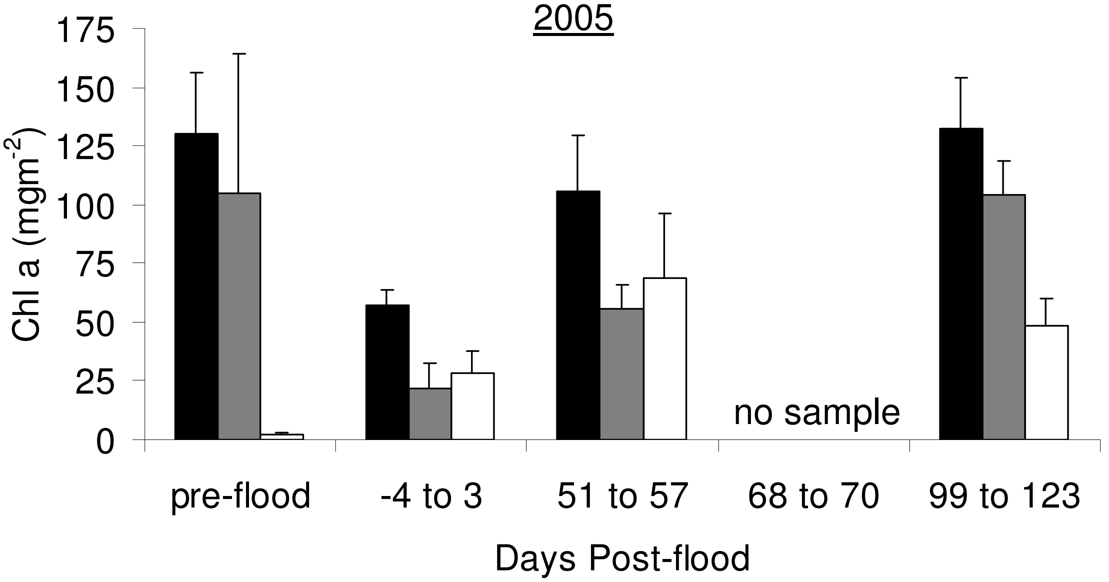
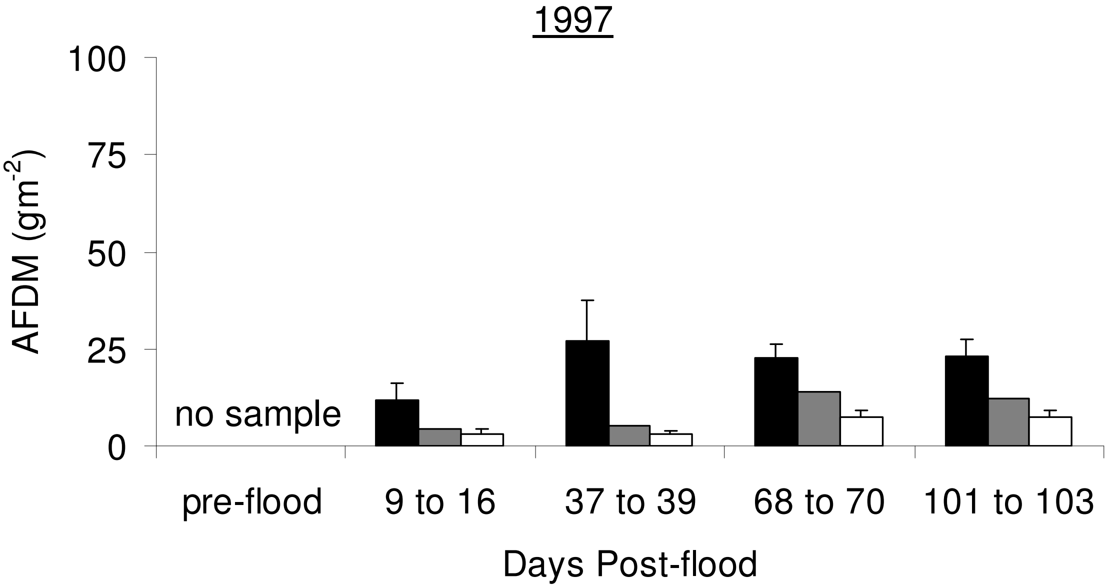


Figure 5. Periphyton chlorophyll *a* values for floodplain habitats pre- and post-flood in 1997 and 2005. Habitats are orthofluvial springbrook (black, n=3 in 1997, n=4 in 2005), parafluvial springbrook (gray, n=1 in 1997, 4 in 2005) and main channel (white, n=5 in 1997, n=4 in 2005). Values are means (±1SE).



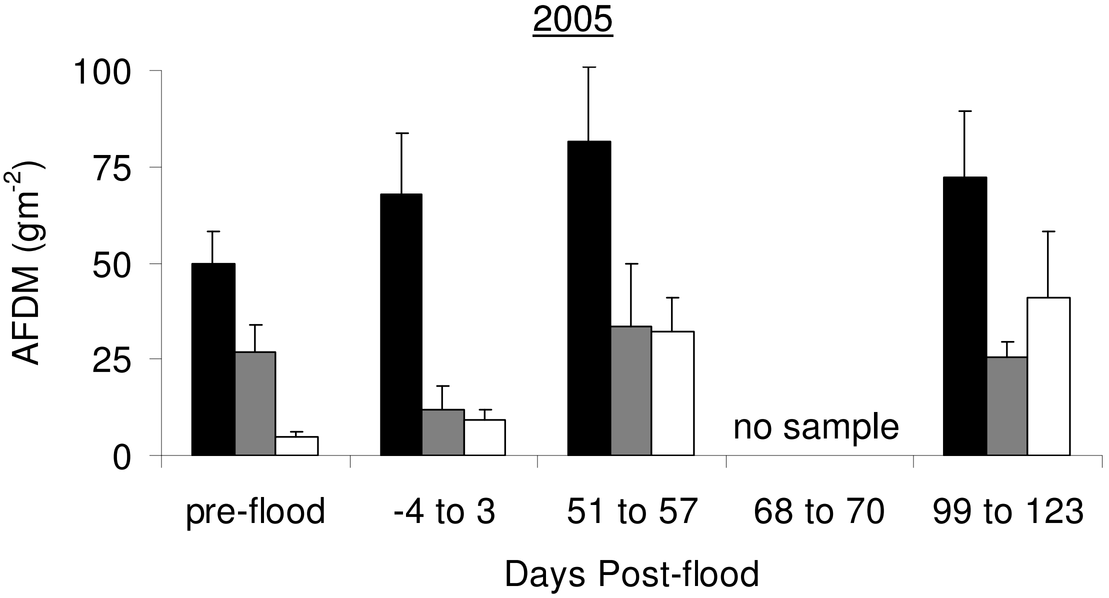
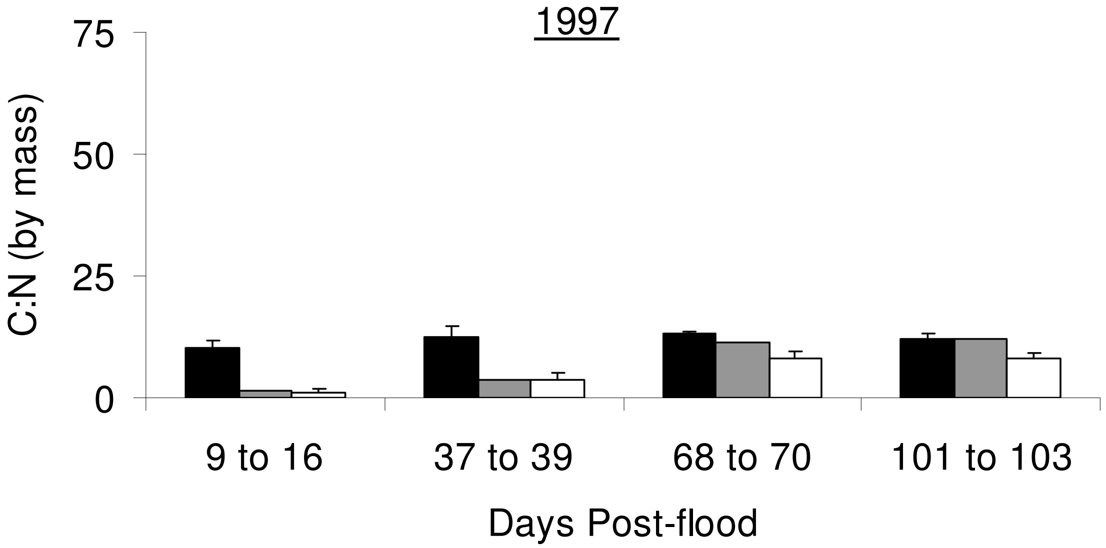


Figure 6. Periphyton ash free dry mass values for floodplain habitats pre- and post-flood in 1997 and 2005. Habitats and sample sizes as in Figure 5. Values are means (±1SE).



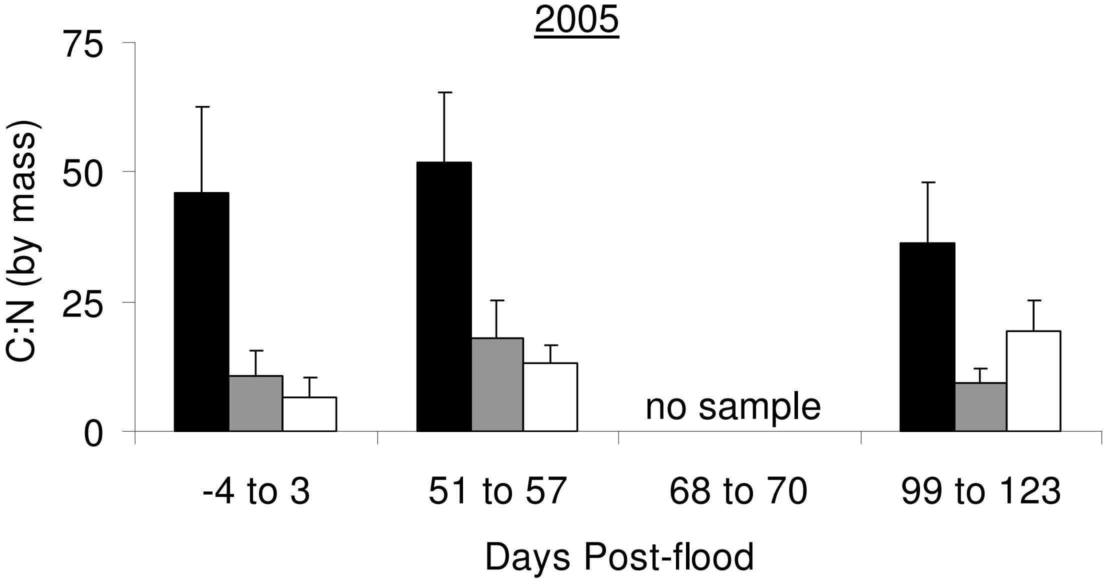


Figure 7. Post-flood periphyton C:N ratio by habitat type in 1997 and 2005. Habitats and sample sizes as in Figure 5. Values are means (±1SE).

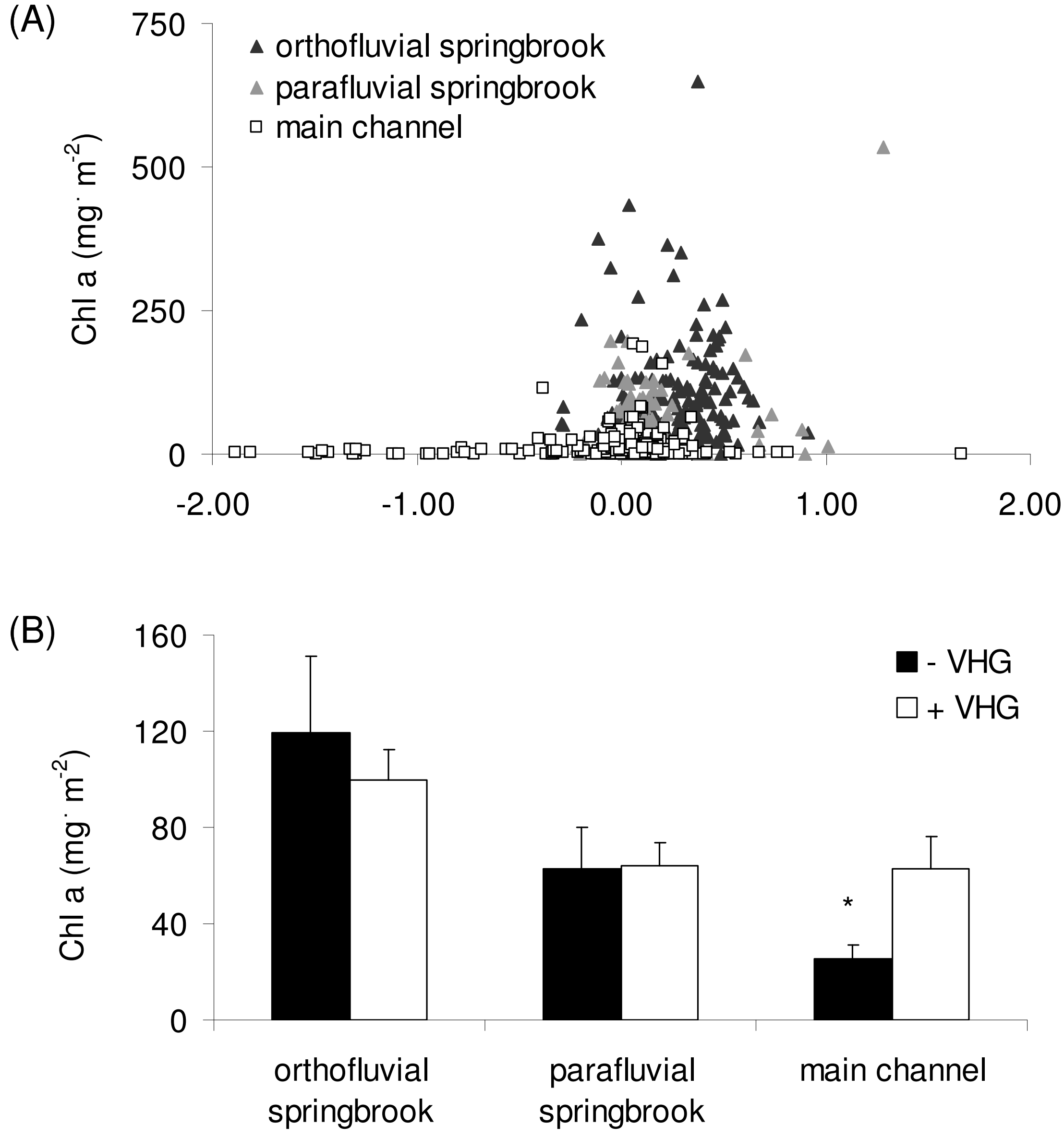


Figure 8. Relationship between chlorophyll *a* and VHG. (A) Point samples of VHG and chlorophyll a by habitat type combined from 1997 and 2005 data. (B) Mean chlorophyll a in relation to VHG by habitat type for all sample dates in 2005 (±1SE). A weak significant difference exists for chlorophyll *a* values between – VHG and + VHG main channel sites (p=0.012, Mann-Whitney).

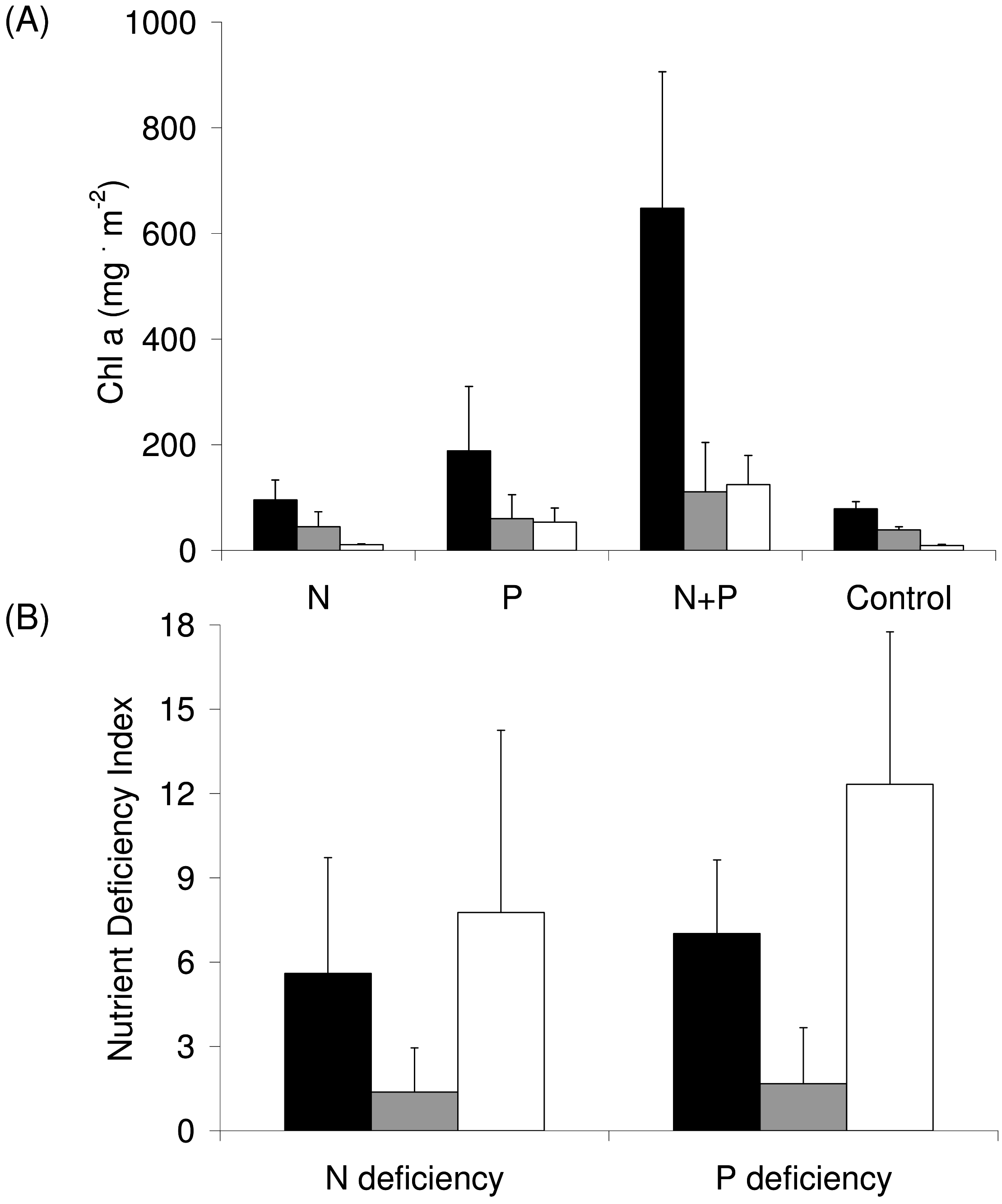
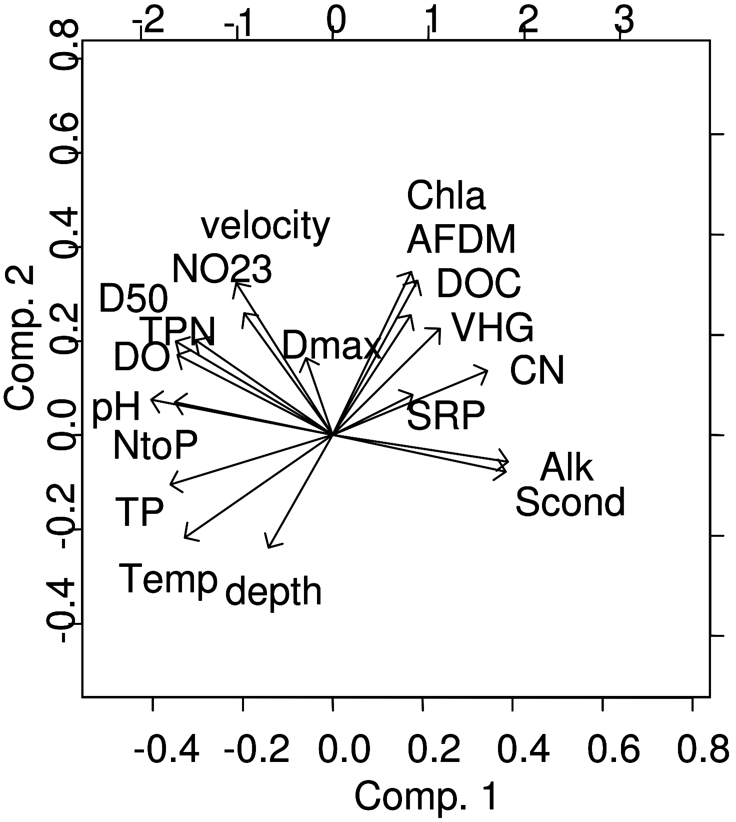


Figure 9. Relative effects of nutrient amendments on (A) chlorophyll a and (B) nutrient deficiency index from NDS experiments (±1SE). Black bars indicate orthofluvial springbrook site (n=1), gray bars indicate parafluvial springbrook sites (n=2) and white bars indicate main channel site (n=1).

(A)



(B)

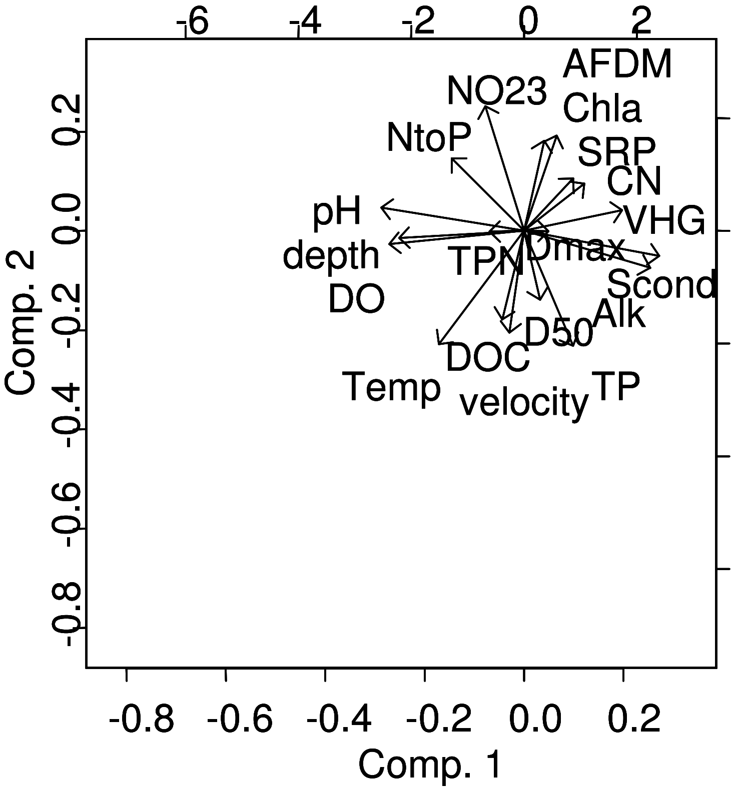


Figure 10. Vectors for the first two principal components from analysis of site type, water chemistry, hydrology and periphyton data in August (A) 1997 and (B) 2005.

main channel (-)	main channel (+)	parafluvial spring	orthofluvial spring
S' = 9.3 ± 2.6	S' = 6.5 ± 3.2	S' = 9.5 ± 3.4	S' = 8.5 ± 4.0
Amphipleura *Diploneis* *Gephyria* *Tabellaria*	*Eunotia* *Merismopedia* *Scenedesmus* *Spirogyra*	*Denticula* *Frustulia* *Lyngbya* *Mastogloia* *Pediastrum*	*Neidium*

Figure 11. Algal community composition across floodplain habitats. Photographs are of rock sampled from main channel downwelling (“-”; n=30) and upwelling (“+”; n=36) sites in mid-summer 2004 as well as from parafluvial (n=4) and orthofluvial (n=4) springbrook sites in mid-summer 2005. Average sample taxa richness (± 1 SD) at each site type is listed below site photographs, along with taxa unique to a habitat type.

Appendix 1. Average number of algal cells per cm^2 per sample by habitat type. –VHG and + VHG from Wyatt (2005).

	- VHG Main Channel	+ VHG Main Channel	Parafluvial Springbrook	Orthofluvial Springbrook
Achnanthidium	5567	1674	268	157
Amphipleura	42	0	0	0
Amphora	0	0	0	0
Cocconeis	95	28	11	1
Cyclotella	95	17	3	5
Cymatopleura	77	0	0	0
Cymbella	753	159	10	22
Denticula	0	0	3	0
Diatoma	764	57	5	59
Didymosphenia	295	23	1	1
Diploneis	77	0	0	0
Encyonema	0	0	5	1
Epithemia	0	0	0	0
Eunotia	0	10	0	0
Fragilaria	649	41	2	0
Frustulia	0	0	2	0
Gephyria	2	0	0	0
Gomphonema	464	69	9	6
Hannaea	95	74	0	0
Hydrurus	496	2866	0	0
Lyngbya	0	0	12	0
Mastogloia	0	0	0	0
Melosira	627	90	0	0
Meridion	31	94	0	0
Merismopedia	0	411	0	0
Mougeotia	0	364	0	5
Navicula	427	28	4	3
Neidium	0	0	0	1
Nitzchia	138	22	0	0
Pediastrum	0	0	1	0
Phormidium	231	440	0	0
Pinnularia	103	14	1	0
Plectonema	0	0	0	59
Scenedesmus	0	12	0	0
Spirogyra	0	119	0	0
Staurosira	0	0	0	1
Stigeoclonium	894	5416	35	71
Synedra	218	98	7	18
Tabellaria	34	0	0	0
Zygnema	0	4240	6	4

APPENDIX 2:
DETAILED DESCRIPTION OF STATISTICAL METHODS USED IN CHAPTER 3

INTRODUCTION

The purpose of this study was to document variation in hydrologic disturbance, water chemistries, surface water-groundwater exchange and periphyton variables across the Nyack floodplain over time. This is essential to understanding how floodplains function as disturbance, water chemistry and periphyton all influence ecosystem productivity through the distribution and abundance of aquatic organisms. The main study area was the Nyack floodplain, across which major aquatic habitats (main channel, parafluvial springbrook, orthofluvial springbrook) were sampled in 1997 after a large flood event and again in 2005 after a much smaller flood event. Sample design was altered between 1997 and 2005 (Fig. A1, A2) in order to create a more balanced factorial design and better assess habitat specific differences in variables. Significance of habitat type and days post-flood (DPF) were tested to explain variation in periphyton response variables. Exploratory data analysis revealed a potential effect of both disturbance and nutrients on periphyton, but I was unable to statistically test the significance of these relationships with the existing data. It was determined that evidence existed to support the view that there are significant differences in disturbance regimes, water chemistry, and periphyton among different habitat types and DPF within and between the years 1997 and 2005. Ideally these issues will be resolved with an expanded, well-balanced sample design coupled with experiments.

OBJECTIVE

Our objective was to document differences in hydrologic disturbance, water chemistries, surface water-groundwater exchange and periphyton variables among habitat types within and between years. The significance of hydrologic disturbance, habitat type and days post-flood were tested to explain variation in chlorophyll *a*.

METHODS

Sampling sites were located in main channel, parafluvial springbrook and orthofluvial springbrook lateral aquatic habitat types in 1997 and 2005. The 1997 study design, though well-designed for sampling periphyton and hydrologic variation within a site, was unbalanced (main channel n=5, parafluvial springbrook n=1, orthofluvial springbrook n=3). In attempting to correct the unbalance and deal with channel change in the intervening 8 years, site location and sample methodology differed between years (Fig. A1, A2, Chapter 3 Methods). This precluded direct, repeated measures comparison of variables between years. There was collection of similar response and explanatory variables in both years at similar time intervals of days post-flood:

<u>Fixed factor variables:</u>

habitat type

time (days post-flood, year)

<u>Periphyton response variables:</u>

chlorophyll *a* (chl *a*)

Periphyton response variables (cont):

ash free dry mass (AFDM)

ratio of chlorophyll a: ash free dry mass (chl a: AFDM)

periphyton molar ratio carbon: nitrogen (C:N)

Environmental response variables:

physical site characteristics:

vertical hydraulic gradient (VHG)

water quality characteristics:

temperature (Temp)

dissolved oxygen (DO)

pH

specific conductivity (SpCond)

alkalinity (Alk)

dissolved organic carbon (DOC)

soluble reactive phosphorous (SRP)

total phosphorous (TP)

nitrate ($NO_{2/3}$)

total persulfate nitrogen (TPN)

nitrogen to phosphorous (N:P)

Data analyses

Exploratory data analyses were used to a) calculate means and variances for data presentation purposes, b) test main assumptions (normality, homogeneity of variances) of statistical tests and c) provide a rational for or against pooling data in space and time. Further statistical tests were chosen to assess significant differences and relationships between variables among habitat types and days post-flood. Most data analyses were performed in SPSS 12.0 except for the principal components analysis (PCA), carried out in S-PLUS 4.5.

Potential lack of independence and autocorrelation in this data set were pressing concerns driving exploratory data analysis. The sample units are sites, either a main channel, orthofluvial or parafluvial springbrook. In order to achieve accurate values for variables of interest, multiple samples were taken within a site to capture potential variability in water chemistries and periphyton metrics. Depending on the year, 1-3 water chemistry and 3-10 periphyton samples were taken per site per sampling event (Fig. A1, A2). The potential for lack of independence in data from upstream-downstream effects was significant. The small number of samples taken within sites also made determination of within site variation nearly impossible. These factors led us to pool results within a site into a single site mean observation per sample event, as opposed to treating replicate water samples on a given date as independent observations. Water chemistry means and standard deviations were calculated across site types, days post-flood and years (Chapter 3 Table 1). Inspection of this data provided evidence for large and erratic differences between sampling events within and between years for some water chemistry variables. This precluded pooling of chemistry data across dates.

Prior to performing any statistical analyses in this study, variables were assessed for their ability to meet normality and homogeneity of variance assumptions. Normality of variables was tested by visually inspecting P-P plots and boxplots and examining the results of Shapiro-Wilk tests. Non-normally distributed data was transformed to meet the assumptions of normality when possible. Homogeneity of variances was assessed using the Levene's test. For examples of tests, see Fig. A3-6.

Due to variation in data collection across sample events and years and the transient nature of floodplain ecosystems, a choice was made not to do a year-to-year comparison between 1997 and 2005. Instead, statistical analyses were focused on the more balanced data collected in 2005 (n=4 for all site types and variables) during the 2nd post-flood sampling period. This event occurred both years in the latter half of August. This sample event represented the most complete set of chemistry data for any one event across both years. This event also coincided with the peak growing season for algae and the period in which stress from temperature and dissolved oxygen variation coupled with nutrient limitation are suspected to be most severe for periphyton. A combination of one-way ANOVA with Tukey's HSD post-hoc tests, Kruskall-Wallis and Wilcoxon Mann-Whitney tests were used to compare water chemistry and periphyton variables between site types in August 2005. Temperature, dissolved organic carbon (DOC), nitrate-nitrite (NO2/3) and vertical hydraulic gradient all had significant departures from normality or equality of variances that could not be corrected using transformations. An analysis of these variables was performed using the Kruskall-Wallis test to determine which variables were significantly different at p=0.05 or less. Variables judged to be significant in the Kruskall-Wallis test were then compared pairwise by habitat type using Wilcoxon Mann-Whitney tests.

In order to address changes in periphyton over days post-flood in different habitat types, a full factorial repeated measures ANOVA was used on chlorophyll *a* data from 2005. Chlorophyll *a* was the only periphyton metric which met ANOVA assumptions of normality and equality of variance, following an *ln* (x+1) transformation of the data (Fig. A3). A suspected interaction between site type and DPF led to the addition of an interaction term, which resulted in the ANOVA generating an extra-sums-of-squares F-test and associated F-statistics and p-values.

A principal component analysis (PCA) based on a correlation matrix was used as an exploratory technique to examine contrasts between variables. Due to strong seasonal and year-to-year differences previously noted, the decision was made to run a PCA only on the 2nd post-flood sample event in 1997 and 2005 for reasons mentioned above. It was hoped that PCA could be used to reduce the number of possible explanatory variables for subsequent analysis if a subset of variables within the PCA explained a high proportion of the total variation in the dataset and exhibited a strong relationship to periphyton metrics. Those variables would then be used in a multiple regression context in an attempt to attribute variation in periphyton to environmental factors.

RESULTS

A robust discussion of results of analyses is located in the text of this chapter. As this appendix focuses on statistical methods, only aspects of results already presented in

Chapter 3 (Tables 1-4) that are pertinent to understanding the statistical aspects of this work with be repeated herein.

Table 2 illustrates results of the repeated measures ANOVA on *ln* (x+1) transformed chlorophyll *a* data from 2005. Mauchly's test of sphericity indicated a possible weak violation ($p = 0.075$). Due to small sample sizes a choice was made to proceed with caution and interpret ANOVA results using the Huynh-Felt correction for sphericity violations. Results of the ANOVA indicated that type ($p = 0.001$), DPF ($p < 0.001$) and the type x DPF interaction ($p < 0.001$) were all highly significant. Levene's tests indicated that equality of variances assumptions were met (p-values ranged from 0.162 to 0.666) so the Tukey's HSD post-hoc test was chosen to evaluate site type differences. Post-hoc tests indicated that contrasts between site types were significant, with main channel versus parafluvial springbrooks ($p = 0.001$) and main channel versus orthofluvial springbrooks ($p = 0.018$) being a more significant differences than between the two springbrook types ($p = 0.11$).

One-way ANOVA and Wilcoxon-Mann-Whitney tests of all variables for differences between site types in August 2005 also indicated differences existed between main channel sites and springbrooks while no such differences existed between springbrooks (Table 1, 3). Main channel sites had higher temperatures, dissolved oxygen, and ph as well as lower specific conductivity, and alkalinity than parafluvial springbrooks. The contrast between main channel and orthofluvial springbrook sites revealed the same pattern with an additional difference in mean negative VHG values in the main channel versus positive VHG values ($p = 0.057$) and higher C: N values in the orthofluvial springbrook ($p = 0.031$).

The PCA analysis revealed distinct patterns of association for August 1997 and 2005, although both held only weak associations across the data set (Table 4, Figure 10). In 1997 the first 4 principle components explained a large degree of variation inherent in the data (92%), with most being explained by the 1st (47%) and 2nd (25%) principle components. Principle component 1 is interpreted to represent springbrook sites due to the positive values for specific conductivity, alkalinity, DOC, SRP, VHG and periphyton metrics and negative values for velocity, depth, mean course sediment grain size (D_{50}), temperature, pH, TP, TPN and N: P. This is consist with general trends in water chemistry, periphyton metrics, and disturbance in springbrook environments previously mentioned. Principal component 2 is interpreted to be the algal response to the main channel environment, with a positive association between algal metrics and the higher water velocities, dissolved oxygen, NO 2/3, TPN, D_{50}, and DOC found in the main channel and negatively associated with the higher SRP values, lower temperatures and less depth found in springbrook environments.

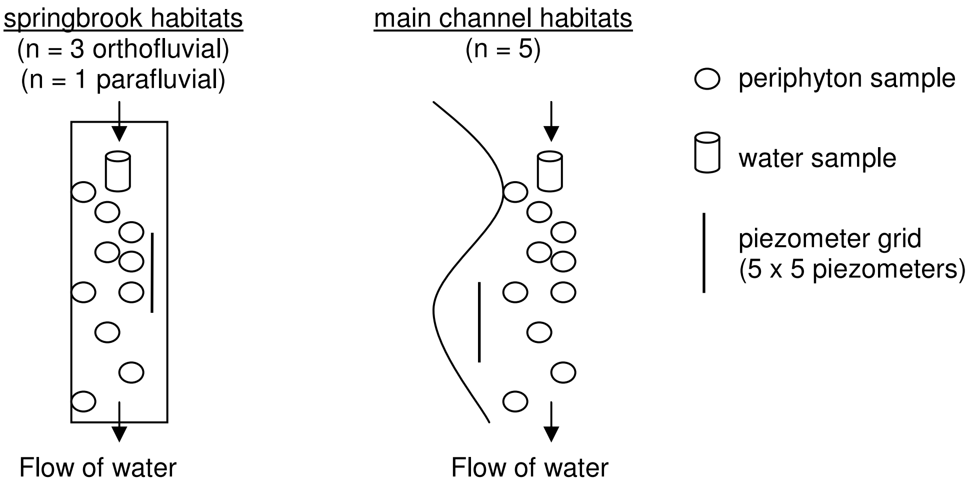
In 2005 the PCA analysis revealed similar patterns to 1997, but weaker trends as it took 5 principle components to explain 87% of the total variation. Principle component 1 comprised 29% of total variation and is again seen to represent springbrook sites, with positive values for C: N, VHG, alkalinity and specific conductivity opposed by negative values for depth, temperature, dissolved oxygen, pH and N: P. This also remained consist with general trends in water chemistry, periphyton metrics, and disturbance previously mentioned. Principle component 2, with 22% of the variation, was interpreted to be environmental variables we suspect are correlated with periphyton chlorophyll *a* and AFDM across site types, including positive associations with the NO2/3, N: P and SRP and a negative relationship to TP, DOC, water velocity, D_{50} and temperature. Component 3 mainly shows the strong association between nitrogen (TPN) and periphyton C: N ratios. Components 4 and 5 respectively associate sediment grain size positively with N: P or DOC and negatively with SRP values, the importance of which remains unclear.

CONCLUSIONS

It was felt there was evidence to support the view that there were significant differences in disturbance regimes, water chemistry, and periphyton among different habitat types and days post-flood in 2005. It also appeared that strong differences in water chemistry and periphyton occur between the main channel and springbrooks but not as much between springbrook types. A relationship likely existed between nutrients and periphyton, yet its exact nature was obscured by variability in hydrologic disturbance and surface water-groundwater exchange. Unfortunately, it proved impossible to statistically assess significant differences in 1997 or between years, or resolve periphyton response to variation in hydrology or water chemistry through regression analysis as had been hoped. A further major drawback of this study was the inability to extrapolate results to systems other than Nyack. In the future a better replicated, more balanced design would make assessment of statistical significance of the variables more robust. It seems likely that experiments will be needed to tease apart the effects of so many potential covariates on water chemistry variation and periphyton growth and nutrition. Ideally a larger data set coupled with experiments would allow us to move into the more predictive framework of multiple regressions.

In 1997 all samples were obtained from within a 15 m long by 5 m wide sample grid, located in one of three habitat types. Sites were not chosen randomly but sample reaches within sites were.

Figure A1. Study site sampling design in 1997.



In 2005 we used the same habitat types as in 1997, but attempted to create a better balance and randomization of the design. Main channel sites were in similar reaches to 1997 and sample area within site was again randomly selected. Parafluvial and orthofluvial springbrooks were randomly selected from the very small pool of available sites. All parafluvial springbrook sites used in 2005 were new, as the 1997 site had backfilled with sediment and was no longer a viable springbrook. One orthofluvial site chosen at random matched a 1997 site (Georgia) while the remaining orthofluvial springbrook sites did not correspond between years. At the within site scale we collected separate samples for chlorophyll a and ash free dry mass and took piezometer readings at each rock location, and at the site scale we sampled over an entire springbrook by breaking the site into head, mid and mouth reaches, each with a subset of periphyton and water chemistry samples.

Figure A2. Study site sampling design in 1997 and 2005.

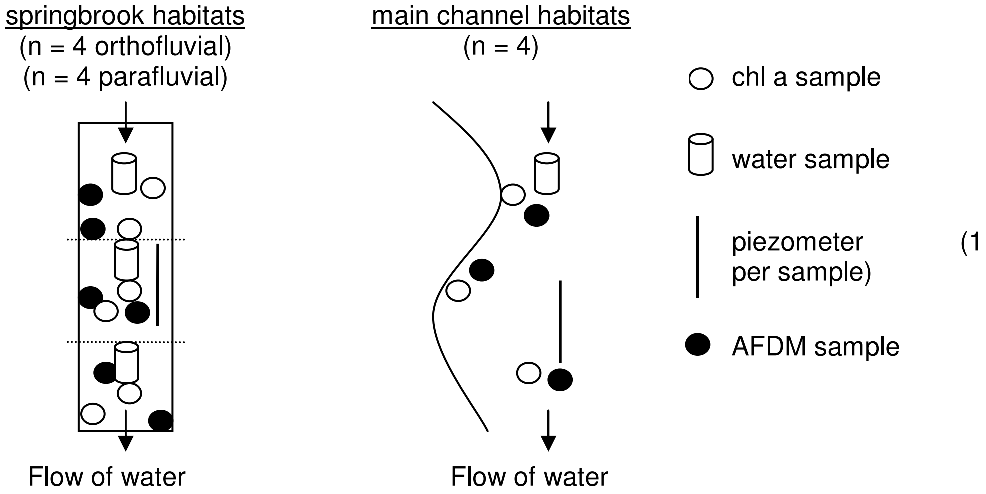


Figure A3. Results of Kolmogorov-Smirnov, Shapiro-Wilk and Q-Q plot tests of normality in data distribution.

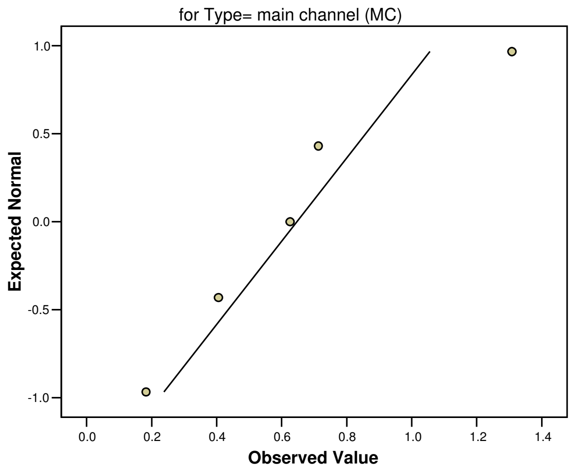
Tests of Normality: Ln (x+1) Chlorophyll a August-November 1997

	Type	Kolmogorov-Smirnov(a)			Shapiro-Wilk		
		Statistic	df	Sig.	Statistic	df	Sig.
August	MC	.238	5	.200(*)	.945	5	.698
	OS	.342	3	.	.845	3	.228
September	MC	.258	5	.200(*)	.880	5	.311
	OS	.362	3	.	.805	3	.125
October	MC	.241	5	.200(*)	.917	5	.509
	OS	.310	3	.	.899	3	.381
November	MC	.145	5	.200(*)	.991	5	.983
	OS	.311	3	.	.897	3	.376

* This is a lower bound of the true significance.

a Lilliefors Significance Correction

Normal Q-Q Plot of Ln (x+1) Chlorophyll a - August 1997



Detrended Normal Q-Q Plot of Ln (x+1) chlorophyll a - August 1997

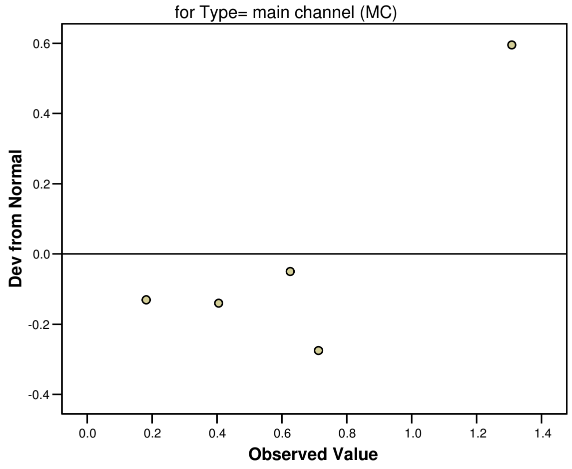
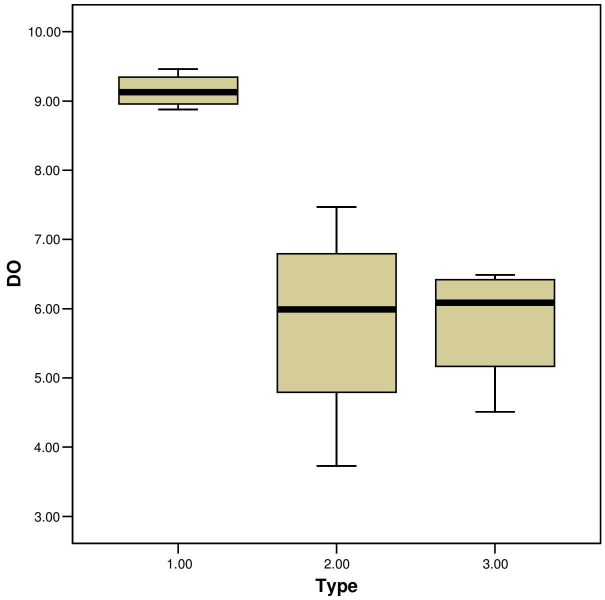


Figure A4. Example of using boxplots to assess normal versus non-normal August 2005 water chemistry data.

Normally distributed data



Non-normally distributed data

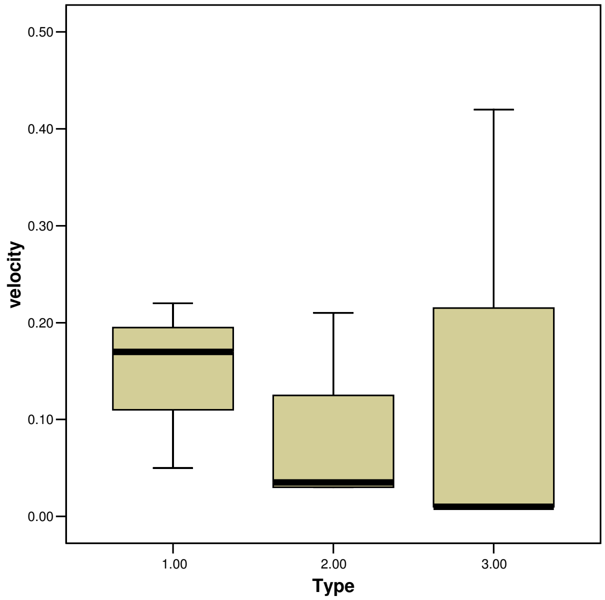


Figure A5. Test of homogeneity of variances for a subset of the August 2005 water chemistry variables. Temperature and DOC are significantly different in terms of variance and cannot be used in a strict ANOVA context.

Test of Homogeneity of Variance

		Levene Statistic	df1	df2	Sig.
Temp	Based on Mean	4.133	2	9	.053
	Based on Median	3.623	2	9	.070
	Based on Median and with adjusted df	3.623	2	3.129	.153
	Based on trimmed mean	4.126	2	9	.053
DO	Based on Mean	1.685	2	9	.239
	Based on Median	1.275	2	9	.325
	Based on Median and with adjusted df	1.275	2	5.010	.357
	Based on trimmed mean	1.572	2	9	.260
pH	Based on Mean	1.715	2	9	.234
	Based on Median	1.287	2	9	.323
	Based on Median and with adjusted df	1.287	2	3.992	.370
	Based on trimmed mean	1.607	2	9	.253
Scond	Based on Mean	4.154	2	9	.053
	Based on Median	1.514	2	9	.271
	Based on Median and with adjusted df	1.514	2	3.529	.335
	Based on trimmed mean	3.570	2	9	.072
Alk	Based on Mean	8.359	2	9	.009
	Based on Median	7.932	2	9	.010
	Based on Median and with adjusted df	7.932	2	4.059	.040
	Based on trimmed mean	8.354	2	9	.009
DOC	Based on Mean	2.448	2	9	.142
	Based on Median	.486	2	9	.630
	Based on Median and with adjusted df	.486	2	4.401	.645
	Based on trimmed mean	1.993	2	9	.192

CHAPTER 4:

AQUATIC HABITATS AND BIODIVERSITY OF AN EXPANSIVE RIVER FLOOD PLAIN

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ABSTRACT

River restoration and management is often directed at creating healthy stream ecosystems. There are perhaps many reasons for this myopic approach, including agencies and laws with species specific mandates; however a fundamental reason is that we lack basic knowledge of the community composition and food web structure in different habitats across river landscapes.Nowhere is this a more pressing concern than in highly productive and diverse river flood plains. Herein we describe biodiversity and food web relationships across aquatic habitats of the Nyack flood plain in northwestern Montana. We relate biodiversity pattern and process to habitat heterogeneity as described in the shifting habitat mosaic (SHM). SHM is fundamentally driven by fluvial geomorphic processes of channel avulsion, cut-and-fill alluviation, which in turn dictates groundwater/surface water exchange processes and associate biogeochemical cycling. We predicted metrics describing organismal densities and diversity and food webs of the flood plain would be greatly increased if off-channel habitats as well as main channel habitats were analyzed. Within the off-channel or "lateral" habitats we expected diversity and density to be: 1) reduced in areas of high hydrologic disturbance, i.e. shallow shorelines and backwaters, 2) moderate to high in low disturbance orthofluvial springbrook habitats, and 3) maximum in the intermediate disturbance parafluvial springbrook habitats. We also anticipated seeing a gradient in carbon resource utilization from reliance on algal carbon near the main channel to more reliance on terrestrial carbon in orthofluvial springbrooks, with a mix of resource utilization in parafluvial springbrooks. Evidence strongly supported the increased biodiversity and density of biotic organisms found in lateral habitats. Support for biotic variation and carbon signature as predicted for different lateral habitat types was mixed and revealed a more

complex suite of biotic interactions than originally envisioned. This warrants further investigation of the unique ecological communities of lateral habitats and their contribution to floodplain ecosystems.

INTRODUCTION

Rivers with expansive flood plains are common world wide but are among the most endangered landscapes on earth owing to human activities (Tockner and Stanford 2002). Anthropogenic change leads to loss of floodplain structure and function in an ecosystem context. This is unfortunate indeed because we have only recently begun to document and understand the biophysical linkages between the main river channel and its lateral and vertical components (Ward et al. 2002). Stanford et al. (2005) noted that floodplain rivers are characterized by a “shifting habitat mosaic” (SHM) created and maintained by the dynamic interaction of flooding, sediment and wood transport and deposition and primary plant succession. In a similar vein, Junk (2005) noted the extreme importance of flooding as a pulse disturbance that is a strong organizer of channel and floodplain habitats. Flooding is a primary attribute of all natural rivers, to which the biota of river ecosystems have adapted and diversified in consequence. These two key papers describe the interactive catenae of habitat types that characterize temperate and tropical rivers as one moves laterally away from the main channel through the aquatic-terrestrial transition zone to the terrace or hill slope environment of the river valley. The conclusion is that regional biodiversity maximizes on river flood plains as a consequence of the myriad of habitats associated with the SHM and the tendency of rivers to transport propagules of potential colonizers. Indeed, Mouw et al., (submitted) documented that 68% of the vascular plant flora known to occur in the central Rocky Mountain region (Glacier NP and adjacent areas) were found on the Nyack flood plain.

Few studies have documented the full range of aquatic habitat types that occur on expansive river flood plains, much less documented the diversity and life history strategies of biota that depend upon them. Long-term datasets exists for a handful of research sites located in gravel-bed river flood plains, including the Nyack (Stanford et al. 2005, Whited et al. 2007), Queets (Latterell et al. 2006, Van Pelt et al. 2006) and Tanana (Van Cleve et al. 1993, Viereck et al. 1993) rivers in North America, the Danube, Val Roseg, and Tagliamento River systems in Europe (Tockner et al. 1999, 2002, 2003), and the Taieri River in New Zealand (Townsend et al. 1997). Publications from each research group describe different aspects of the expansive nature of river flood plains. The Tanana work for example has focused on dynamic interactions between flooding, soil nutrients and riparian vegetation. In only three of these rivers have researchers attempted to document the full range of habitats and associated biota in an SHM context– the Tagliamento, Queets and Nyack.

The habitat catena of free-flowing rivers is organized into parafluvial and orthofluvial zones. Aquatic habitats in the parafluvial zone encompass the portion of the channel network that is flooded annually. Parafluvial habitats are characterized by cut, scour and fill alluviation by water and sediment. Aquatic habitats of the orthofluvial zone occur in topographic depressions where the water table intersects channel surfaces. River stage controls the degree of connectivity through overbank flooding and surface water-groundwater interactions. Orthofluvial habitats are dominated by depositional processes through flooding and terrestrial inputs.

SHM is fundamentally driven by fluvial geomorphic processes of channel avulsion, cut-and-fill alluviation, which in turn dictates groundwater/surface water exchange processes and associate biogeochemical cycling. This sets the stage for the regeneration of riparian vegetation and fuels primary production which sustains complex organismal organization, food webs and feedback loops of interaction between organisms and the floodplain itself. Hence, management plans or river restoration efforts that are not based in the concept of SHM that first take care of the primary fluvial geomorphic drivers (e.g. lacking normative flow) will fail because the fundamental structures and processes that shape, form and change the mosaic of habitats.

The SHM produces a network of aquatic habitats in off-channel areas that have very different habitat attributes in comparison with the main channel. Dynamic resource patches are available to biota living in off-channel or “lateral” habitats. These habitats provide vulnerable taxa with thermal, velocity, and depth refuges from disturbance and predators (Collier and Smith 2006, Anderson in prep). We expected SHM lateral habitat diversity would support a large suite of organisms that occur uniquely in the off-channel habitats. Biota living in off-channel habitats of the parafluvial zone must be responsive to stochastic changes in hydrology, temperature, substrate and nutrient availability. Organisms living in orthofluvial habitats have greater access to stable habitats and abundant resources but may face intense competition in obtaining those assets.

Herein we describe the spatial distribution and temporal variation in aquatic biota occupying lateral habitats of the Nyack flood plain, including macroinvertebrate, fish and amphibian assemblages. We predicted densities and diversity of organisms and food webs of the flood plain would be greatly increased if off-channel habitats as well as main channel habitats were analyzed. Within the off-channel or “lateral” habitats we expected diversity and density to be: 1) reduced in areas of high hydrologic disturbance, i.e. shallow shorelines and backwaters, 2) moderate to high in low disturbance orthofluvial springbrook habitats, and 3) maximum in the intermediate disturbance parafluvial springbrook habitats. We anticipated observing a gradient in carbon resource utilization, from reliance on algal carbon near the main channel to greater reliance on terrestrial carbon in orthofluvial springbrooks, with a mix of resource utilization occuring in parafluvial springbrooks. In order to document the structure and change in the biotic communities of different lateral habitats, we combined quantitative, seasonal sampling of benthic macroinvertebrates, fish and amphibians with a stable isotope analysis of food web structure. We also describe physical structure and organic matter availability in lateral habitats as a template for biological community development (see also Chapter 2 and 3).

METHODS

Study Site

The Nyack Flood Plain Research Natural Area (hereafter referred to as Nyack) is is a 20 km^2 aggraded reach of Middle Fork of the Flathead River in northwestern Montana (Fig. 1). The anastamosing channel network is embedded in an expansive forested and ranched landscape. The annual hydrograph is spring snowmelt driven, with discharges ranging from from 541 m^3 s^{-1} in May-June to 17 m^3 s^{-1} in December-January (Whited et al. 2007). As the Nyack is a long-term research site, many aspects of physical and biological site characteristics are described in a large array of recent papers. Two major projects were undertaken in the last 5 years to synthesize existing information and create a modeling framework for testing novel hypotheses regarding floodplain ecosystems.

The Nyack Biocomplexity Project was designed to model the dynamic biophysical processes that make this flood plain a regional center of ecological organization. The overarching project goal was to create a process model linking water, heat and materials flux and retention to the organization of the SHM (Poole et al. 2004, 2006). Nested within the larger Biocomplexity Project, investigators pursued focused studies of hydrology, forest structure and geomorphic dynamics (Harner and Stanford 2003, Whited et al. 2007, Mouw et al. submitted), along with the aquatic biota of parafluvial ponds (Chilcote 2004) and the aquifer (Reid 2007). The Nyack Microbial Observatory Program was established in 2004 to explore microbial diversity in the hyporheic zone of the aquifer. The intent of this project is to characterize microbial diversity in the context of factors influencing community structure and linkages between the microbial community and higher organisms such as insects and plants. To this end a grid of over 100 wells have been monitored and collected samples analyzed using innovative molecular, microbial and hydrologic techniques. Data from the Biocomplexity Project and Microbial Observatory Program projects, as well as previous work at Nyack (Bansak 1998, Ellis et al. 1988, Case 1998, Cavallo 1997, Pepin and Hauer 2002) that pertained to the objectives of this study were available through the Nyack Floodplain Database (described below).

In the study presented herein, sampling sites were chosen to represent the primary habitat types found at Nyack moving laterally from the main channel across the flood plain (Fig. 1; Fig. 2). Sites were located in one of five study reaches representing regional (floodplain scale) differences in groundwater upwelling and downwelling that arose longitudinally down the river corridor (Harner and Stanford 2003, Stanford et al. 2005). Using multispectral imagery managed in an ArcGIS platform (Lorang et al. 2005), reaches were divided into a series of 100 meter long stream segments. In each reach we randomly chose two of these stream segments along the main channel as study units in which to sample shallow shoreline and backwater habitats. Within the study unit a section of shallow shoreline habitat 30 meters in length was sampled. We defined the area to be sampled by including only the wetted region parallel to the shoreline that was less than 0.25 meters in depth. Backwater area was defined as all connected surface water channel down to the confluence with the main channel. Springbrooks are clustered on the landscape and could not be sampled as randomly as main channel reaches. Instead we located all major parafluvial and orthofluvial springbrooks within the floodplain (n = 5-6 per springbrook type) and randomly chose three to four of each springbrook type of study site from within this group. As these sites also possess a large surface area, multiple random sample sites within springbrooks were established to fully capture site variability.

Change in habitat structure associated with the flood-baseflow hydrograph

Sampling of variables defining the physical structure of lateral habitats occurred over the falling limb of the hydrograph in early summer (June-July), late summer (August-September) and fall (October-November) of 2003 and on the rising limb of the hydrograph in spring (March-April) of 2004. Because the lateral habitats are fed by upwelling groundwater from the alluvial aquifer, the volume of these habitats changes with river stage. Thus, during sampling events a single longitudinal and multiple horizontal transects were laid out in a grid across the habitat area. Point measures of channel width, water depth, and channel bottom temperatures were taken at 2-10 meter intervals depending on the length of the habitat. As part of a separate temperature study, thermographs were also placed at sample sites. In-steam percent cover of woody material and aquatic vegetation in the form of filamentous algae and macrophytes was estimated visually during each sampling event. Canopy cover of above stream vegetation was determined from digital photo interpretation of 1-4 photos taken at random intervals along the longitudinal transect.

Temperature and chemical patterns vary among the habitat types (see Chapters 2 and 3). Springbrooks exhibit less variable water temperatures year-round, providing cool water refugia in summer and warm water refugia in winter warm. This is especially true in orthofluvial springbrooks fed by water that has spent a longer residence time in the aquifer. In contrast, shallow shoreline areas of the main channel can 18-20^{o}C during the hottest parts of summer, and remain frozen for much of the winter. These same areas of the main channel annually lose most of their biofilm in late spring due to scouring flood flows. Biofilm communities recover pre-flood levels of biomass within 3-4 months following an annual flood, but recovery time is longer following bankfull or above flood flows. This same general pattern exists in parafluvial springbrooks, but large biomass of biofilms are maintained at a constant level in orthofluvial springbrooks. These habitats remain buffered from disturbance and only experience scouring flows in long return intervals (ca. 20 years). Springbrooks also exhibit higher alkalinity and phosphorous levels and lower dissolved oxygen and nitrogen levels in comparison with the main channel.

Invertebrates

Quantitative aquatic macroinvertebrate sampling coincided with physical habitat data collection. Our purpose was to sample as many habitats as possible and obtain the greatest diversity of organisms so we sacrificed some within site replication for between site replication. We collected 3 samples per major substrate site and pooled samples into a single jar per substrate type for a total of 1-4 samples per site per event.

Fixed area samples were obtained using a 0.25 m^2 surbur sampler (125 µm mesh) and or a fixed area bilge pump apparatus. The pump sampler was constructed using a vacuum hose attached to a bilge pump with a funnel head to break the vacuum seal created by pumping and allows placement even placement on the stream bottom. A plastic bucket with the bottom cut off was used as a sample frame by pushing the bucket into the substrate until a seal was formed with the bottom. The substrate in the surbur frame or in the bucket was disturbed to a depth of 5-10 cm to collect surface and shallow bed organisms. After disturbing the bottom, water in the bucket was pumped into a bolus net (125 µm mesh). All fixed area samples regardless of method were collected for 1 minute. In addition to the fixed area samples, we completed a timed search at each site in order to sample underrepresented aquatic microhabitats (vegetation, wood, shoreline edges) and collect rare taxa that might have been missed in quantitative samples. All invertebrate samples were preserved in the field in 50-80% ethanol and brought to 70-80% in the lab.

Sample processing in the lab depended on the sample volume. Small volume samples were drained through a small (15 x 20 cm) subsampling frame (125 µm mesh) partitioned into 15 grids while large sample volumes were drained through a similiarlu designed but larger (20 x 30 cm) frame sectioned into 30 grids. A 1:1 pick was done with the naked eye to remove large, rare taxa. Grids were selected using a random number generator for microscope sorting at 25 x power and sampled until a minimum of 300 organisms or the entire sample was picked clean. The Plecoptera, Trichoptera, Ephemeroptera, Coleoptera, Odonata, and Gastropoda were consistently identified to lowest possible taxonomic order and used in all analyses. The Diptera, and Hemiptera (Family Corixidae) were sorted and counted but not consistently identified to lowest taxonomic level. These two groups were included in total invertebrate density estimates but excluded from diversity metrics. The Arachnida (water mites), Tricladida, Branchipoda, Maxillopoda, Clitellata, Cladocera, Hydra and Glossiphonidae were present in samples but consistency in sorting and counting these specimens could not be assured, thus they were excluded from formal density and diversity analyses. All samples were sorted by the first author with the help of three laboratory assistants. All identifications were performed by R. Newell or the first author. Data for Ephemeropta, Plecoptera, and Trichoptera distinct taxa (hereafter referred to as EPT taxa) were plotted using seasonal habitat specific taxa rank abundance plots. We selected EPT taxa richness because of its extensive use both in the United States and world-wide as a measure of water quality (Lenat and Penrose 1996). EPT taxa were also assigned to functional feeding group classifications adapted from Merritt, Cummins, and Berg (2007).

Vertebrates

As many aquatic vertebrates are diurnally active, day and night visual surveys were used in the early summer, late summer and fall of 2004 to ensure a complete assessment of vertebrate community structure. Surveys consisted of snorkeling in habitat reaches with water deeper than 0.5 meters (main channel, backwaters, springbrooks) and visual surveys along bank edges of shallower waters (shallow shoreline, backwater and springbrook channel edges). Surveys were conducted along 20-100 meter transects depending upon the length of the habitat, while width varied from habitat to habitat as described in the physical characteristics section above. Day surveys occurred between 10:00 to 14:00 hours while night surveys were conducted with a divelight between the hour after dusk and 01:00 hours. All snorkeling was performed by the author (M. Anderson) while data on vertebrate species' identity, number and size (1-5 cm increments) were recorded by a bank observer. The bank observer also performed a visual survey of shallow stream edges inaccessible to the snorkeler. Unadjusted densities of fish and amphibians per 100 m^2 were calculated from these field surveys.

Diversity Metrics

Seasonal habitat specific diversity metrics were analyzed using the quantitative measures of species distribution and abundance outlined above. Analysis was restricted to taxa that could be identified to the level of genera. The average number of taxa per site (site average taxa richness, α_s) was combined with abundance data to calculate Shannon (H') and Simpson (1/D) indices of diversity and evenness (E). These measures complement one another, with indices biased towards richness (α_s, H') offset by an index biased towards evenness (1/D). Turnover of species (β) across the four lateral habitat types in a given season was assessed using Whittaker's measure. Each of these diversity indices was calculated as described in Magurran (1998).

Using data for the Nyack from a wide variety of sources (see the "Data management" section below), we derived total species richness by habitat type (α_h) and regional species richness for the entire floodplain (γ_f). We compared γ_f to Western United States regional diversity (γ_W) for Ephemeroptera, Plecoptera, Trichoptera and Odonata. The γ_W measure was developed from taxa occurrence tables in Merritt, Cummins, and Berg (2007).

Organic Matter

A relative index of benthic organic matter (BOM) in different aquatic habitats was created from the quantitative benthos sample material processed in the laboratory. We deemed the index relative as somewhat different sediment fractions are likely sampled depending upon the method of benthos sampling (i.e. surbur versus benthic pump samples). After removal of macroinvertebrates from benthos subsample grids, the remaining sediment and organic material was placed in tinfoil packets, dried overnight at 60^{o} C and weighed the following day. Material was then ashed at 500^{o} C for one hour, rewetted, dried at 60^{o} C overnight and reweighed to determine the final ash-free dry mass of BOM. Subsample BOM weights were averaged by site and season.

Leaf litter samples were collected from stands across the flood plain. Stands were classified as young *Populus* (10-15 years), pole *Populus* (15-20 years), mature *Populus* (20-50 years), old mixed conifer and *Populus* (50-100 years), and old conifer (>100 years). Age classes were previously determined by Harner and Stanford 2000). In general, young and pole *Populus* stands where in proximity to actively scoured lateral habitats (shallow shorelines, backwaters, parafluvial springbrooks). Mature stands occurred in depositional parafluvial and orthofluvial zones. Old growth stands were strictly orthofluvial and flooded rarely. Some parafluvial and all orthofluvial springbrooks were located in these older stands. Leaf litter was collected in the fall following leaf abscission using three mesh hoop baskets (1 m^2 opening) placed on the forest floor at 3 to 10 sites per stand type. Leaf litter was taken back to the Flathead Lake Biological Station Freshwater Research Laboratory where it was dried, weighed and analyzed for carbon, nitrogen and phosphorous content. This provided a measure of annual aerial loading of nutrients in forest stands.

Food Web

Samples of biota were collected at two field sites per habitat to describe seasonal food web structure using stable isotope analysis. Isotope samples were collected in the summer of 2003 and the spring, summer, and fall of 2004. Multiple specimens were placed in chemically inert plastic vials on dry ice and transported to the FLBS Freshwater Laboratory, where they were frozen for later processing. In order to sample more habitats and achieve the mass necessary for analysis of certain sample types, we pooled multiple individuals or leaves within taxa per sample event to obtain an average site value for vegetation and macroinvertebrate samples. Individual fish were sampled and processed separately using dorsal muscle tissue. Samples were dried in tinfoil envelopes at 60^o C until free of moisture, which was 6 to 48 hours depending on the type of sample. Dried samples were ground into a fine powder using a ball-mill grinder, transferred into glass scintillation vials and re-dried at 60^{o} C. A 1 to 10 µg sample of dried material was weighed out into tin capsules. Sample weight varied by specimen type to achieve a single sample balance of 50-1500 µg carbon and 20-200 µg nitrogen content for optimal dual stable isotope analysis, based on preliminary isotope analyses. All materials used in sample preparation were rinsed with dissolved ionic water and dried with heat or nitrogen gas between samples.

Samples were shipped to the University of California-Davis Stable Isotope Facility where dual δ13C and δ15N isotope analysis was performed with a Europa 20/20 continuous-flow isotope-ratio mass spectrometer (PDZ Europa Ltd., Cheshire, U.K.). Isotope data is presented as δ, the parts per thousand differences from standards of Pee Dee Belemnite limestone for δ13C and atmospheric nitrogen for δ15N, using the following equations (Peterson and Fry 1987):

$$\delta\ ^{13}C = \{(^{13}C/^{12}C \text{ sample} /\ ^{13}C/^{12}C \text{ standard})-1\} \times 10^{3}$$

and,

$$\delta\ ^{15}N = \{(^{15}N/^{14}N \text{ sample} /\ ^{15}N/^{14}N \text{ standard})-1\} \times 10^{3}$$

Isotope data points where organized by season and trophic level as primary producers, mid-level consumers and predators. At the data analysis stage we combined data points from shallow shoreline and backwater sites. This decision was based on the small number of samples collected and the observed low variability among data points, which was attributed to the proximity of these habitats to each other and the main channel. Furthermore, data presented in seasonal dual isotope plots was mainly 2004 data. As it appeared there were few differences in values across years we felt comfortable including a few select data points from 2003 for taxa not well sampled in 2004. Trophic level was assessed using a combination of known species life history characteristics and dual isotope plot results. Finding a well-distributed, long-lived taxon as suggested by Post (2002) to serve as a baseline for food web analysis proved impossible. Instead we chose a group of primarily herbivorous mayflies (*Cinygmula, Ameletus, Baetis*) that were common and had an overlapping distribution across sites and seasons to serve as the isotopic baseline. We assumed trophic transfers resulted in a trophic enrichment of >1‰ for δ^{13}C and 3-4‰ for δ^{15}N (Post 2002). Basic isotope metrics of food web structural complexity, including the overall δ^{15} N range of vertical food web structure and the δ^{13} C range in values indicative of niche diversification, were calculated as described by Layman et al. (2007).

Data management

In order to assess floodplain wide patterns of aquatic diversity we supplemented data mentioned above with taxonomic records and habitat data from all previous studies at Nyack organized by habitat type, spatial location and taxonomic descriptor. This included the records of all known taxa ever collected at Nyack. A reference collection of taxonomic species is stored in museum format at the FLBS Freshwater Laboratory and maintained by the FLBS curator of aquatic invertebrates. Taxonomic identifications were confirmed by a wide array of experts in the USA and abroad, as noted in the data base that describes the collections. All Nyack biophysical data and associated metadata, including taxonomic records, are maintained by the FLBS data manager, as a single, spatially explicit Nyack Floodplain Database.

RESULTS

Seasonal changes in physical habitat

The physical characteristics of habitat types varied by location and season; surface area (and volume) varied with river stage and temperature patterns were spatially and seasonally complex (Table 1 – see Chapter 2 for a more detailed analysis of temperature patterns). Peak surface area and temperatures in backwaters and all springbrooks followed early summer flooding. In contrast, shallow shoreline habitats exhibited greatest surface area and temperatures in late summer. Parafluvial springbrook surface area was high in both early summer and fall. Average depth ranged from 0.2 to 0.3 meters at all sites except for backwaters in late summer, with an average depth of 0.6 meters. Instream wood and aquatic vegetation cover was low in shallow shorelines and backwaters (0-10%) in comparison to both springbrook types (10-40%). Canopy cover was consistently below 25% across habitats and seasons.

Variation in density and diversity of invertebrate taxa

Densities of major invertebrate groups counted from fixed area samples varied seasonally by habitat type (Fig. 3), with the least annual variation occurring in orthofluvial springbrooks (5,250 to 9,550 invertebrates / m^2) as opposed to a high degree of annual density variability in shallow shorelines (3,540 to 20,210 invertebrates / m^2). Parafluvial springbrooks, shallow shorelines and to a lesser extent backwaters had similar high peak abundances but in different seasons. Shallow shoreline and backwater densities were at maximum in the late summer while parafluvial springbrooks in were greatest in fall.

The density and diversity of macroinvertebrate taxa showed subtle patterns across season and habitat (Table 2). While densities of taxa in shallow shorelines remained highest in late summer, backwaters were greatest in early summer, while orthofluvial springbrooks reached a zenith in spring. Densities of taxa in all habitats were associated with large standard deviations and percent coefficient of variation, indicated major sample differences within sites, particularly in spring. Average site α remained similar across habitats within season except for the large α = 18 for parafluvial springbrooks in late summer, 8 taxa higher than any other habitats and the highest value observed across seasons. Generally α values across and within sites were higher in summer and lower in spring and fall, with the exception of maximum seasonal α = 13 for orthofluvial springbrooks in the spring. The absolute values of H' and 1/D indices were well correlated within and across seasons. As these metrics are biased alternately towards richness (H') and evenness (1/D), this supports the reliability of our diversity measurements. Percent coefficient of variation did not necessarily correspond and did not reveal a discernable pattern. Within season absolute values were higher in both springbrook types than either of the other two habitats, with maximum values for shallow shorelines, backwaters and springbrooks occurring in late summer and orthofluvial springbrooks in the spring. Except for a low evenness value of 0.4 in parafluvial springbrooks in the late summer and high evenness of 0.7 in parafluvial springbrooks in the late summer and orthofluvial springbrooks in the spring, evenness of diversity was similar at 0.5 to 0.6 across seasons and habitats. Sample-β was consistent across sites in early summer but varied across habitat types in other seasons, remaining low in parafluvial springbrooks in late summer and orthofluvial springbrooks in the spring while reaching high levels of turnover in the spring for shallow shorelines and backwaters.

Many of these same diversity and abundances patterns were observed in finer detail in the EPT rank abundance curves (Fig. 4). All habitats showed large shifts in rank abundance distributions across seasons. In early summer and spring the orthofluvial springbrook curve appeared to fit the geometric series with high species abundance and evenness, while lower and more variable species richness and evenness produced a log normal model fit in late summer and a log series model in the fall. The three remaining habitat types fit the log normal series across seasons most seasons. The exceptions to this were backwater habitats in late summer and both backwaters and shallow shorelines in spring, all of which more closely approximated the log series. The log series is viewed with caution as the appearance of model fit may have been an artifact of the small number of species sampled (n = 9-11) as opposed to a biologically relevant pattern (May 1975). Greatest EPT species richness (n=21) and abundance was observed in the shallow shoreline data in late summer. The lowest species richness (n=9) and abundance was found in backwaters during late summer.

The mayflies *Ameletus* and *Cinygmula* dominated EPT abundances of all habitat types in early and late summer, but were more restricted to parafluvial springbrooks in fall and backwater and shallow shoreline habitats in spring. Another common mayfly, *Paraleptophlebia* was prevalent across habitats in late summer and in orthofluvial springbrooks in the spring. Two taxa of seasonal high abundance in specific habitats were *Rhyacophila* (Trichoptera) in late summer and fall in orthofluvial springbrooks and *Utacapnia* (Plecoptera) in backwaters and shallow shorelines in the spring. Within a season each habitat contained 2 to 4 unique taxa not found in other habitats during that season. Across seasons 5 taxa were unique to both springbrooks, 3 were unique to backwaters and 1 taxon was unique to shallow shorelines. However, comparison of these records to the global dataset confirmed the presence of most taxa more broadly across other habitats. The exception to this was *Asynarchus (Trichoptera)*, which was restricted to orthofluvial springbrooks in both the seasonal EPT samples and the global dataset.

Omnivores dominated the EPT taxa across habitats (Fig. 5), especially in fall, while the contribution of predators and grazers was most variable in space and time. Grazers are most dominant across sites in late summer, although their proportional abundance remains fairly consistent in parafluvial springbrooks throughout the year. Predators are almost equally abundant in early and late summer, in all but the orthofluvial springbrook sites which showed a marked proportional late summer decrease. Detritivores contributed most to dominance measures in the summer. A strong contrast arose in spring when detritivores are at their maximum seasonal percent dominance in backwaters and their minimum in orthofluvial springbrooks.

Variation in density and diversity of vertebrate taxa

The density of aquatic vertebrates was low in all habitats in early summer and high in late summer (Fig. 6-9). From late summer through the fall, fish nighttime abundance increased as daytime abundance decreased, while the opposite was true for amphibians. No clear pattern of seasonal diversity existed across sites. Diel variation did occur in all seasons with fish diversity much higher across habitats at night, while amphibian diversity was slightly elevated during the day.

Species abundance and occurrence varied across lateral habitats. Suckers (*Cattastomus cattastomus*) dominated backwaters, ponds and parafluvial springbrooks, brook trout (*Salvelinus fontinalis*) prevailed in orthofluvial springbrooks and sculpin (*Cottus* spp.) were most prevalent in shallow shorelines (Fig. 6-7). Whitefish (*Prosopium williamsoni*) were widespread but their numbers varied greatly by habitat and season. Native westslope cutthroat (*Onycorhyncus clarki lewisi*) and bull trout (*Salvelinus confluentus*) were rare in all habitats but were observed more often in all seasons occupying parafluvial springbrooks at night (Fig. 7).

Amphibians had limited overlap in distribution, with boreal toads (*Bufo boreas*) occupying ponds and to a lesser extent parafluvial springbrooks and backwaters, while large numbers of Columbia spotted frog (*Rana lutrievensis*) occurred only in the orthofluvial springbrooks (Fig. 8-9). Garter snakes (*Thamniopsis* spp.) were observed twice during the course of surveys, once in a shallow shoreline at night and once in a backwater during the day. Tailed frogs (*Ascaphus trueii*), although not observed as part of this study, are known from the global dataset to occur rarely in the shallow shoreline and main channel habitats.

Species richness across the flood plain

The comparison of aquatic habitat diversity using the Nyack Floodplain Database revealed that orthofluvial springbrooks contained the most taxa (148), while hyporheic environments contained the least (30) (Fig. 10). Among groups of macroinvertebrate taxa considered, hyporheic environments harbored only the stoneflies (Plecoptera; 19), mayflies (Ephemeroptera; 7) and beetles (Coleoptera; 4). Mayflies and vertebrates achieved maximal species richness in orthofluvial springbrooks and minimal species richness in parafluvial ponds. In contrast coleopteran, gastropod, and odonate species richness peaked in parafluvial ponds. Values for all three groups were similar across habitats, with some decline in beetle taxa diversity near the main channel. Caddisfly and stonefly diversity varied widely across habitats. Caddisfly richness (Trichoptera; 47 species) was highest in orthofluvial springbrooks and declined to 16 taxa or less in backwater, shallow shoreline, and main channel habitats. Stonefly species richness was bimodal, with a peak in both the main channel (43) and orthofluvial springbrooks (38) and minimum richness in parafluvial ponds (10). Vertebrate taxa richness varied little across surface water habitats, with only a slight reduction in parafluvial ponds (7 of 10 taxa).

Less than half of the 168 taxa occurred widely among the habitat types (Fig. 10b). Moreover, only 10 species were unique to the main channel while 88 were spread among the off-channel habitats. As a group, Odonata and Gastropoda were entirely restricted to lateral habitats, as were most Coleoptera. Eleven taxa of mayfly and 15 of caddisfly taxa were restricted to lateral habitats, while in the main channel only a small subset of total stonefly and caddisfly were restricted. Most genera were broadly distributed among lateral habitat types, with few taxa restricted to a single type of lateral habitat.

Total diversity (γ) for the entire flood plain included 168 taxa of aquatic organisms, of which insects were by far the dominant group whereas the ichthyofauna (6 species) and amphibians (4 species) was notably depapurate. Comparing the regional diversity of aquatic insect fauna at Nyack to regional diversity of fauna in Western streams, we find a remarkably high percentage of all known stonefly and mayfly taxa occur at Nyack. Nearly 70% of Plecoptera taxa ($\gamma_f = 40$; $\gamma_W = 62$) and 42% of Ephemeroptera taxa ($\gamma_f = 24$; $\gamma_W = 57$) in Western streams are found at Nyack. Odonata were at 36% of Western taxa ($\gamma_f = 12$; $\gamma_W = 33$) and Trichoptera ($\gamma_f = 32$; $\gamma_W = 114$) were at 28% of Western taxa, but we suspect these percentages at Nyack will grow with inclusion of thorough sampling in orthofluvial pond habitats.

Organic matter availability

Aerial loading of allochthonous nutrients increased with age of the cottonwoods in the vegetation chronosequence to reach a maximum in old mixed forest stands, providing 2 to 3 times greater nutrient availability than in young stands. Loading rates dropped off sharply in old-growth stands dominated by conifers (Fig. 11).

No significant differences were found in benthic organic matter collections among the habitat types across seasons (Fig. 12). However, BOM in spring channels was much higher overall than in the main channel shallow shorelines as a consequence of increased nutrient availability in the upwelling ground water (see Chapter 3).

Lateral habitat food web structure

We were unable to discern clear differences in isotope signatures for primary producers that would separate values along habitat or seasonal lines (Fig. 13). However, a general pattern of signature variation emerged when comparing groups of primary producers. Nitrogen values of primary producers were depleted and varied by species across seasons, ranging from a low of -8.46‰ $\delta^{15}N$ for *Picea* to a high of -1.06‰ $\delta^{15}N$ for *Salix*. The carbon signatures of terrestrial plants fell in a narrow range of -29.59‰

δ^{13}C to -26.80‰ δ^{13}C. CPOM and FPOM appeared to be derived from terrestrial carbon sources and were enriched in carbon and nitrogen over the original terrestrial plant signatures. Orthofluvial springbrook CPOM and FPOM values were slightly depleted in both carbon and nitrogen in relation to other habitats across seasons. Biofilm samples showed the most variation in carbon signatures of any primary producer, with no obvious seasonal or habitat specific clustering. Nitrogen values for biofilm were more constrained, falling between -2‰ to +1‰ δ^{15}N with one suspiciously low value at -5.05‰ δ^{15}N in the main channel in summer. This broad spectrum of δ^{13}C values among biofilm samples precluded use of a two end-member mixing model analysis of ultimate carbon sources supporting the trophic food web of different habitats at Nyack.

Minimal fall collection of mid-trophic level consumers restricted analysis to spring and summer samples, in which we found marked seasonal and habitat specific differences in isotopic signatures (Fig. 14). In the spring a high degree of overlap in carbon and nitrogen signatures of consumers was present across habitats. Carbon values of consumers fell within or were depleted beyond the range of terrestrial carbon sources, with the low value occurring in a chironomid sample (-36.27‰ δ^{13}C). Nitrogen values ranged 2‰ δ^{15}N (+0.39‰ to +2.54‰ δ^{15}N). Assuming a trophic enrichment of 3-4‰, this points to consumer intake of riparian vegetation carbon sources such as *Populus*, *Salix* and *Alnus*. In summer a clear habitat separation in values was visible, with orthofluvial springbrook carbon signatures consistently falling below -30‰ δ^{14}C while parafluvial springbrook and main channel signatures were consistently enriched above this value. The range in nitrogen values was greater across habitats in summer, indicating a longer and more varied food chain. Ephemeroptera expressed the most variation in N and C signatures of any consumer group, which matches their broad dietary differences among species.

As was the case for primary producers, no clear habitat specific relationships in isotopic signatures were observed among predators (Fig. 15). Seasonally, nitrogen and carbon signatures were most variable across habitats in summer and least variable in the fall. Fish nitrogen signature spanned a wide range of values in summer, but carbon signatures banded more closely between -29.32‰ to -24.66‰ $\delta^{13}C$. This range of carbon values corresponds with terrestrial carbon and FPOM signatures, which may indicate significant feeding by fish on terrestrial insects. Aquatic and terrestrial insect predators exhibited carbon isotope signatures on the same level as sculpin (*Cottus* spp.) and amphibians, indicating all of these groups are likely feeding on similar invertebrate prey sources. Brook trout adults were the group most enriched in nitrogen across the entire food web (+6‰ $\delta^{15}N$), indicative of feeding on other predatory taxa.

The total range in $\delta^{13}C$ and $\delta^{15}N$ values across seasons and habitats was 26.96‰ $\delta^{13}C$ (-39.84‰ to -12.88‰) and 14.84‰ $\delta^{15}N$ (-8.46‰ to 6.38‰) which was interpreted as a sign of a remarkable degree of vertical structure and niche diversification.

DISCUSSION

Predictions: density, diversity, and food web structure

We predicted density of organisms would be low but variable across habitats post-flood due to a combination of spring seasonal emergence of aquatic insects coupled with flood disturbance of benthic habitats. We expected densities, diversities and food web complexity to be lowest in areas of high hydrologic disturbance, i.e. shallow shorelines and backwaters, moderate in the low disturbance orthofluvial springbrook habitats, and highest in the intermediate disturbance parafluvial springbrook habitats. Finally we anticipated seeing a gradient in carbon resource utilization from reliance on algal carbon near the main channel through to reliance on terrestrial carbon in orthofluvial springbrooks, with a mix of resource utilization in parafluvial springbrooks.

Invertebrate densities followed expected pattern within habitats in time but not across habitats. Shallow shoreline, backwater and parafluvial springbrook invertebrate densities increased steadily over the post-flood season through the fall and declined into the spring. We assume this is due to insect emergence from these habitats. Orthofluvial springbrook densities remained constant across seasons, which we attribute to a lack of seasonal temperature cues triggering emergence. When the subset of identifiable EPT, beetle, dragonfly, damselfly and gastropod taxa were counted, backwater invertebrate densities fell sharply across seasons following an early summer peak, parafluvial springbrook densities remained relatively constant across seasons and orthofluvial springbrook densities bottomed out in late summer and peaked in the fall.

Regardless of which grouping was used and contrary to our expectations, shallow shoreline invertebrate densities were highest of all habitats in early summer. We attribute this as a response to flood disturbance opening up niche space coupled with resource availability of periphyton in late summer (see Chapter 3). This explanation could also apply to parafluvial springbrook peak invertebrate abundances between early and late summer, as these areas are flooded but less severely and their algal base rebounds more quickly. The converse scenario of niche stability and seasonal consistency of algal resources would explain continuity in overall invertebrate abundance in orthofluvial springbrooks. Temperature dynamics (Chapter 2) in orthofluvial springbrooks may explain the high density estimates of the narrow focus group as this estimate was driven by delayed maturity of *Paraleptophlebia*, *Diphetor*, *Baetis*, and *Neophylax* (Table 4).

Vertebrate density patterns followed our expectation of highest densities in late summer but differed from our expectations of spatial distribution. This was often driven by the extremely high densities of a single species life history stage in a particular habitat. For example, early summer backwater and shallow shoreline density is driven by large numbers of juvenile suckers. Parafluvial ponds had the highest late summer vertebrate densities again due to large numbers of suckers coupled with boreal toad tadpoles. Orthofluvial springbrooks had elevated densities in the fall of spotted frogs, as they apparently moved towards thermally stable wintering habitats.

Diversity was more equitable across habitats than expected and did not follow the seasonal flux in disturbance. All measures of invertebrate and vertebrate diversity remained high throughout habitats in summer, and appeared to decline through the fall. Spring may have been the period with lowest diversity but it is difficult to tell as we lacked winter samples of invertebrates and both winter and spring vertebrate samples. The most interesting patterns appeared, as with density, when we looked at species distribution as a driver of diversity within habitats across seasons. Less than half of species were found within a habitat were observed in sequential seasons, indicating a high degree of turnover in conjunction with environmental heterogeneity as a possible temporal niche separating mechanism as has been observed in lake systems (Hutchinson 1957). A high degree of species variation may be driving divergence in species rank abundance patterns if distinct species use resources in different ways. In early summer the orthofluvial springbrook curve (Fig. appeared to fit the geometric series, indicating species abundance at these sites was proportional to resource utilization in that the most abundant species take advantage of the most abundant resources (Magurran 1988). The curves for many of the habitats fit the log normal series, indicative of systems in which species abundance is suspected to be proportional to niche space apportionment (Sugihara 1980).

Our ability to predict food web pattern was confounded by the variable signature of periphyton and the high overlap in signatures of common groups across habitats. Although there is some evidence that terrestrial inputs to shallow shoreline and backwater habitats are less than other lateral habitats (Fig. 11-12), it was difficult to rule out the importance of terrestrial subsidies without a distinct algal carbon signature. We do see a division of carbon signature between orthofluvial springbrooks and other habitats in mid-trophic consumers in summer (Fig. 14). We suggest this issue will only be resolved by more work to determine factors governing algal carbon variability. Finlay et al. (2004) suggests DIC may play a role which, coupled with our understanding of the complexity in groundwater and surface water interactions at Nyack, would explain this variation. The only known source of carbon signatures lower than terrestrial vegetation at Nyack comes from sampling carbon from the aquifer (Reid 2007).

There is evidence that seasonality exists in food web structure within different taxa as well. Brook trout nitrogen signatures were more variable early in the summer between juvenile brook trout, which appear to be feeding at lower trophic levels, and adult brook trout, which are eating other predatory taxa (Fig. 15). By late summer the larger juvenile brook trout have a nitrogen and carbon signature nearly indistinguishable from adult brook trout, suggesting a common diet. We also observed a shift in overall range of carbon and nitrogen values seasonally, with the greatest variation occurring in summer when it appears both resources and taxa are abundant.

Community structure and the SHM

Perhaps the most remarkable result of this analysis is the clarity and uniqueness of habitat specific biotic diversity (Fig. 10). Lateral habitats contribute greatly to floodplain regional diversity. This is evidenced in the rich beetle and gastropod fauna of parafluvial ponds and caddisfly fauna of orthofluvial springbrooks. Our records of lateral habitats are also not yet complete as a survey of orthofluvial ponds has not yet been comprehensively undertaken. Uniqueness of off-channel habitats was also observed at Nyack in parafluvial ponds by Chilcote (2008) and for the Taglimento River in Italy (Arscott et al. 2005). Habitat heterogeneity, frequently cited as a driver of diverse animal assemblages (MacArthur 1972, Hansen 2000), is high across the Nyack flood plain as a result of hydrologic disturbance reorganizing sediment, wood, water and with these, nutrients (Stanford et al. 2005, Anderson in prep.). We believe this habitat heterogeneity is provides the diversity of niches allow creation of the diverse assemblages of biota observed in this study.

Mathematical modeling (Roxburgh et al. 2004), lab experiments (Cardinale and Palmer 2002) and field studies (Whiles and Goldowitz 2001) indicate that coexistence occurs if competitors occupy a spatially and temporally patchy landscape shaped by disturbance. Organisms respond differently to disturbance and disturbance itself creates spatial and temporal variation in resource availability across the landscape (Stanford et al.

2005). The prevalence of omnivory in our system is not surprising, as it has been observed in other systems that omnivory may be a successful strategy to dealing with disturbance mediated pulses of food resources in streams (Huang et al. 2007).

Teasing apart the important elements of diversity in a system as complex as the Nyack floodplain relates to recent debates by ecologists on the role and importance of "functional diversity" in regulating ecosystem processes (Petchey and Gaston 2002). For example, the strength of the diversity-productivity relationship appears to be influenced by disturbance gradients, with greater biomass accumulation in disturbed environments with species rich aquatic communities of algae (Cardinale et al. 2005). Most studies have focused on tractable manipulations of plant communities (Tilman et al. 1996) or aquatic biofilms (Jackson et al 2001) as opposed to the daunting challenge of manipulating a fluctuating environment like a floodplain. Due to their physical complexity, disturbance regimes, successional trajectory and diverse assemblages, floodplains ecosystems present significant challenges to addressing functional roles and diversity of organisms.

In order to discern factors regulating habitat heterogeneity and biodiversity in floodplain environments, we will need a better understanding of the relationship between productivity, biomass, dispersal and species interactions in these systems (Mittelbach et al. 2001, Urban 2004), especially in the context of flood disturbance as some rivers become more flashy. Lateral habitats likely support a large flux of organisms across the landscape, creating a subsidy to upper level food web consumers (Nakano et al. 1999, Baxter et al. 2004).

It is now apparent that lateral habitats and their rich fauna must be considered in the management and protection of floodplain biodiversity. Pervasive alteration to rivers has severely impacted floodplain ecosystems throughout North America (Stanford and Tockner 2002). Additionally, climate change is expected to impact the aquatic biota of mountainous landscapes severely and in potentially difficult to predict ways (Fureder 2006, Harper and Peckarsky 2006). Restoration efforts have mainly focused on smaller streams (Bernhardt et al. 2005), with re-establishment or maintenance of collective stream ecosystem health frequently cited as a management objective. Yet we rarely create management plans that address the ecology of entire communities of organisms. Instead we have focused on conserving a small, and thus tractable suite of species, mainly fish (Schindler et al. 2003), amphibians (Alford and Richard 1999), molluscs (Lodge and Kelly 1985) or riparian trees (Braatne et al. 1996). Lateral habitat physical and biological structure and function are driven by hydrogeomorphic processes. These process drivers will need to be brought back into balance first and then the primary structure and functional drivers will reset the system so that the biota can respond.

The rich biodiversity and complexity of geomorphic processes that makes floodplains so valuable will also then make them a challenge to study, conserve and restore. One of the major justifications for studying gravel bed river flood plains is that they have disturbance intervals conducive to human observation. Coupled with the opportunity to manipulate whole large scale systems, this ability to document variation in disturbance affects should advance ecological thought. Furthermore, we expect a large variety of species will need to be maintained to insure that vital ecosystem goods and services provided by floodplains are protected (Elmqvist et al. 2003, Hooper et al. 2005).

In order to preserve this species diversity, we will need to protect or restore the lateral habitats of the expansive flood plain. Recent restoration work to re-connect rivers with their flood plains on the Green River (Modde et al. 2001) in Utah, the Colorado River below Glen Canyon Dam (Stevens et al. 2001) in Arizona, the Tummel River in England (Parsons and Gilvear 2002), and the Main and Rodach Rivers in Germany (Speierl et al. 2002) have produced hopeful results. In these systems it appears that when off-channel habitats are re-connected to their flood plain a significant level of habitat and biotic diversity is restored within years to decades.

LITERATURE CITED

Alford, R., and S. J. Richards. 1999. Global amphibian population declines: a problem in applied ecology. Annual Review of Ecology and Systematics **30**: 133-165.

Arrington, D. A., and K. O. Winemiller. 2006. Habitat affinity, the seasonal flood pulse, and community assemble in the littoral zone of a Neotropical floodplain river. Journal of the North American Benthological Society **25**: 126-141.

Arscott, D. B., K. Tockner, and J. V. Ward. 2003. Spatio-temporal patterns of benthic invertebrates along the continuum of a braided Alpine river. Archiv fuer Hydrobiologie **158**: 431-460.

Arscott, D. B., K. Tockner, and J. V. Ward. 2005. Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. Journal of the North American Benthological Society **24**: 934-954.

Bansak, T. 1998. The influence of vertical hydraulic exchange on habitat heterogeneity and surficial primary production on a large alluvial floodplain. M.S. Thesis. University of Montana, Missoula, Montana, USA.

Barquin, J., and R. G. Death. 2006. Spatial patterns of macroinvertebrate diversity in New Zealand springbrooks and rhithral streams. Journal of the North American Benthological Society **25**: 768-786.

Beechie, T. J., M. Lierman, E. M. Beamer, and R. Henderson. 2005. A classification of habitat types in a large river and their use by juvenile salmonids. Transactions of the American Fisheries Society **134**: 717-729.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. brooks, J. Carr, J. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B.

Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science **308**: 636-637.

Braatne, J. H., S. B. Rood, and P. E. Heilman. 1996. Life history, ecology and conservation of riparian cottonwoods in North America. In: Biology of *Populus*: Implications for management and conservation. National Research Council of Canada, Ottawa: 57-85.

Cardinale B.J., M. A. Palmer, A. R. Ives, and S. S. Brooks. 2005. Diversity-productivity relationships in streams vary as a function of the natural disturbance regime. Ecology **86**: 716-726.

Cardinale, B. J, and M. A. Palmer. 2002. Disturbance moderates biodiversity-ecosystem function relationships: experimental evidence from caddisflies in stream mesocosms. Ecology **83**: 1915-1927.

Case, G. L. 1995. Distribution and abundance of zoobenthos in channel, springbrook and hyporheic habitats of an alluvial floodplain, M.S. Thesis, University of Montana, Missoula, Montana, USA.

Cavallo, B. J. 1997. Floodplain habitat heterogeneity and the distribution, abundance, and behavior of fishes and amphibians in the Middle Fork Flathaed River Basin, Montana. M.S. Thesis, University of Montana, Missoula, Montana, USA.

Chilcote, S. 2004. The ecology of parafluvial ponds on a Rocky Mountain floodplain. Ph.D. Dissertation, University of Montana, Missoula, Montana, USA.

Ellis, B. K., J. A. Stanford, and J. A. Ward. 1998. Microbial assemblages and production in alluvial aquifers of the Flathead River, Montana, USA. Journal of the North American Benthological Society **17**: 382-402.

Elmquist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment **1**: 488-494

Fureder, L. 2007. Life at the edge: Habitat condition and bottom fauna of alpine running waters. International Review of Hydrobiologia **92**: 491-513

Harner, M. J. and J. A. Stanford. 2003. Differences in cottonwood growth between a losing and gaining reach of an alluvial floodplain. Ecology **84**: 1453-1458.

Hansen, R. A. 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology **81**: 1120-1132.

Herwig, B. R., D. A. Soluk, J. M. Dettmers, and D. H. Wahl. 2004. Trophic structure and energy flow in backwater lakes of two large floodplain rivers assessed using stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences. **61**: 12-22.

Hoeinghaus, D. J., K. O. Winemiller, and A. A. Agostinho. 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. Ecosystems

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Lorveau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75**: 3-35.

Huang, I., Y. Lin, C. Chen, and H. Hsieh. 2007. Food web structure of a subtropical headwater stream. Marine and Freshwater Research **58**: 596-607.

Hutchinson, G. E. 1957. The paradox of the plankton. The American Naturalist **95**: 137-145.

Jackson, C. R., C. F. Perry, and E. E. Roden. 2001. Successional changes in bacterial assemblage structure during epilithic biofilm development. Ecology **82**: 555-566.

Junk, W. J. 2005. Flood pulsing and the linkages between terrestrial, aquatic, and wetland systems. Verhein Internationale Vereinigung Limnologie **29**: 11-28.

Latterell, J. J., J. Scott Bechtold, T. C. O'Keefe, R. Van Pelt, and R. J. Naiman. 2006. Dynamic patch mosaics and channel movement in an unconfined river valley of the Olympic mountains. Freshwater Biology **51**: 523-544.

Lenat, D. R., and D. L. Penrose. 1996. History of the EPT taxa richness metric. Bulletin of the North American Benthological Society **13**: 1-2

Lodge, D.M., and P. Kelly. 1985. Habitat disturbance and the stability of freshwater gastropod populations. Oecologia **68**: 111-117.

Lorang, M. S., D. C. Whited, F. R. Hauer, J. S. Kimball, and J. A. Stanford. 2005. Using airbone multispectral imagery to evaluate geomorphic work across flood plains of gravel-bed rivers. Ecological Applications **15**: 1209-1222.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough, L. 2001. What is the observed relationship between species richness and productivity? Ecology **82**: 2381-2396.

MacArthur, R. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York. 269 pp.

Modde, T., R. T. Muth, and G. B. Haines. 2001. Floodplain wetland suitability, access and potential ise by juvenile razorback suckers in the Middle Green River, Utah. Transactions of the American Fisheries Society **130**: 1095-1105.

Mouw, J. E. B., J. A. Stanford, and P. B. Alaback. In review. Influences of flooding and hyporheic exchange on floodplain plant richness and productivity. Submitted to River Research and Applications.

Pachepsky, E., J. W. Crawford, J. L. Brown, and G. Squire. 2001. Towards a general theory of biodiversity. Nature **410**: 923-926.

Parker, S. M., A. D. Huryn. 2006. Food web structure and function in two arctic streams with contrasting disturbance regimes. Freshwater Biology **51**: 1249-1263.

Pepin, D. M. and F. R. Hauer. 2002. Benthic responses to groundwater-surface water exchange in two alluvial rivers in northwestern Montana. Journal of the North American Benthological Society **21**: 370-383.

Petchey, O. L. and K. J. Gaston. 2002. Functional-diversity (FD), species richness, and community composition. Ecology Letters **5**: 402-411.

Pollis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics **28**: 289-316.

Poole, G. C. J. A. Stanford, S. W. Running, C. A. Frissell, W. W. Woessner and B. K. Ellis. 2004. A patch hierarchy approach to modeling surface and subsurface hydrology in complex flood-plain environments. Earth Surface Processes and Landforms **29**: 1259-1274.

Poole, G. C., J. A. Stanford, S. W. Running, C. A. Frissell. 2006. Multiscale geomorphic drivers of groundwater flow paths: subsurface hydrologic dynamics and hyporheic habitat diversity. Journal of the North American Benthological Society **25**: 288-303.

Reid, B. 2007. Energy flow in a floodplain aquifer ecosystem. Ph. D. Dissertation. Uniersity of Montana, Missoula, Montana, USA.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal environments. Frontiers of Ecology and the Environment **1**: 31-37.

Sommer, T.R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival, Canadian Journal of Fisheries and Aquatic Sciences **58**: 325-333.

Speierl, T. K. H. Hoffman, R. Klupp, J. Schadt, R. Krec, and W. Voelk. 2002. Fish communities and habitat diversity: the effect of river restoration on the Main and Rodach. Nat. Landschaft **77**: 161-171.

Stanford, J. A., M. S. Lorang, and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems, Verhein Internationale Vereinigung Limnologie **29**:123-136.

Stevens, L. E., T. J. Ayers, M. J. C. Kearsley, J. B. Bennett, R. A. Parnell, A. E. Springer, K. Christensen, V. J. Meretsky, A. M. Phillips, J. Spence, M. K. Sogge, and D. L. Wegner. 2001. Planned flooding and Colorado River riparian trade-offs downstream from Glen Canyon Dam, Arizona. Ecological Applications **11**: 73-94.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**: 718-720.

Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer, and J. V. Ward. 1999. Hydrologic connectivity, and the exchange of organic matter and nutrients in a dynamic river floodplain system (Danube, Austria). Freshwater Biology **41**: 521-535.

Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: Present state and future trends. Environmental Conservation **29**: 308-330.

Tockner, K., F. Malard, U. Uelinger, and J. V. Ward. 2002. Nutrients and organic matter in a glacial river-floodplain system (Val Roseg, Switzerland). Limnology and Oceanography **47**: 266-277.

Tockner, K., J. V. Ward, D. B. Arscott, P. J. Edwards, J. Kollmann, A. M. Gurnell, G. E. Petts, and B. Maiolini. 2003. The Tagliamento River: a model ecosystem of European importance. Aquatic Sciences **65**: 239-253.

Townsend, C. R. and A. G. Hildrew. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology **31**: 265-275.

Townsend, C. R., S. Doledec, and M. Scarsbrook. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat-templet theory. Freshwater Biology **37**: 367-387.

Van Cleve, K., C. T. Dyrness, G. M. Marion, and R. Erickson. 1993. Control of soil development on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research **23**: 941-955.

Viereck, L. A., C. T. Dyrness, and M. J. Foote. 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. Canadian Journal of Forest Research **23**: 889-898.

Urban, M. C. 2004. Disturbance heterogeneity determines freshwater metacommunity structure. Ecology **85**: 2971-2978.

Van Pelt, R., T. C. O'Keefe, J. J. Latterell, and R. J. Naiman. 2006. Riparian forest stand development along the queets river in Olympic National Park, Washington. Ecological Monographs **76**: 277-298.

Ward, J. V., K. Tockner, D. B. Arscott and C. Claret. 2002. Riverine landscape diversity. Freshwater Biology **47**: 517-539.

Whiles, R. M., and B. S. Goldowitz. 2001. Hydrologic influences on insect emergence production from central Platte River wetlands. Ecological Applications **11**: 1829-1842.

Whited, D. C., M. S. Lorang, M. J. Harner, F. R. Hauer, J. S. Kimball, J. A. Stanford. 2007. Hydrologic disturbance and succession: Drivers of floodplain pattern. Ecology **88**: 940-953.

Wyatt, K. H. 2005. The influence of hyporheic-surface water exchange on benthic algal biomass, abundance, and community composition in the Middle Fork Flathead River, Montana. M.S. Thesis. University of Southern Mississippi, Mississippi, USA.

Table 1. Seasonal changes in the physical environments of lateral habitats. Percent cover of wood and aquatic vegetation and algae estimated visually. Percent canopy cover estimated from digital photo interpretation. *Temperatures from thermographs as opposed to transects.

Lateral habitat type	Sample period	No. of sites (n)	Surface area (m^2)	Avg. Depth (m)	Temp. (^oC)	Wood cover (%)	Aquatic veg. cover (%)	Canopy cover (%)
shallow shoreline	early summer	3	68 ±29	0.2 ±0.1	13 ±1	0-10	0-10	0
backwater	early summer	3	828 ±170	0.2 ±0.2	17 ±0	0-10	0-10	0-25
parafluvial springbrook	early summer	2	4322 ±4627	0.3 ±0.0	13 ±1	10-20	30-40	0-5
orthofluvial springbrook	early summer	3	4024 ±2040	0.3 ±0.1	11 ±1	10-20	20-30	5-20
shallow shoreline	late summer	3	218 ±126	0.2 ±0.0	14 ±1	0-10	0-10	0
backwater	late summer	2	723 ±590	0.6 ±0.1	12 ±1	10-20	0-10	0-20
parafluvial springbrook	late summer	3	3370 ±2851	0.2 ±0.0	11 ±1	10-20	30-40	0-5
orthofluvial springbrook	late summer	3	3541 ±1679	0.2 ±0.1	11 ±3	10-20	10-20	0-5
shallow shoreline	fall	0	-	-	2 ±0*	-	-	-
backwater	fall	0	-	-	4 ±2*	-	-	-
parafluvial springbrook	fall	2	4536 ±2751	0.2 ±0.1	9 ±6	0-10	30-40	0-10
orthofluvial springbrook	fall	2	2357 ±119	0.3 ±0.2	5 ±0	10-20	10-20	0-5
shallow shoreline	spring	3	-	0.2 ±0.0	3 ±1*	0-10	0-10	-
backwater	spring	3	-	-	3 ±1*	0-10	0-10	-
parafluvial springbrook	spring	0	-	-	5 ±1*	-	-	-
orthofluvial springbrook	spring	3	-	0.3 ±0.1	4 ±1*	10-20	20-30	-

Table 2. Densities and diversities of select invertebrate taxa (Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Odonata, Gastropoda) across lateral habitats and time. Values are presented as means ± standard deviation. Values in parentheses are percentages of covariation.

	n	Density	(ind/m^2)		ά			H'			1/D			E	β
early summer					36										
shallow shoreline	3	954	±373	(39.1)	11	±4	(32.8)	1.21	±0.54	(44.7)	2.75	±1.55	(56.4)	0.5	2.3
backwater	3	777	±247	(31.8)	10	±2	(14.8)	1.05	±0.08	(7.3)	1.83	±0.13	(7.3)	0.5	2.6
parafluvial springbrook	2	585	±386	(66.1)	10	±6	(67.0)	1.35	±0.55	(41.2)	4.02	±2.92	(72.6)	0.6	2.6
orthofluvial springbrook	3	971	±857	(88.3)	11	±6	(55.3)	1.45	±0.46	(31.6)	3.51	±1.34	(38.3)	0.6	2.3
late summer					36										
shallow shoreline	3	2205	±1938	(87.9)	10	±6	(55.7)	1.25	±0.48	(38.4)	2.89	±0.84	(28.9)	0.5	2.6
backwater	3	293	±345	(118)	8	±5	(66.0)	1.13	±0.04	(13.3)	2.53	±0.19	(7.5)	0.6	3.5
parafluvial springbrook	2	527	±33	(6.2)	18	±2	(12.1)	1.88	±0.04	(1.9)	6.08	±2.54	(41.9)	0.7	1.0
orthofluvial springbrook	2	396	±264	(66.6)	10	±1	(7.4)	1.25	±0.41	(32.7)	2.87	±1.58	(55.0)	0.6	2.6
fall					24										
shallow shoreline	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
backwater	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
parafluvial springbrook	2	659	±382	(58.0)	9	±8	(94.3)	0.87	±0.39	(45.0)	1.72	±0.38	(21.8)	0.4	1.7
orthofluvial springbrook	2	437	±347	(79.4)	6	±2	(38.6)	1.01	±0.37	(36.3)	2.53	±0.79	(31.4)	0.6	3.0
spring					28										
shallow shoreline	3	205	±472	(230)	6	±3	(57.7)	1.06	±0.20	(19.3)	2.19	±0.28	(12.8)	0.6	3.7
backwater	3	229	±490	(214)	6	±1	(10.2)	0.84	±0.29	(35.1)	1.73	±0.39	(22.7)	0.5	3.7
parafluvial springbrook	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
orthofluvial springbrook	3	1161	±1622	(140)	13	±6	(44.9)	1.73	±0.42	(24.4)	4.68	±2.51	(53.6)	0.7	1.2

Table 3. Species sequences and densities of EPT taxa (± 1 SD) used to construct seasonal rank-abundance curves.

Early summer

	Habitat type											
	orthofluvial springbrook			parafluvial springbrook			backwater			shallow shoreline		
Spp. #	Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)	
1	Diphetor	275	±275	Cinygmula	101	±101	Ameletus	571	±190	Ameletus	628	±283
2	Ameletus	174	±158	Ameletus	101	±101	Ephemerella	62	±47	Cinygmula	188	±68
3	Ephemerella	139	±139	Epeorus	31	±31	Paraleptophlebia	31	±20	Suwallia	30	±30
4	Psychoglypha	94	±37	Siphlonurus	20	±20	Siphlonurus	30	±3	Baetis	26	±13
5	Acentrella	82	±82	Paraleptophlebia	18	±18	Suwallia	26	±16	Ephemerella	22	±10
6	Siphlonurus	42	±18	Drunella	16	±16	Cinygmula	22	±13	Epeorus	20	±13
7	Suwallia	37	±24	Rhithrogena	9	±9	Isoperla	12	±12	Seratella	10	±7
8	Paraleptophlebia	32	±16	Seratella	8	±8	Lepidostoma	9	±9	Diphetor	9	±5
9	Rhyacophila	23	±18	Paraperla	8	±8	Psychoglypha	4	±3	Paraleptophlebia	7	±4
10	Seratella	17	±17	Diphetor	6	±6	Drunella	3	±2	Malenka	5	±5
11	Limnephilus	14	±14	Pteronarcella	3	±3	Diphetor	2	±1	Drunella	4	±1
12	Lepidostoma	10	±10	Callibaetis	3	±3	Rhithrogena	2	±2	Siphlonurus	2	±2
13	Dicosmoecus	6	±6	Suwallia	1	±1	Seratella	1	±2	Neophylax	1	±1
14	Neophylax	5	±4	Onocosmoecus	1	±1	Sweltsa	1	±1	Paraperla	1	±1
15	Paraperla	4	±4	Kogotus	1	±1	Dicosmoecus	1	±1	Pteronarcella	1	±1
16	Kogotus	4	±2				Hydropsyche	1	±1	Acentrella	1	±1
17	Caudatella	3	±3							Claasenia	1	±1
18	Pteronarcella	3	±3									
19	Amphicosmoecus	2	±2									
20	Sweltsa	1	±1									

Table 3. (cont.)

Late summer

	Habitat type											
	orthofluvial springbrook			parafluvial springbrook			backwater			shallow shoreline		
Spp. #	Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)	
1	Paraleptophlebia	108	±108	Ameletus	208	±13	Paraleptophlebia	152	±124	Rhithrogena	853	±482
2	Rhithrogena	85	±85	Paraleptophlebia	103	±23	Ameletus	109	±102	Ameletus	463	±194
3	Rhyacophila	79	±77	Drunella	47	±28	Siphlonurus	17	±10	Paraleptophlebia	395	±143
4	Ameletus	38	±38	Apatania	43	±16	Isoperla	4	±4	Ephemerella	335	±273
5	Drunella	28	±28	Ephemerella	36	±24	Rhithrogena	2	±2	Diphetor	82	±82
6	Baetis	18	±18	Siphlonurus	30	±1	Sweltsa	2	±2	Drunella	62	±40
7	Sweltsa	13	±13	Rhithrogena	12	±2	Drunella	1	±1	Sweltsa	26	±13
8	Neophylax	5	±5	Baetis	9	±8	Epeorus	1	±1	Epeorus	24	±24
9	Hydroptila	3	±3	Rhyacophila	5	±5	Timpanoga	1	±1	Skwala	20	±15
10	Lepidostoma	3	±3	Malenka	4	±4				Acentrella	15	±12
11	Glossosoma	2	±2	Epeorus	4	±3				Isoperla	14	±12
12	Siphlonurus	1	±1	Timpanoga	3	±2				Baetis	14	±14
13	Timpanoga	1	±1	Sweltsa	3	±2				Rhyacophila	10	±10
14	Psychoglypha	1	±1	Zapada	2	±2				Pteronarcella	2	±2
15	Onocosmoecus	1	±1	Cinygmula	1	±1				Siphlonurus	2	±2
16				Skwala	1	±1				Hydropsyche	1	±1
17				Glossosoma	1	±1				Apatania	1	±1
18				Diura	1	±1				Arctopsyche	1	±1
19				Mesocapnia	1	±1				Brachycentrus	1	±1
20				Megarcys	1	±1				Glossosoma	1	±1
21										Lepidostoma	1	±1

Table 3. (cont.)

Fall

	Habitat type											
	orthofluvial springbrook			parafluvial springbrook			backwater			shallow shoreline		
Spp. #	Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)	
1	Ephemerella	159	±159	Cinygmula	322	±322	-	-	-	-	-	-
2	Rhyacophila	92	±92	Ephemerella	61	±61						
3	Psychoglypha	59	±59	Ameletus	28	±28						
4	Sweltsa	53	±53	Paraleptophlebia	25	±25						
5	Onocosmoecus	35	±35	Siphlonurus	24	±24						
6	Hydroptila	35	±35	Callibaetis	12	±12						
7	Limnephilus	1	±0	Drunella	9	±9						
8	Asynarchus	1	±1	Rhithrogena	5	±5						
9	Siphlonurus	1	±1	Apatania	4	±4						
10				Kathroperla	3	±3						
11				Glossosoma	2	±2						
12				Skwala	2	±2						
13				Malenka	1	±1						
14				Pteronarcella	1	±1						
15				Zapada	1	±1						

Table 3. (cont.)

Spring

	Habitat type											
	orthofluvial springbrook			parafluvial springbrook			backwater			shallow shoreline		
Spp. #	Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)		Taxon	Density (ind./m^2)	
1	Paraleptophlebia	196	±192	-	-	-	Utacapnia	426	±412	Ameletus	363	±236
2	Diphetor	184	±182				Ameletus	125	±48	Cinygmula	153	±116
3	Baetis	157	±133				Epeorus	82	±82	Utacapnia	68	±62
4	Neophylax	100	±100				Cinygmula	34	±7	Skwala	11	±11
5	Cinygmula	74	±64				Rhithrogena	5	±5	Epeorus	4	±4
6	Ephemerella	73	±54				Paraleptophlebia	4	±2	Ephemerella	4	±2
7	Siphlonurus	64	±39				Ephemerella	2	±2	Paraleptophlebia	3	±3
8	Epeorus	51	±51				Capnia	2	±2	Diphetor	1	±1
9	Paraperla	20	±20				Isocapnia	2	±2	Drunella	1	±1
10	Rhithrogena	13	±13				Isoperla	2	±2	Glossosoma	1	±1
11	Ameletus	11	±6				Prostoia	2	±2	Paraperla	1	±1
12	Rhyacophila	8	±4							Baetis	1	±1
13	Drunella	7	±4									
14	Sweltsa	5	±4									
15	Ecclisomyia	2	±2									
16	Glossosoma	2	±2									
17	Kogotus	2	±2									
18	Limnephilus	1	±1									
19	Pteronarcella	1	±1									

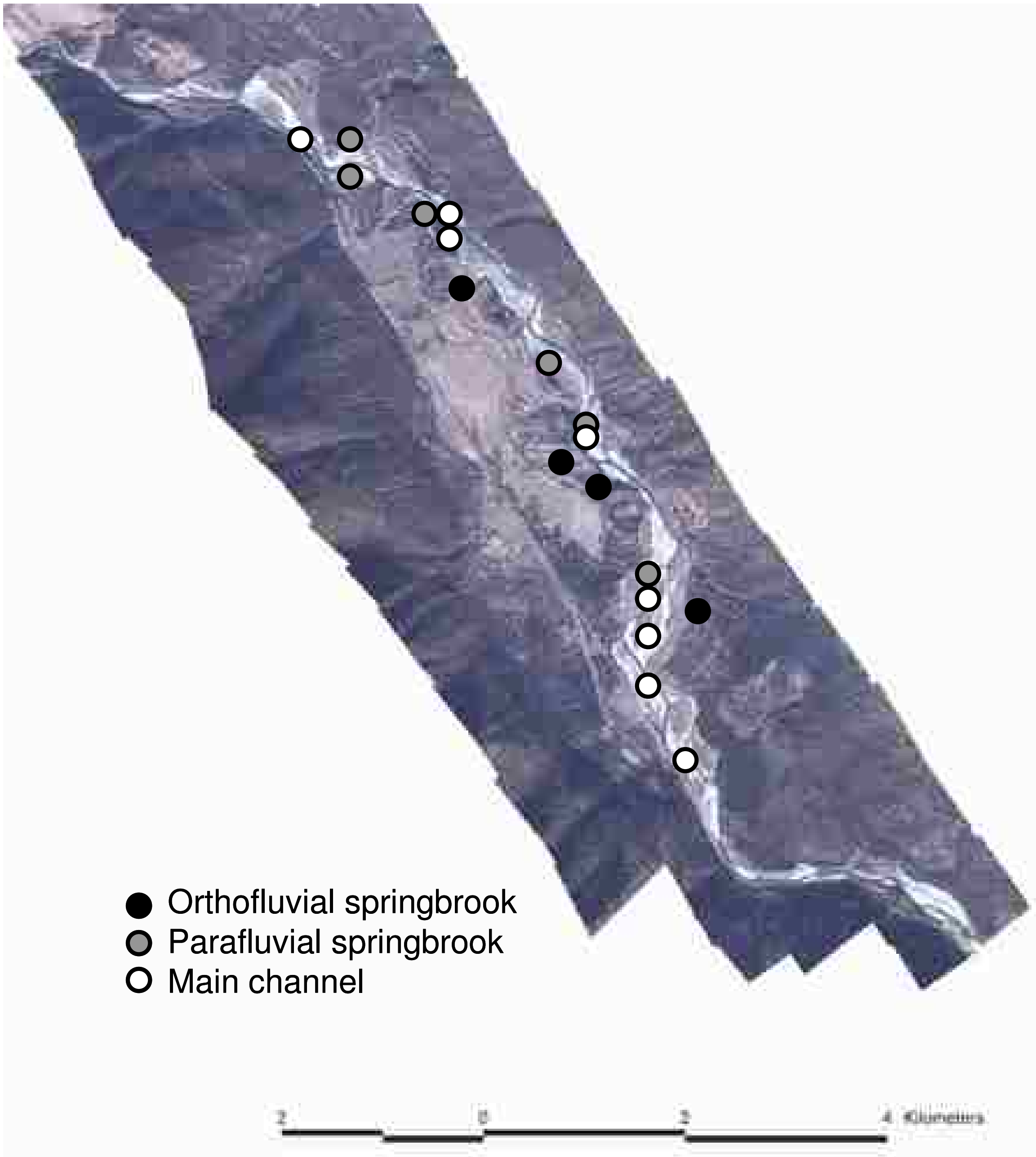


Figure 1. Nyack floodplain map labeled with 2003-2004 sampling sites. Sites designated main channel also include shallow shoreline and backwater habitats.

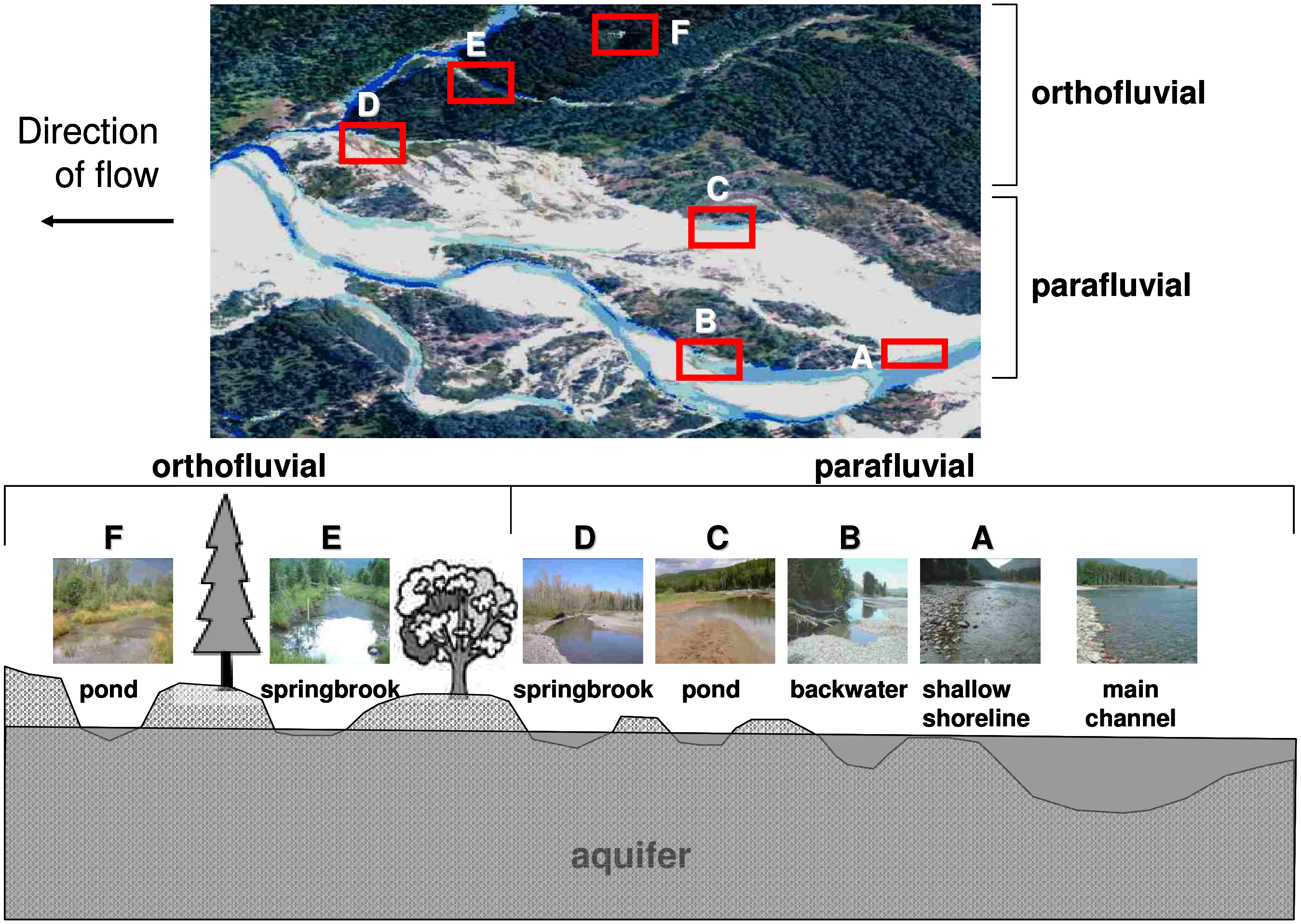


Figure 2. Commonly-occurring habitats that characterize the lateral gradient of aquatic-terrestrial transition across the Nyack Flood Plain. Examples of sites selected for study are shown along a lateral gradient across the flood plain from the main channel to the valley wall. A – C occur in the frequently flooded parafluvial zone, whereas D-F are in the less-frequently flooded orthofluvial zone. Habitats are: parafluvial (A) shallow shorelines, (B) backwaters, (C) ponds and (D) springbrooks, and orthofluvial (E) ponds and (F) springbrooks. Image of the Nyack floodplain, Middle Fork of the Flathead River in Montana, USA.

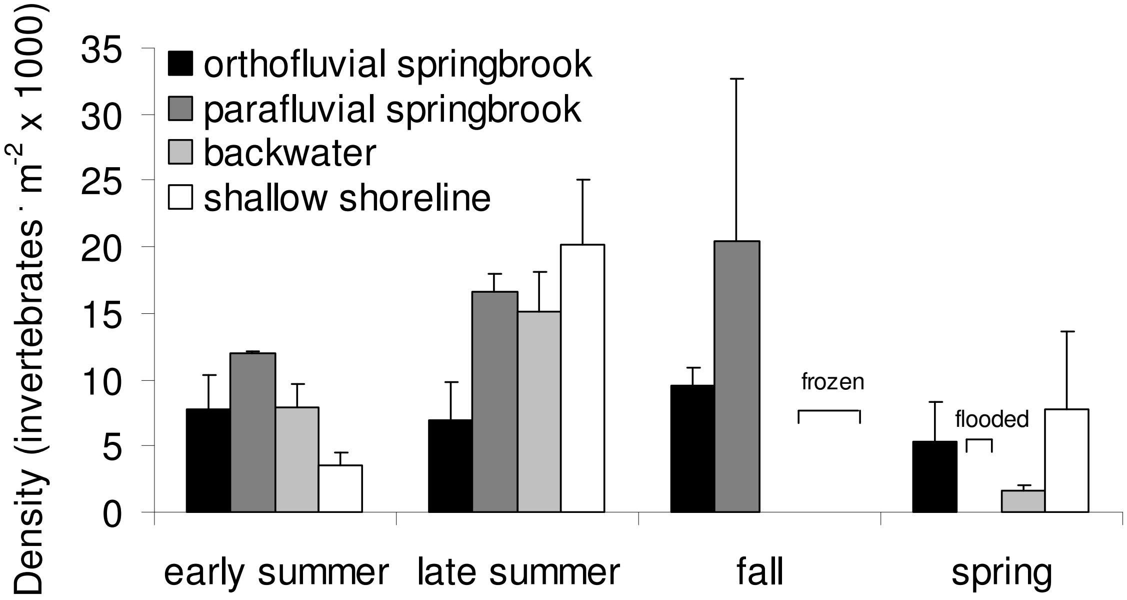


Figure 3. Densities of macroinvertebrates (±1SE) by type of lateral habitat and sample date in 2003-2004.

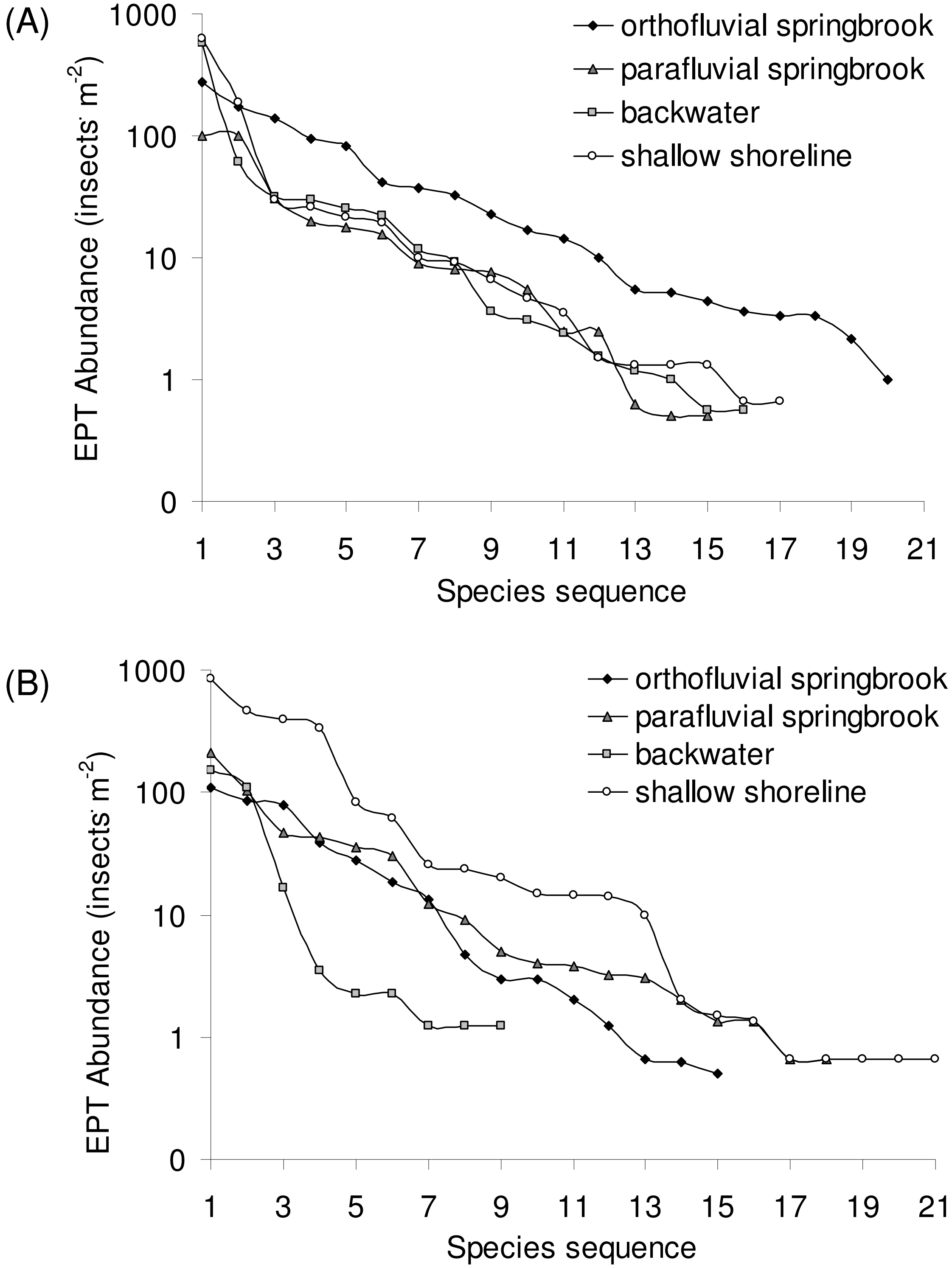
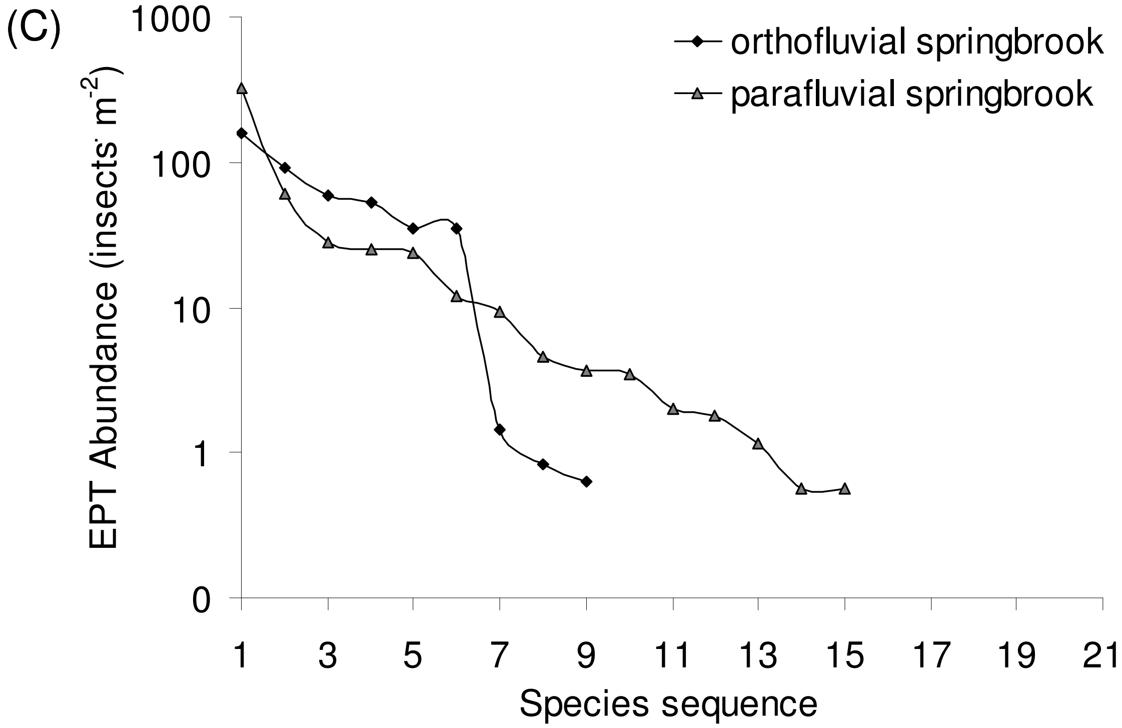


Figure 4. Rank abundance curves for EPT taxa illustrate diversity by habitat type in (A) early summer, (B) late summer, (C) and fall 2003, and (D) early spring 2004.



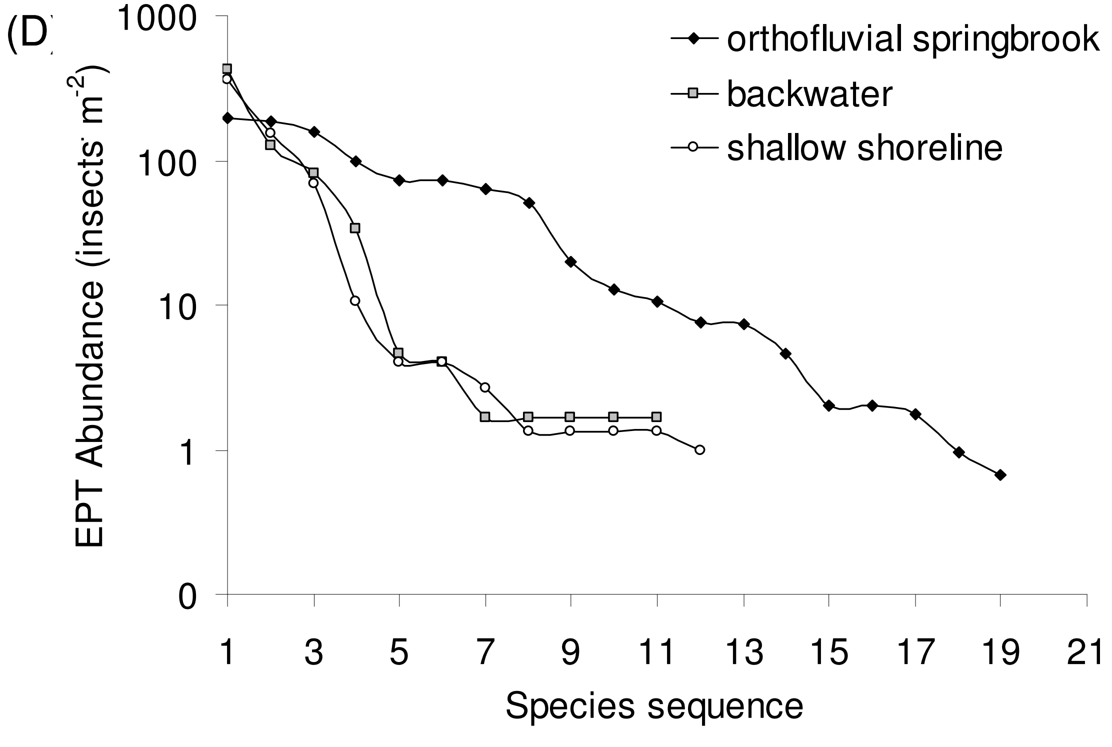


Figure 4. (cont.)

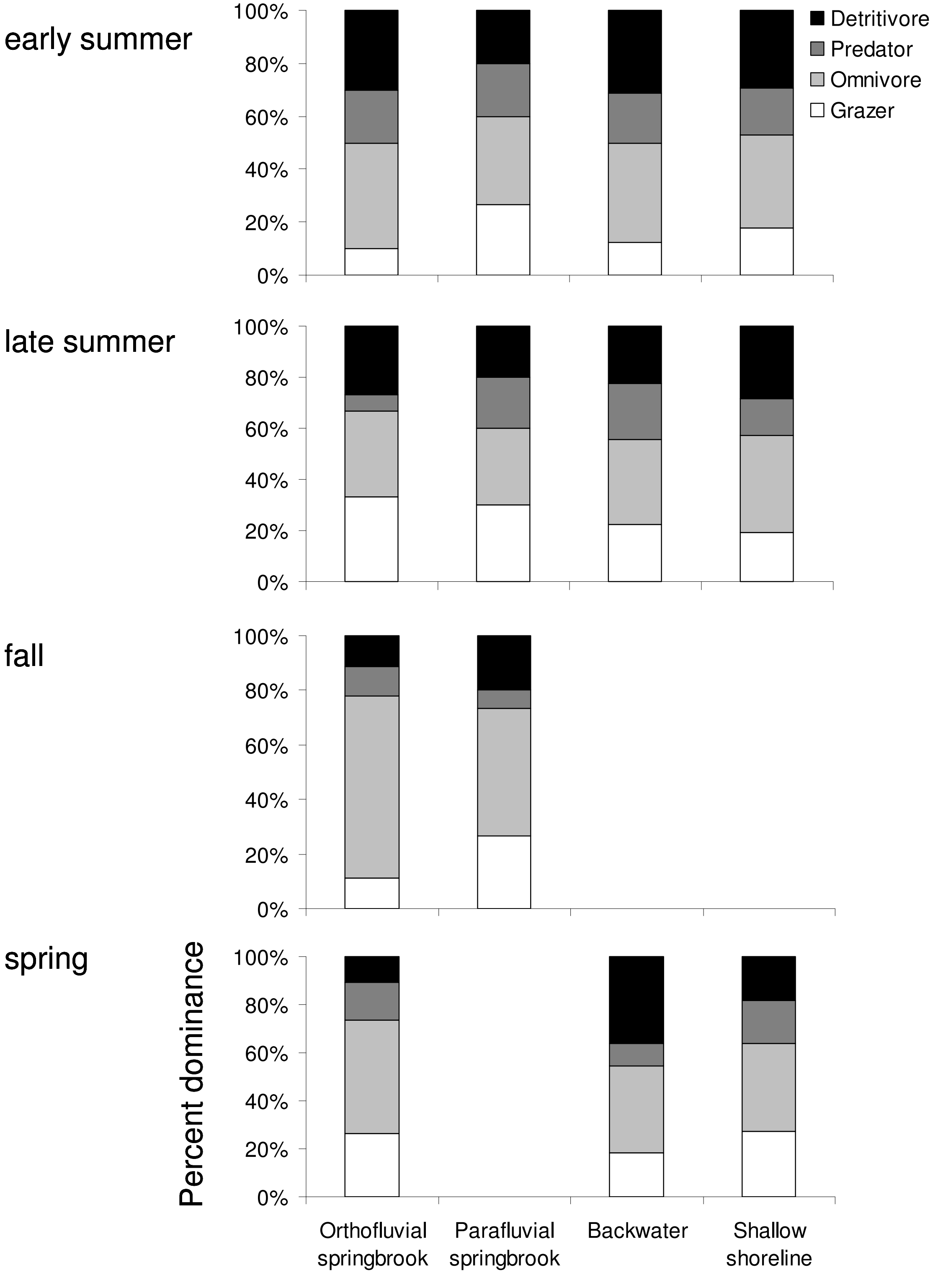


Figure 5. Percent dominance by functional groups of EPT taxa observed in samples grouped by habitat and season in 2003-2004.

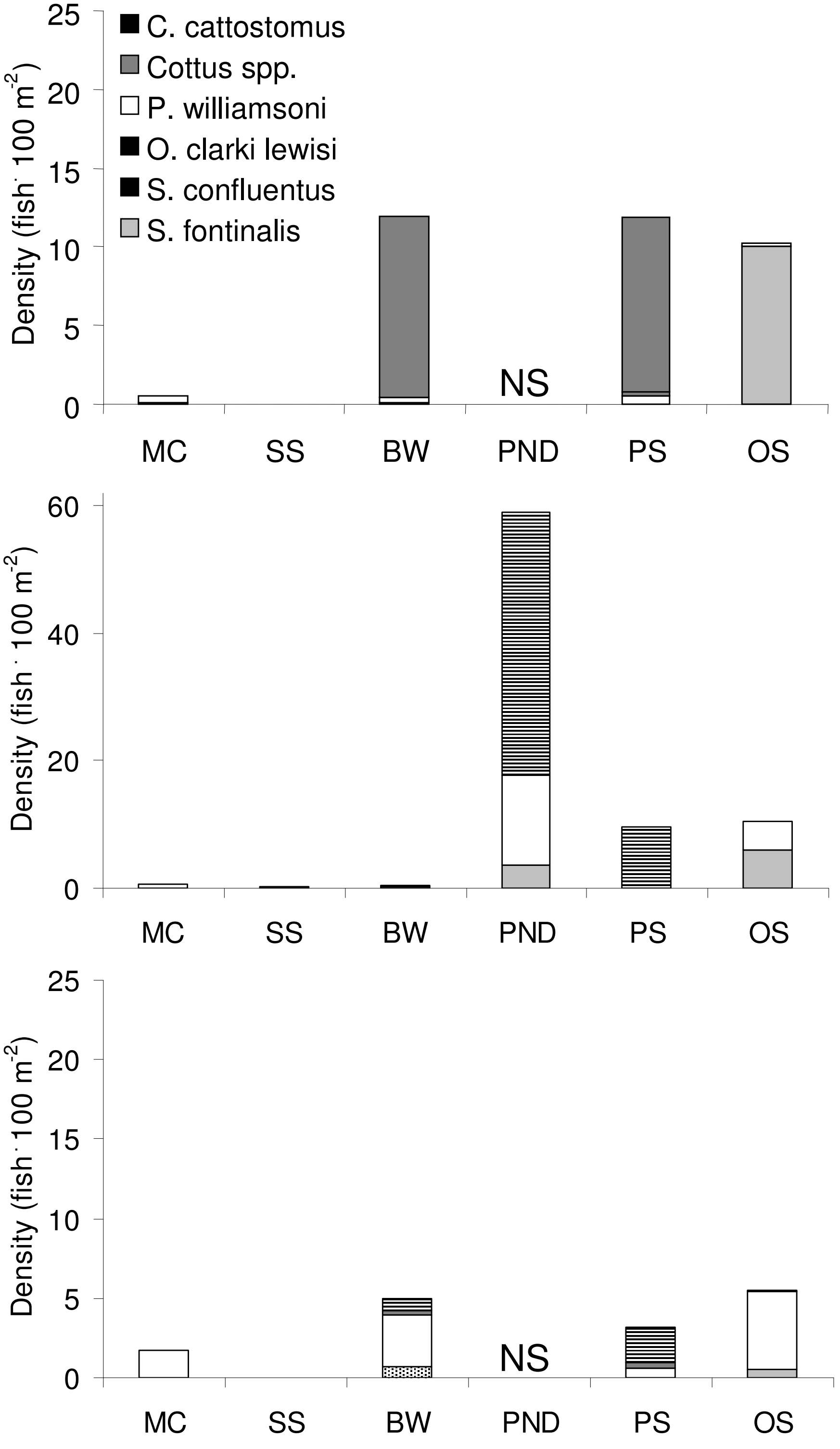


Figure 6. Densities of fish oberved in daytime during visual surveys in (A) early summer, (B) late summer and (C) fall. Surveys conducted in 1995 (pond) and 2004 (all other habitats). MC = main channel, SS = shallow shoreline, BW = backwater, PND = pond, PS = parafluvial springbrook, OS = orthofluvial springbrook). NS = no sample

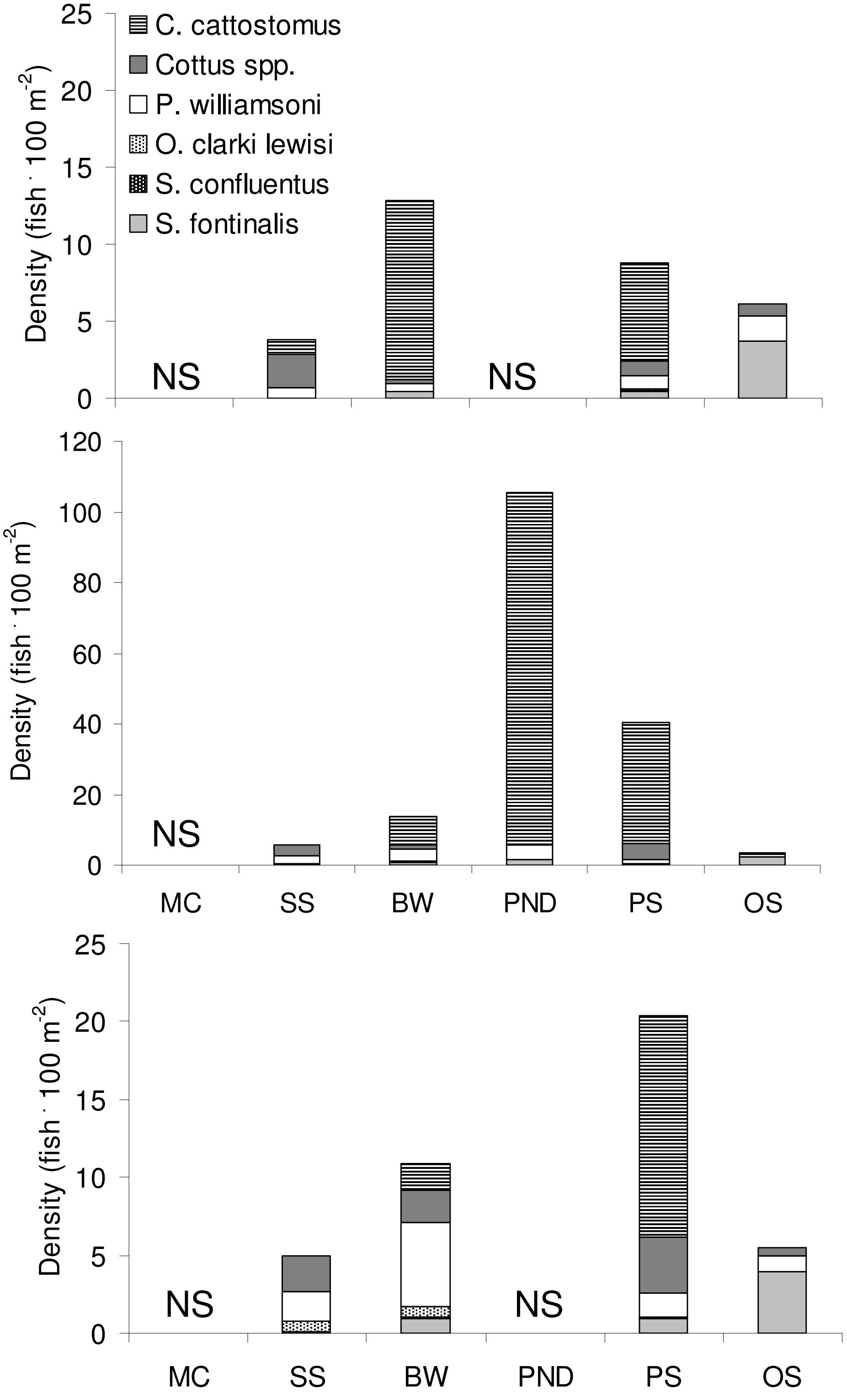


Figure 7. Densities of fish observed at night during visual surveys in (A) early summer, (B) late summer and (C) fall. Surveys conducted in 1995 (pond) and 2004 (all other habitats). MC = main channel, SS = shallow shoreline, BW = backwater, PND = pond, PS = parafluvial springbrook, OS = orthofluvial springbrook). NS = no sample

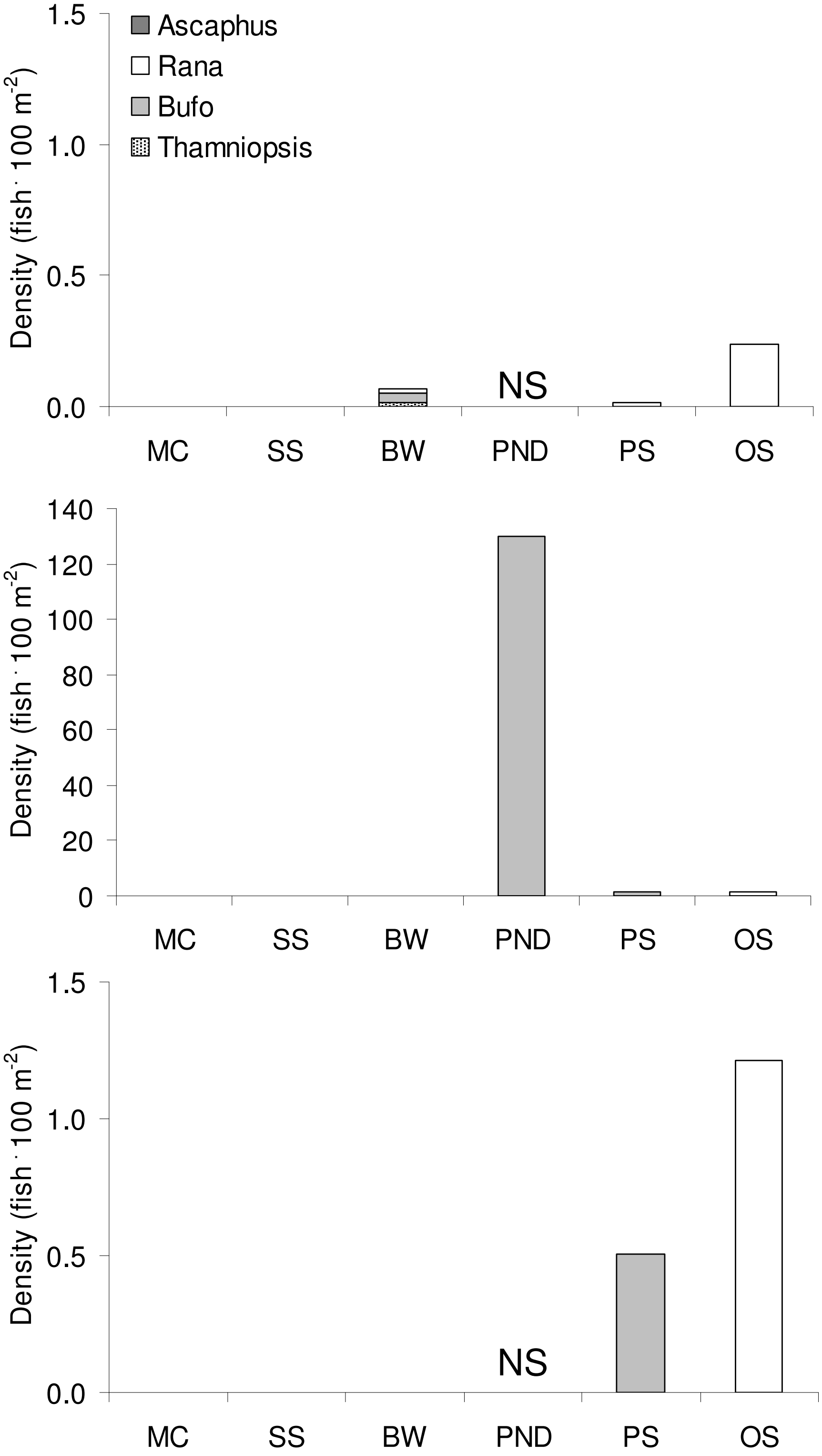


Figure 8. Densities of amphibians observed in daytime during visual surveys in (A) early summer, (B) late summer and (C) fall. Surveys conducted in 1995 (pond) and 2004 (all other habitats). MC = main channel, SS = shallow shoreline, BW = backwater, PND = pond, PS = parafluvial springbrook, OS = orthofluvial springbrook). NS = no sample

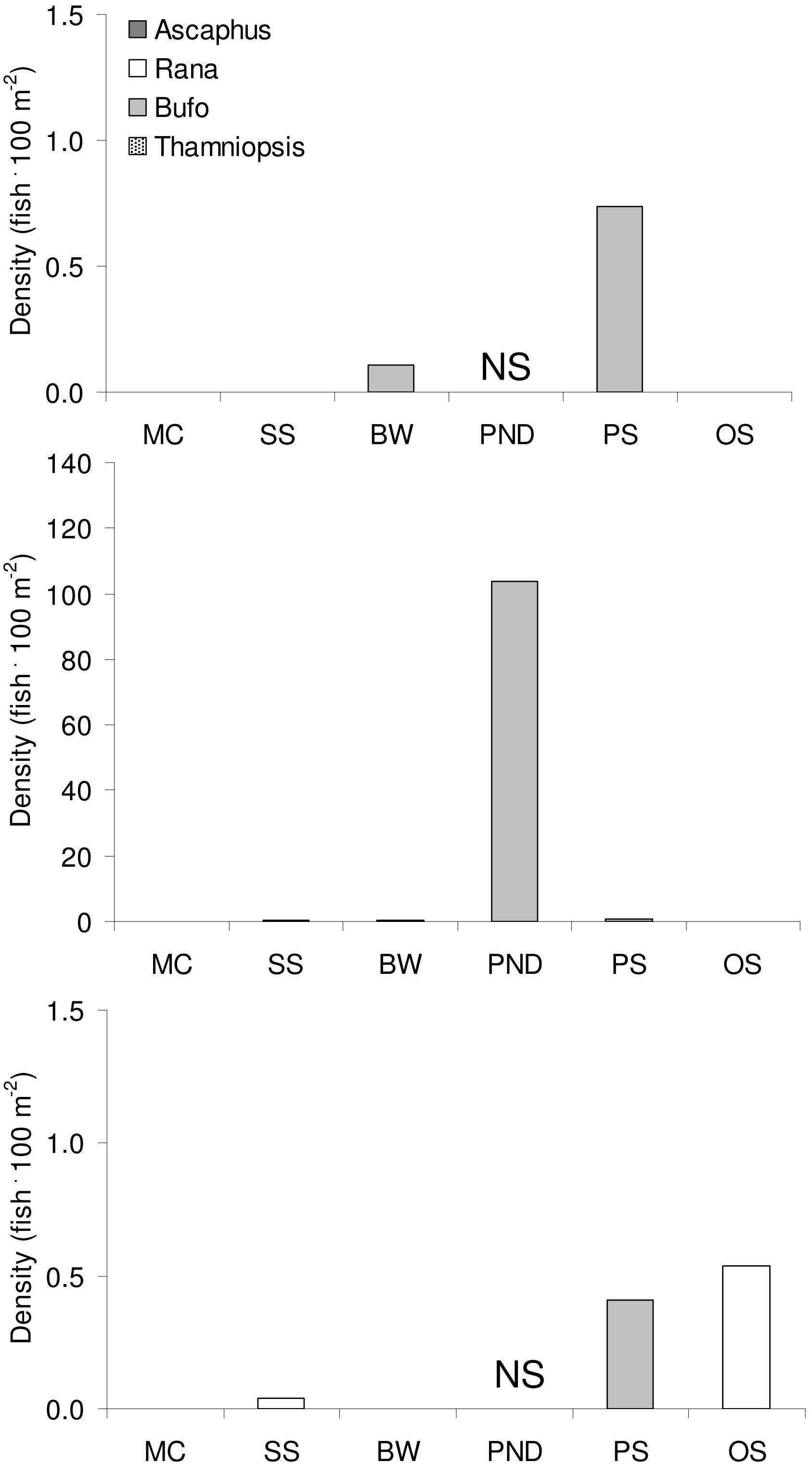


Figure 9. Densities of amphibians observed at night during visual surveys in (A) early summer, (B) late summer and (C) fall. Surveys conducted in 1995 (pond) and 2004 (all other habitats). MC = main channel, SS = shallow shoreline, BW = backwater, PND = pond, PS = parafluvial springbrook, OS = orthofluvial springbrook). NS = no sample

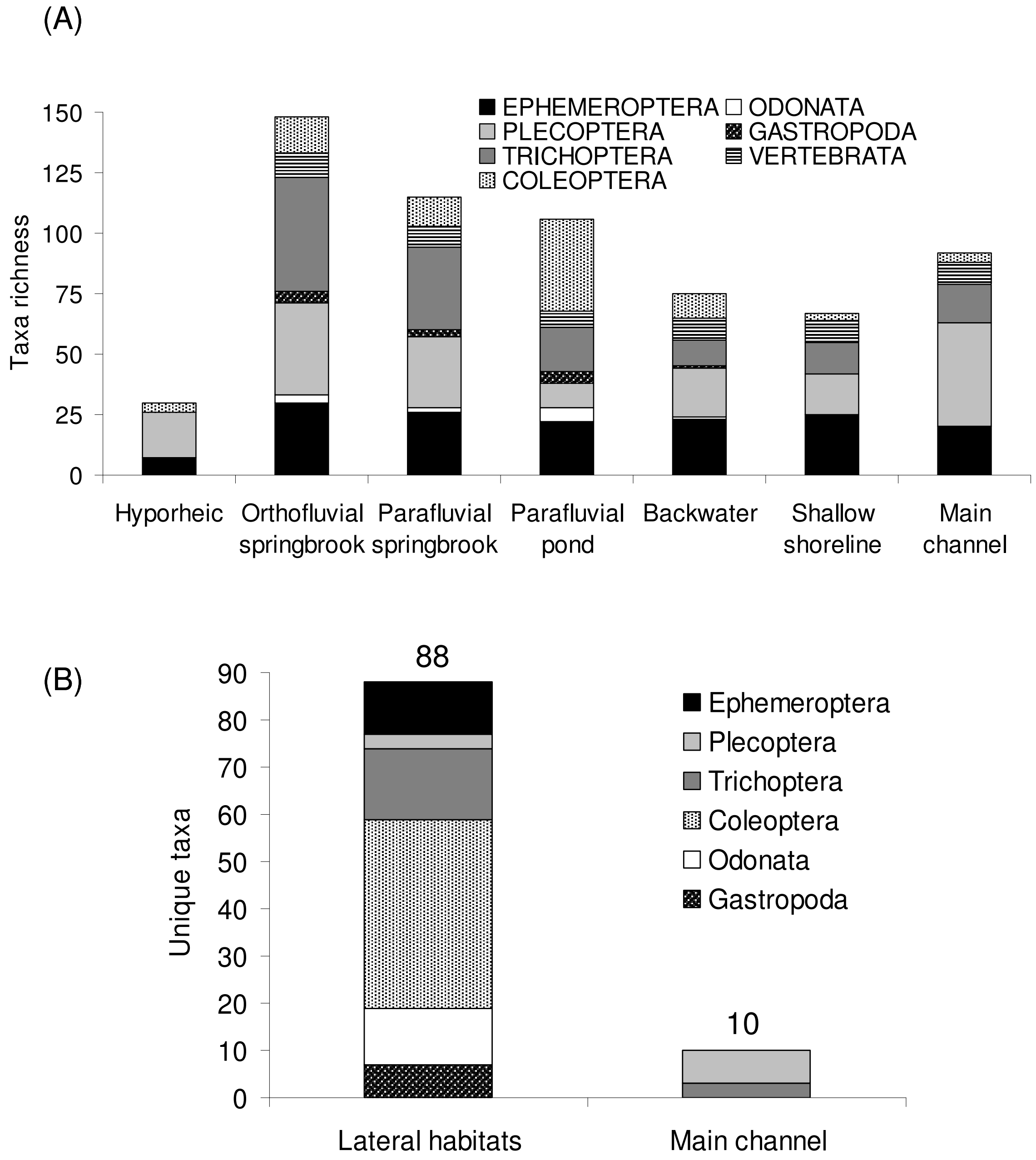


Figure 10. Taxonomic (A) richness and (B) uniqueness in major groups of organisms found in aquatic habitats of the expansive flood plain. Data compiled from studies at Nyack conducted in 1995-2005.

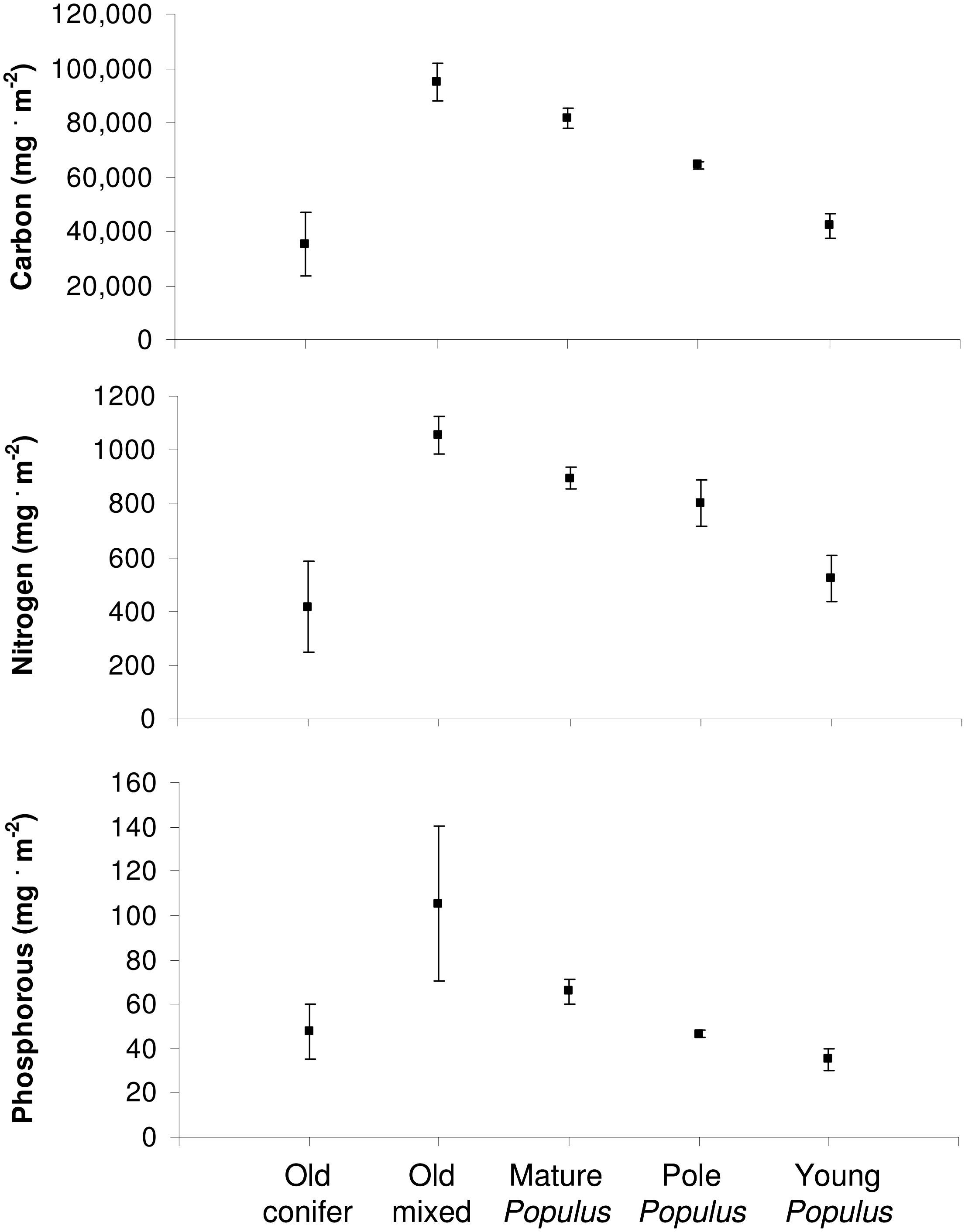


Figure 11. Aerial loading of carbon, nitrogen and phosphorous from leaf litter across a forest chronosequence at Nyack in fall 2003. (Mean ± 1SE)

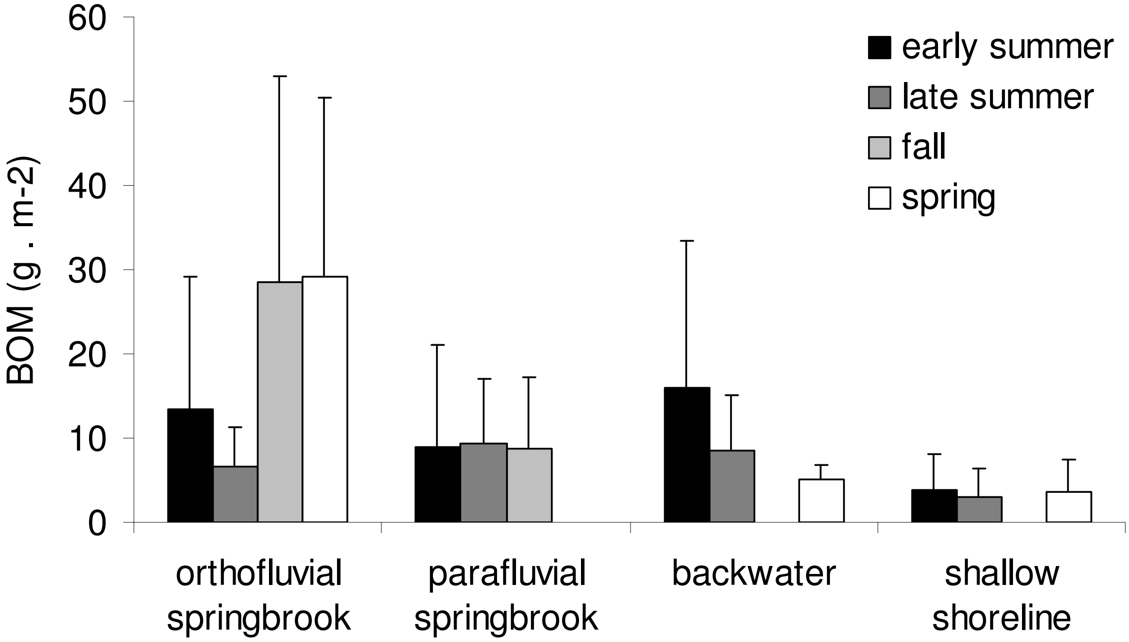


Figure 12. Habitat and seasonal variation in relative density estimates (mean±1SD) of benthic organic matter (BOM) from quantitative benthos samples in 2003-2004.

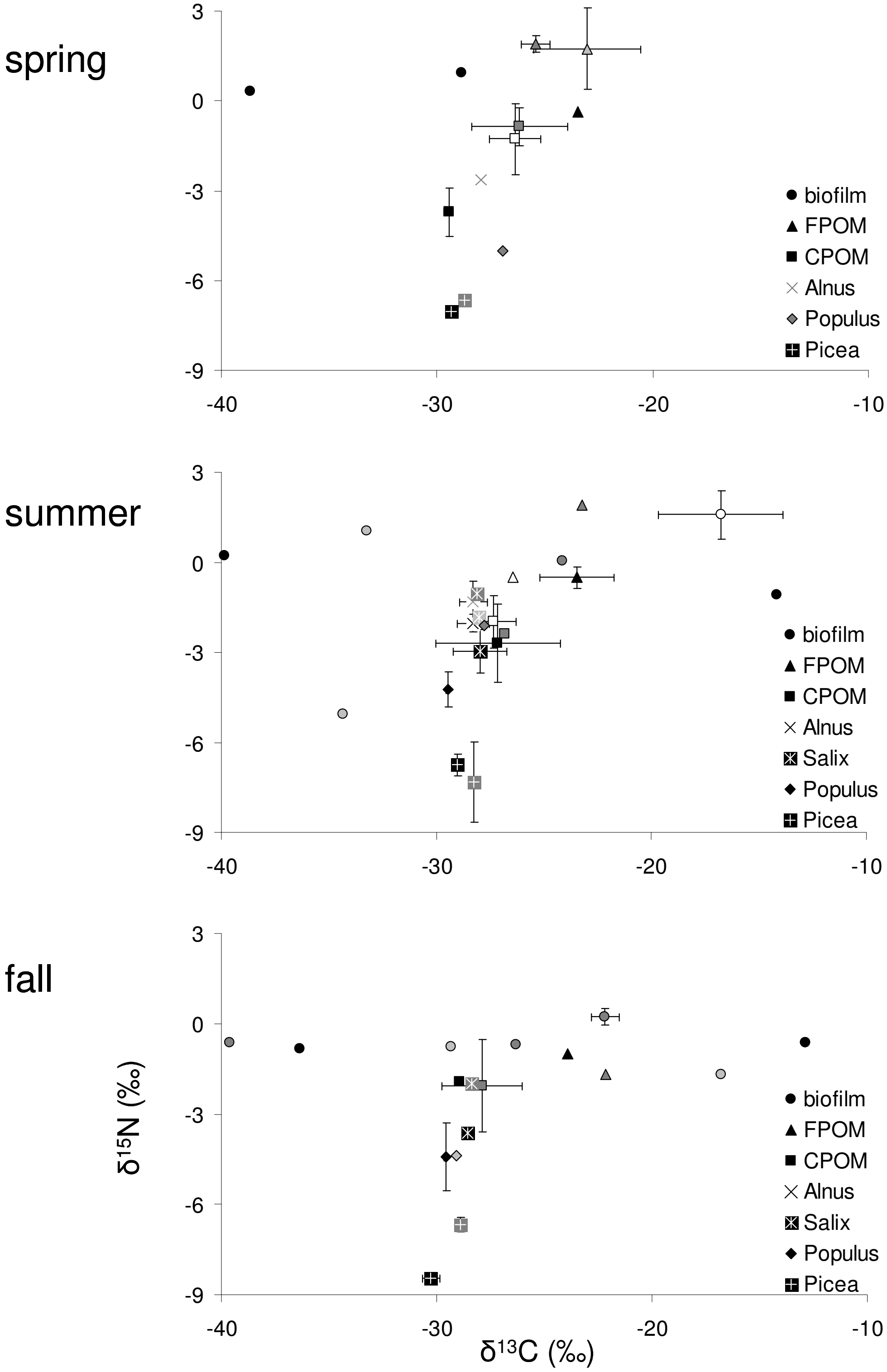


Figure 13. Isotopic signatures of primary production at main channel shallow shoreline/ backwater (light gray), parafluvial springbrook (dark gray), and orthofluvial springbrook (black) sites across three different seasons in 2004.

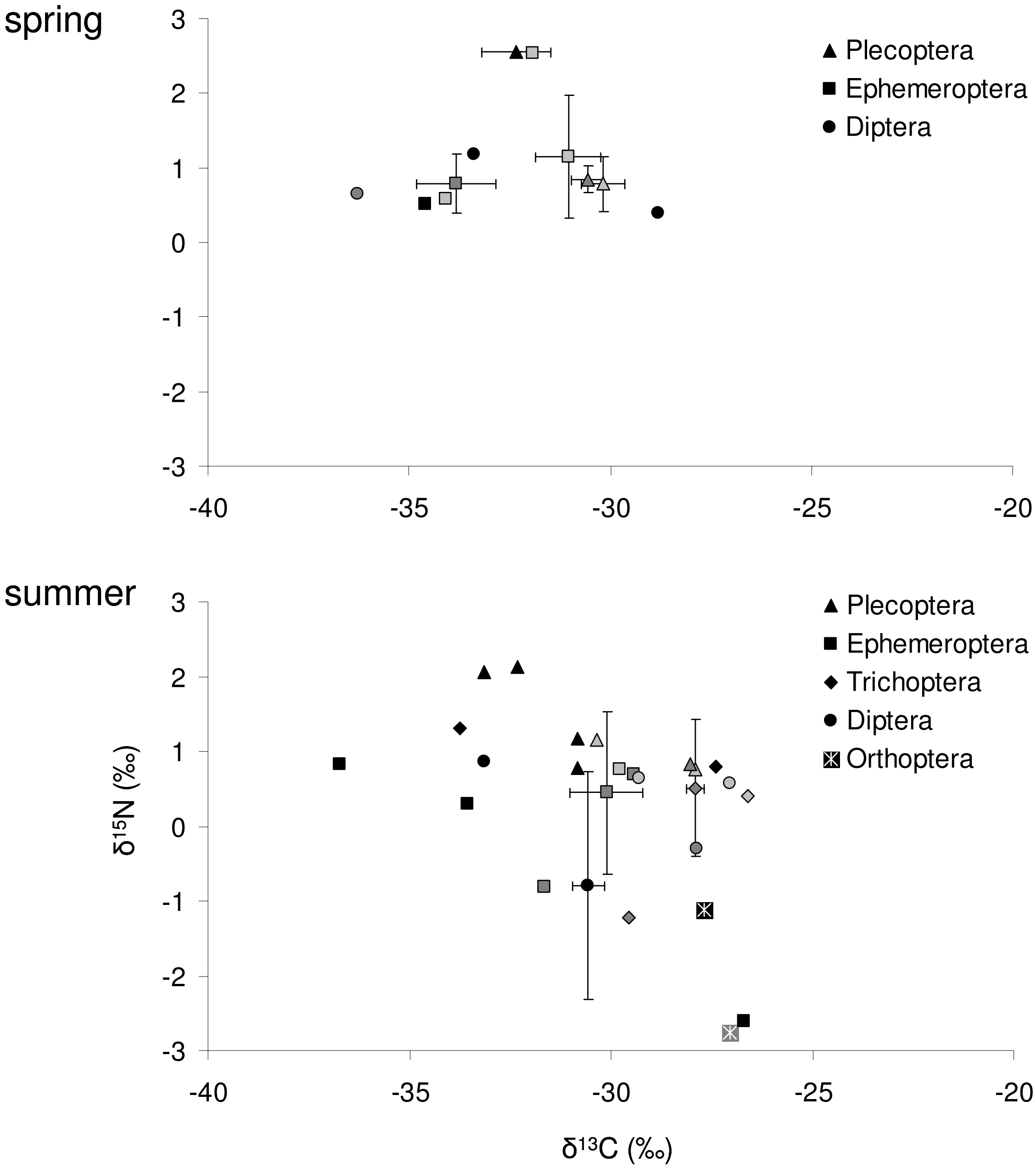


Figure 14. Isotopic signatures of mid-trophic level consumers at main channel shallow shoreline/ backwater (light gray), parafluvial springbrook (dark gray), and orthofluvial springbrook (black) sites across two different seasons in 2004.

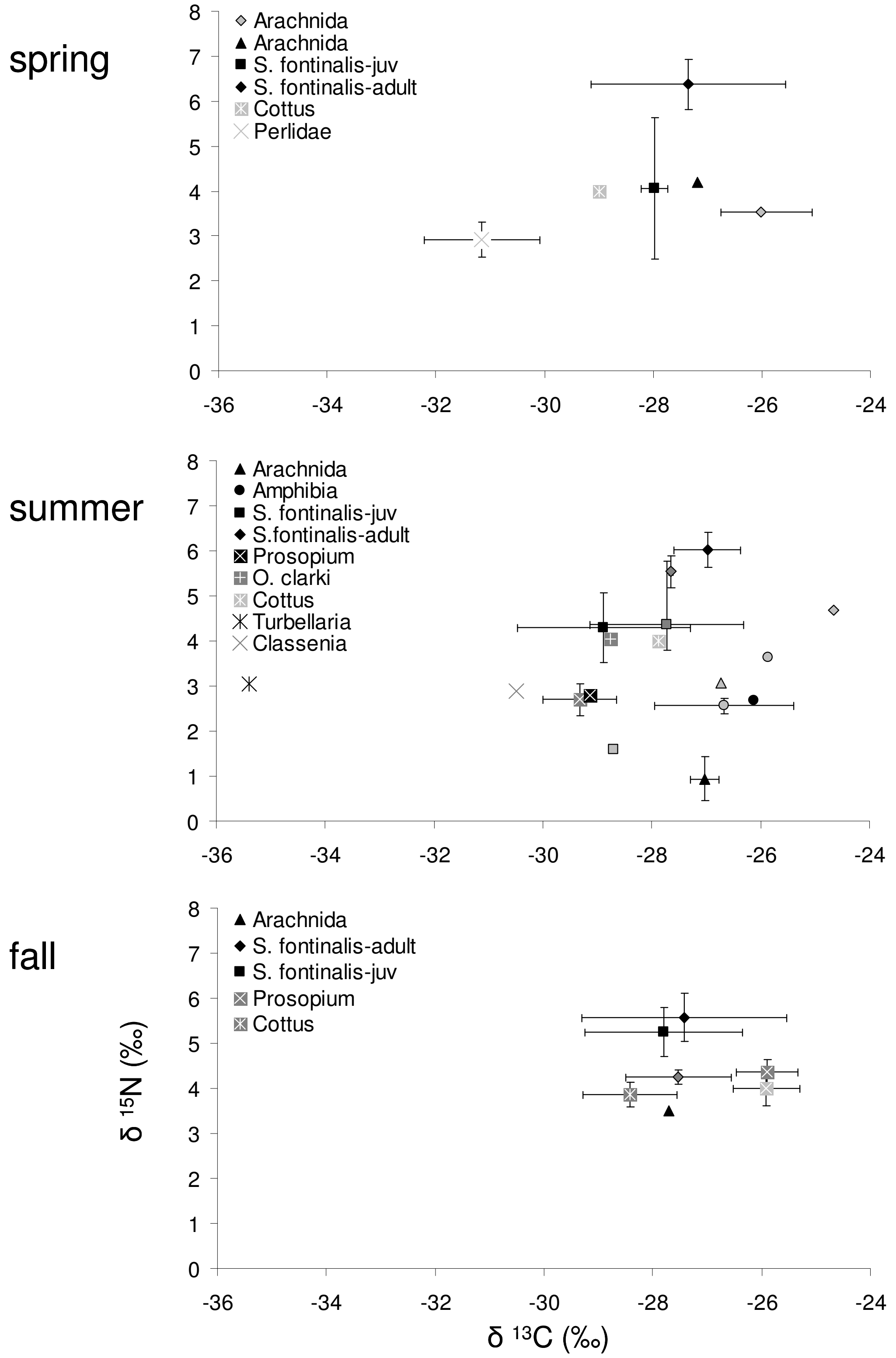


Figure 15. Isotopic signatures of top predators at main channel shallow shoreline/ backwater (light gray), parafluvial springbrook (dark gray), and orthofluvial springbrook (black) sites across three different seasons in 2004.