Response of physical processes and ecological targets to altered hydrology in the Connecticut River Basin

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July 2006

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“The Nature Conservancy’s mission is to preserve the plants, animals and natural communities that represent the diversity of life on Earth by protecting the lands and waters they need to survive.”

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Executive summary

Ecologists have formed general hypotheses about potential changes in aquatic community structure and function resulting from flow alterations. However, most of the studies in the United States used to form these hypotheses were conducted in the west and southeast, and hydroecological relationships can differ considerably among ecoregions. We have limited data on the response of species in rivers of the northeast, as well as the degree of alteration that may lead to changes in aquatic and riparian communities. The goal of this report was to examine: (1) links between hydrology and physical and ecological processes in the Connecticut River Basin, (2) specific flow needs for various life stages of The Nature Conservancy’s ecological targets in the basin, including migratory and resident fish, aquatic invertebrates, floodplain forests, and estuarine communities, (3) potential effects of hydrologic alteration on these ecological targets, and (4) areas of research needed to expand our knowledge of ecological effects of hydrologic alteration in the Connecticut River and its tributaries.

Individual dams in the Connecticut Basin typically store a lower proportion of mean annual discharge compared with dams in other regions, notably the west and southeast U.S. (Graf 1999). Because of these lower ratios of storage to annual runoff, the potential for individual dams in the Connecticut Basin to cause large-scale changes in river flow regimes may be low relative to rivers in other regions. However, the number of dams per watershed area in the Connecticut is among the highest of all rivers in North America, Europe, and the former Soviet Union (Dynesius and Nilsson 1994; Graf 1999). Thus, altered hydrology due to both individual dams and cumulative effects of dams may be a primary stressor to aquatic and riparian communities in the Connecticut River and its tributaries.

Specific data linking hydrologic alteration to physical and ecological processes and ecological targets are scarce for the Connecticut Basin. Additional research is needed on specific links between altered hydrology and ecological response. However, studies conducted in the Connecticut Basin and in rivers of the eastern U.S. have examined some links between hydrology and response of physical processes, ecological processes, species, and communities. Some relationships between components of the hydrograph (defined by The Nature Conservancy as environmental flow components; The Nature Conservancy 2005) and rate of change of flows...
with physical processes, ecological processes, and biological targets in the Connecticut Basin are summarized below. This summary is based on approximate recurrence intervals of environmental flow components, rather than specific discharge values, because discharge relating to flow recurrence intervals varies widely among tributaries to and reaches of the Connecticut River.

Large floods (>10 year recurrence interval)
- Induce meandering, scouring, and filling of channel
- Scour riparian vegetation and deposit alluvial soils
- Supply a diverse seed bank to floodplains and enhance recruitment and diversity of riparian species (when timed with seed drop of riparian species)
- Develop young floodplain forest communities

Small floods (2-10 year recurrence interval)
- Maintain floodplain landforms (e.g., side channels, oxbows, wetlands, deposition bars, sandy and cobblestone beaches) and transport nutrients from the floodplain to the channel
- Regularly inundate riparian vegetation and maintain existing floodplain communities
- Provide habitat for spawning and rearing of river herring (alewife and blueback herring) on floodplains when timed with spawning (flood duration must be sufficient to allow for egg hatch and rearing of juveniles)
- High spring discharge is a cue for Atlantic salmon smolt migration, and is likely a cue for life history stages of other fishes; delayed timing of spring floods outside of spawning window of shortnose sturgeon (defined by temperature and photoperiod) results in delay or cessation of spawning
- Increase invertebrate production by connecting floodplain habitat to the main channel

Bankfull flows (1.5-2 year recurrence interval)
- Define and maintain channel shape and prevent vegetation growth in the channel
- Effective discharge for sediment transport
- Provide maximum area of channel and riverbank (snags, undercut banks, overhanging vegetation) for habitat for fish and invertebrates
- Increase invertebrate production by maximizing riverbank habitat

Seasonal low flows (<Q70)
- Increase water temperature and decrease dissolved oxygen
- Decrease available habitat
- Concentrate prey for fish predators
- Increase available habitat for some riparian species, such as cobblestone tiger beetle and puritan tiger beetle

In addition to information linking hydrology and response of physical and ecological processes and targets, some data are available that indicate how alteration of the above flow components may influence species and communities. Some potential physical and ecological impacts of flow alteration are summarized below.
Elimination of large floods
- Loss of floodplain meandering
- Vegetation encroachment on floodplains
- Decreased regeneration of floodplain forests
- Shifts in species composition at higher floodplain sites

Reduction or elimination of small floods
- Decreased input of terrestrial nutrients and organic material to aquatic systems
- Shifts in sediment dynamics that may lead to degradation of floodplain landforms
- Shifts in species composition at lower floodplain sites, potential decrease in regeneration
- Loss of habitat for fish that spawn on floodplains
- Potential loss of migratory or spawning cues for some fish species

Decreased frequency of bankfull flows
- Vegetation encroachment in the channel
- Change in channel shape and sediment transport to adjust to new hydrograph
- Loss of habitat (snags, undercut banks, overhanging vegetation) for fish and invertebrates

Increased duration and/or lower magnitude of low flows
- Increased water temperature and decreased dissolved oxygen
- Decrease in available habitat
- Shifts in fish communities to species that prefer slower water velocities (favor habitat generalist species over fluvial specialists)
- Elimination of habitat for some fish and invertebrates, resulting in reduced diversity and abundance of fishes and freshwater mussels

Increased short-term flow fluctuations
- May result in bank erosion, loss of stable shallow water habitats, and increased water temperature at stream margins
- Stranding and displacement of fish and aquatic invertebrates
- Reduce or eliminate the fish and mussel assemblage dependent on stream margin habitat, resulting in reduced diversity and abundance of fishes and freshwater mussels
- Lead to low species diversity and total abundance of benthic invertebrates
- Reduce or eliminate stable beach habitat for puritan tiger beetle and cobblestone tiger beetle

Based on the most prevalent patterns of hydrologic alteration in the Connecticut River Basin and available information linking hydrology with physical and ecological process and biota, I recommend to focus flow restoration efforts on reintroducing small floods that link rivers with their floodplains in tributaries to the Connecticut River, and reduce diurnal (short-term) flow fluctuations below dams, both in the mainstem and in tributary rivers. Flow restoration plans should include a research component, to examine links between flows and physical and ecological response specific to the Connecticut River and its tributaries. In particular, research is needed on the effects of decreased flood frequency for stream geomorphology, riparian communities, and nutrient dynamics. I suggest that studies be designed to examine response of
geomorphic and ecological processes and riparian communities in the Connecticut River Basin to reductions in overbank flows using experimental floods or taking advantage of natural flood events, accounting for interactions between reduced flood flows and other stressors, such as land uses in riparian areas that have decreased site availability and seed sources for floodplain forest communities. Research on diurnal flow fluctuations is also needed, particularly examining species that use river margins and effects of flow fluctuations on river margins and shallow water habitat.
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Introduction

A river’s flow regime is considered a “master variable” structuring physical and biotic components of aquatic ecosystems (Power et al. 1995b; Poff et al. 1997). Patterns of river flow determine physical habitat in streams and on floodplains and influence organic matter and nutrient availability, water temperature, and water quality (Stanford et al. 1996; Bunn and Arthington 2002; Whiting 2002). Five critical components of a natural flow regime, including magnitude of discharge, frequency of occurrence, duration, timing, and rate of change of flows, maintain aquatic biodiversity and ecosystem processes (Poff et al. 1997). Life history strategies of aquatic and riparian species have evolved in response to natural flow regimes in the species’ native rivers and streams (Poff et al. 1997; Bunn and Arthington 2002). Changes in components of the natural flow regime, such as loss of overbank flows due to dams or water diversions, may result in loss of aquatic biodiversity, changes in aquatic food webs, and reductions in fish species and abundance (Power et al. 1995a; Power et al. 1995b; Wootton et al. 1996).

Ecologists have formed general hypotheses about potential changes in aquatic community structure and function resulting from altered flow regimes. However, most of the studies in the United States used to form these hypotheses were conducted in the west and southeast. Ecological effects of hydrologic alteration are dependent on physical and ecological context; thus, specific relationships will vary among ecoregions. Overall, we have limited data on the response of species in rivers and floodplains of the northeast U.S., as well as the degree of hydrologic alteration that may lead to changes in aquatic and riparian communities. The goal of this report was to synthesize published information that links river flow regimes with ecological response in the Connecticut River and tributaries. Specifically, I examined: (1) links between hydrology and physical and ecological processes, (2) flow needs for various life history stages of The Nature Conservancy’s ecological targets in the basin, including floodplain forests, migratory and resident fish, aquatic and riparian invertebrates, and estuarine communities, (3) potential effects of hydrologic alteration on these ecological targets, and (4) areas of research needed to expand our knowledge of ecological effects of hydrologic alteration in the Connecticut Basin. To the greatest extent possible, I have restricted the scope of literature reviewed in this report to studies specifically focused on some aspect of the Connecticut Basin. Where data were not available, I expanded the scope of the literature to include studies conducted in humid regions of the eastern United States.

The Connecticut River flows 660 km from its source near the Canadian border to Long Island Sound, draining a 29,137 km² basin. Land use in the watershed is approximately 77% forested, 9% agricultural, 7% wetlands and water, and 7% developed (Jacobson et al. 2004). Land use is generally rural agrarian and undeveloped at the headwaters in northern Vermont and New Hampshire, and transitions to densely populated urban areas in the south-central river valley in Connecticut (Garabedian et al. 1998). Down-river from the city of Hartford, Connecticut, the basin is again largely undeveloped, and the Connecticut River is the only major river in the northeastern U.S. without a major port, harbor, or urban area at the mouth (Jacobson et al. 2004). The estuary contains high-quality tidal wetlands selected as Wetlands of International Importance under the Ramsar convention (Jacobson et al. 2004). The upper Connecticut River in New Hampshire and Vermont flows mainly through a confined valley, limiting channel sinuosity and floodplain width (Nislow et al. 2002), although meander bends are
present in some unconfined reaches (Field Geology Services 2004). The river in southern Massachusetts and Connecticut flows through the Hartford Basin, an area of relatively soft sedimentary strata, and the river becomes slow-moving and meandering (Connecticut Department of Environmental Protection 1994). South of Hartford the river crosses the Eastern Border Fault and flows through the Eastern Crystalline Highlands, an area of hard metamorphic rock that constricts the river and allows only narrow tidal wetlands. At the mouth, the river flows across a broad coastal plain, forming extensive brackish and salt marshes (Connecticut Department of Environmental Protection 1994).

Mean annual precipitation ranges from 1200mm near the coast to about 900mm in the northern part of the basin, and precipitation is evenly distributed throughout the year (Garabedian et al. 1998; Magilligan and Nislow 2001). Mean annual discharge of the Connecticut is 19,200 cfs (Garabedian et al. 1998). Peak flows typically occur in late winter and early spring (primarily March and April) resulting from snowmelt or rain falling on frozen ground (Magilligan and Graber 1996). Low flows typically occur in late summer, and less frequent high flows often occur in the fall (October through December, often associated with hurricanes), although the frequency of high flows in autumn decreases with increasing latitude and distance from the coast (Magilligan and Graber 1996). Forty-four major tributaries (each with a drainage basin of at least 78 km², or 30 mi²) flow into the Connecticut.

**Hydrologic alteration in the Connecticut River Basin**

Dams and impoundments are a primary source of hydrologic alteration in the Connecticut Basin. The ratio of dam storage capacity to mean annual runoff of a river provides a general measure of the potential for dams to alter river flow (Graf 1999). Generally, storage of individual dams in the Connecticut Basin is more limited than storage of dams in other regions of the United States. This limited storage, combined with the high precipitation characteristic of this humid region, yields low capacity to runoff ratios. On average, dams in New England store a volume of water equal to 26% of mean annual runoff, whereas mean storage of dams in the southeast is almost equal to mean annual runoff, and dams in the Rocky Mountains and southwest are capable of storing three to four times mean annual runoff (Graf 1999). Although maximum storage of Quabbin Reservoir is 275% of mean annual runoff for its watershed, the next largest dam in the Connecticut Basin can store 62% of annual discharge (unpublished data).

Although the potential for individual dams in the Connecticut Basin to cause large-scale changes in river flow regimes may be low relative to rivers in other regions, the number of dams per watershed area in the Connecticut is among the highest of all rivers in North America, Europe, and the former Soviet Union (Dynesius and Nilsson 1994; Graf 1999). Based on dams listed in the National Inventory of Dams database (NID; US Army Corps of Engineers 2006), Graf (1999) estimated a watershed area to dam ratio of 43km² in New England, the lowest ratio of any region in the United States. Dynesius and Nilsson (1994) ranked the Connecticut River as one of the top three fragmented rivers in North America (along with the Columbia and the Mobile), with the longest main-channel segment without a dam less than 25% of the length of the entire main channel. Thus, altered hydrology due to both individual dams and cumulative
effects of dams is a primary stressor to aquatic and riparian communities in the Connecticut River and tributaries.

There are 65 major dams on the mainstem of the Connecticut River and its tributaries, with a major dam defined as a structure capable of storing at least 10% of total annual runoff at its location. Mainstem dams in the Upper Connecticut (the portion of the river flowing through Vermont and New Hampshire) impound approximately 54% of the length of the river, converting free-flowing, lotic environments into lentic habitat (Fallon-Lambert 1998). Overall, the basin contains 16 flood-control reservoirs and at least 125 reservoirs used for power generation (Garabedian et al. 1998). Water withdrawals for water supply, snowmaking, and other uses also impact river flow throughout the basin. Eighty major surface water withdrawals and hundreds of groundwater withdrawals have been identified in the upper basin alone, although detailed data on water withdrawals are limited (Fallon-Lambert 1998).

Patterns of hydrologic alteration in the Connecticut Basin depend on types of dams present and the prevalence of water withdrawals. Flow in the mainstem of the Connecticut is altered mainly by hydropower dams on the mainstem and flood control dams on the tributaries. General patterns of flow alteration in the mainstem include: increased within-day variation in flows due to hydropower peaking, decreased flood frequency and maximum flows because of flood control dams on tributaries, and potential for decreased magnitude, increased frequency, and increased duration of low flows, particularly in areas with flow diversion. Small floods (2-5 year recurrence interval) are more common on the mainstem Connecticut than in most tributaries with flood control dams, but larger floods are almost nonexistent (Magilligan and Nislow 2001; Nislow et al. 2002; Zimmerman 2006). An analysis by Nislow et al. (2002) showed that a flood in the Upper Connecticut River with a 10-year recurrence interval prior to construction of Wilder dam had a recurrence interval of ≥100 years after the dam was in place.

Tributaries in the Connecticut Basin with flood control dams are generally characterized by increased flow stability and absence of extreme flows. An analysis of the effects of flood control dams on hydrology of the Ashuelot River, New Hampshire, and West River, Vermont found that flood control dams led to decreased frequency of both floods and extreme low flows and lower between-day variability (Zimmerman 2006). Within-day variability increased in the West River, likely due to operations of Ball Mountain dam, which has equipment and an operations schedule that make dam operators unable to make small, frequent modifications to flow releases (Jay McMenemy, Vermont Agency of Natural Resources, personal communication). The most significant flow alteration in both rivers was the reduction or elimination of bankfull and overbank flows (flows with ≥2-year recurrence interval). Flood control dams were not related to significant changes in timing of flood events or high flows (Zimmerman 2006), but spring high flows in New England rivers may be occurring 1-2 weeks earlier than 30 years ago, likely due to increased spring air temperatures (Hodgkins et al. 2003).

Most tributaries in the Connecticut Basin, including those with flood control dams, tend to have multiple small dams with limited storage, but may also have water withdrawals, such as water supply reservoirs, diversions, or groundwater pumping, that impact flows. Presence of dams and culverts that fragment habitat and likely alter sediment dynamics are prevalent throughout the basin, and many tributaries to the Connecticut River also have the potential for
water withdrawals that increase the frequency and decrease the magnitude of low flows. Tributaries in the lower basin, particularly those in Connecticut, may have increased flashiness of flows as a result of high levels of urbanization and impervious surfaces in tributary basins (Burchsted 2005). For example, the watershed of the Salmon River in Connecticut had 2.7% impervious surfaces in 2002 (an increase from 2.3% in 1985), which likely increased both the magnitude of runoff during storm events and variability in stream flows (Burchsted 2005).

Overall, the major causes of hydrologic alteration in the Connecticut River Basin are dams (mainly for flood-control and hydropower production) and water withdrawals. However, potential future changes in land use and/or climate may become increasingly important factors in determining river flows. Urbanization in a basin commonly results in the following hydrologic changes that may have ecological effects: increased frequency and magnitude of high flows, redistribution of water from base flow to storm flow, increased daily variation in flows, and reduced low flows (Konrad and Booth 2005). In watersheds around Boston, Massachusetts, urbanization (Urban Intensity Index, UII) was correlated with increased stream discharge, channel incision, and increased loading of fine sediment to streams (Short et al. 2005). A review of previous studies of effects of urbanization on streams indicated that negative effects on aquatic biota may be expected to occur when impervious surfaces in a basin exceed 5 to 18%, equivalent to UII values of 10-40 for the Boston area (Tate et al. 2005). A study of patterns of land use change and ecological effects in the Hudson River Valley showed an increasing trend of conversion of agricultural land and abandoned fields to new housing developments, with most of the new growth spreading north and east along transportation corridors (Limburg et al. 2005), which may be a predictable future pattern of urbanization in the Connecticut River Basin. Macroinvertebrate indices (EPT index, biotic assessment profile) were negatively correlated with increased urbanization, and nutrients (total N, % inorganic N, total P) increased in urbanized basins (Limburg et al. 2005).

Seasonal patterns in the Connecticut River hydrograph are driven by the ratio of precipitation falling as snow to total precipitation in the basin (S/P). Water is stored as snow during the winter and released as snowmelt in the spring, with snow stored for longer periods in the northern portion of the basin. Rain falling on snow or frozen ground usually results in annual peak flows in March and April. Climate change is predicted to alter the ratio of snow to total precipitation in the region (Huntington et al. 2004). Eleven out of 21 sites in northern New England have significantly lower S/P ratios from 1949 to 2000 compared with earlier periods, predominately from decreased snowfall (Huntington et al. 2004). In addition, future climate predictions for New England suggest a shift to warmer and drier conditions (Moore et al. 1997; Huntington 2003). A water balance model suggests that annual stream flow could be reduced by 21-31% in New England and the Mid-Atlantic regions, with higher reductions in the north. The greatest reductions would occur in fall and winter, although summer thunderstorms are projected to be less frequent but of greater intensity (Moore et al. 1997). A more recent study indicated that an increase in mean annual temperature of 3 °C would result in a decrease of mean annual runoff of 11-13% for streams in New England, due to longer growing seasons (thus, increased evapotranspiration) and less precipitation falling as snow (Huntington 2003). The greatest total decrease in runoff would likely occur in the high flow months of April and May, although the largest proportional decreases are expected to occur in the low flow months of July – September.
Overall, lower S/P ratios may shift the timing and reduce the magnitude of spring peak flows, and climate models suggest decreased annual discharge.

Future changes in hydrology of the Connecticut Basin from climate change or land use, or even perhaps natural flow restoration, may make the Connecticut River and its tributaries more vulnerable to invasive species. Approximately 25% of fish species in New England are introduced (Bain and Meixler 2000), and this high diversity of non-native fishes suggests that adaptive management approaches will be needed to ensure that restoration of natural flows benefit conservation targets rather than introduced species. For example, increased minimum flows and decreased diurnal variation in Colorado River flows below Glen Canyon dam resulted in increased abundance of non-native rainbow trout (McKinney et al. 2001). Overall, development of restoration scenarios for the Connecticut River Basin should include consideration of additional stressors that may influence or interact with current patterns of altered hydrology, including climate change, land use trends, and non-native species.

Response of physical and ecological processes

Predicting effects of hydrologic alteration on biota is difficult due to complex interactions between species and physical and ecological processes in streams. Linking changes in river flow regimes to changes in physical and ecological processes, rather than biological targets, may be simpler in some circumstances, with a greater accuracy of predictions (Benda et al. 2002). For example, bankfull discharge, with an average recurrence interval of 2 years, is considered “effective discharge”, or the flow that transports the greatest amount of sediment over time and does most of the work of maintaining channel shape and condition (Wolman and Miller 1960; Gordon et al. 2004). Doyle et al. (2005) used the concept of effective discharge to investigate a range of flows important for multiple ecological processes, including organic matter transport, algal growth, nutrient retention, macroinvertebrate disturbance, and habitat availability. A range of discharge events drives various ecological processes, indicating that base flows are important for some processes, whereas moderate or large floods dominate others (Doyle et al. 2005; Table 1). Flows just above bankfull are effective for many ecological processes because these flows link the river channel with the floodplain, capturing additional nutrients and habitats. The above physical and ecological processes in turn have effects on aquatic and riparian species. Thus, determining relationships between discharge and processes in streams is often simpler and more direct than focusing only on relationships between discharge and aquatic biota.

Even though relationships between flow regimes and physical and ecological processes may be less complex, specific relationships for the Connecticut River are not well known. In the following section, I examine links between hydrologic alteration and fluvial geomorphology and temperature. I give examples specific to the Connecticut River when available; however, data for the Connecticut Basin are scarce. In addition to fluvial geomorphology and temperature, hydrologic alteration alters organic matter and nutrient transport, which in turn determines the food base available for aquatic organisms. For example, flows that inundate the floodplain capture organic matter that is transported to the stream channel (Doyle et al. 2005). Changing rivers into reservoirs alters biogeochemical cycles, including changes in nutrient ratios, reductions in oxygen levels, and interruptions in the flow of organic carbon (Friedl and Wüest
Although this is an important issue to be considered when examining effects of river regulation, relationships between flow and organic matter and nutrients have not been studied in the Connecticut River Basin.

**Fluvial geomorphology**

Hydrologic alteration can affect aquatic and riparian species and communities directly, through changes in water availability and discharge events linked to life history strategies, and indirectly, through changes in habitat, water temperature and quality, and ecological processes. River hydrology drives changes in fluvial geomorphology, including sediment transport, channel shape, floodplain topography, and valley form. Changes in fluvial geomorphology in turn affect habitat availability and diversity, river hydraulics, and water quality, all factors that have direct effects on aquatic and riparian biota. In some instances, dams may have changed fluvial geomorphology to such an extent that flow prescriptions may not be adequate to restore ecological processes. For example, sediment trapped behind a dam on the Oconee River, Georgia lowered bed elevations downstream, creating an incised channel (Ligon et al. 1995). Although high flows were not altered by the dam, changes in geomorphology led to decreased duration of flows that inundate the floodplain.

Flows necessary to maintain physical processes in stream and rivers include flows that maintain natural sediment sizes, channel form, longitudinal connectivity of the channel, connectivity of the channel with the floodplain, natural features and habitat diversity, and the hyporheic zone (Whiting 2002). Dams typically trap sediment, decreasing the supply of sediment downstream and increasing the size of particles (Table 2). Reductions in high flows below dams may also cause fine particles deposited by downstream tributaries to accumulate in the channel. Sediment may be deposited near channel margins, causing channels to narrow and become incised. Flushing flow releases may be designed to scour the channel and remove fine sediments that may have accumulated downstream (Kondolf and Wilcock 1996). However, for flushing flows to be effective, objectives must be defined that translate into quantitative flows and have measurable results. For example, flows may be designed for the objectives of eroding channel banks, depositing sediment on floodplains, or removing sand from pools. Table 3 outlines general recurrence intervals of discharge events needed for specific physical processes, broadly categorized as channel maintenance, floodplain maintenance, and valley forming flows.

Fluvial geomorphologists define “effective discharge” as the discharge that transports the greatest amount of sediment over time (Gordon et al. 2004). The interaction between frequency and magnitude of discharge events results in a moderate discharge (recurrence interval between 1 and 5 years) that is the most effective in transporting sediment over time, thus also the most effective in creating geomorphic change and maintaining the channel (Wolman and Miller 1960). Effective discharge is often approximately equal to bankfull discharge, although the recurrence interval of effective discharge may increase in rivers with armored channels and large-sized bedload material (Emmett and Wolman 2002). Although bankfull discharge events still occur in the mainstem Connecticut River (Magilligan and Nislow 2001), these events have been greatly reduced or eliminated in many tributaries (Magilligan and Nislow 2001; Zimmerman 2006).
The loss of bankfull flows in tributaries likely has effects on sediment dynamics and channel morphology that are dependent on geology of the basin. Relationships between geology and hydrologic patterns of New England rivers, including the Connecticut River and its tributaries, were reviewed by Apse (2000). Geologic subregions that comprise the Connecticut River Basin include the Connecticut Valley Lowlands, the Eastern Highlands, and the Western Highlands. The mainstem Connecticut River flows through the Connecticut Valley Lowlands, over sedimentary deposits of sandstone, siltstone, and shale. Tributaries drain the Eastern and Western Highlands, areas of resistant igneous and metamorphic rock. Rivers draining the highlands tend to have non-alluvial channels that are underlain by glacial till, bedrock, or weathered coarse sediment and resistant to erosion. These channels also tend to have low levels of infiltration and groundwater recharge due to the absence of coarse-grained stratified drift material (primarily sand and gravel), and so may have higher flow variability and be particularly sensitive to reductions in low flows. Dynamics and shape of non-alluvial channels are governed largely by geology, and less by river flows. In contrast, larger rivers and low-gradient rivers in the basin tend to have alluvial channels formed by sedimentary deposits. Alluvial channels tend to be more dynamic, with frequent changes in channel morphology through erosion and redeposition by river flows. Some of these streams may be underlain by coarse-grained stratified drift, and so have the potential for groundwater recharge during low flow periods. Overall, flow determines channel shape and floodplain formation to a greater extent in alluvial channels than non-alluvial channels.

Although the above section outlines potential effects of hydrologic alteration on geomorphic processes, there is no comprehensive geomorphic assessment of the Connecticut River or its tributaries that fully assess specific responses to changes in river flows. Two geomorphic studies conducted in the upper Connecticut Basin are described below, although the study area in each report is small and observed effects of flow alteration and other river modifications (e.g., channelization) are likely site-specific. The study of the main channel assessed the main natural and anthropogenic factors determining channel morphology and causing bank erosion for a 137 km reach of the northern Connecticut River, between Murphy Dam (Pittsburg, NH) and Gilman Dam (between Gilman, NH and Lunenburg, VT) (Field Geology Services 2004). A subsequent examination of fluvial geomorphology of two tributaries to the Connecticut River examined a 16 km reach of the Mohawk River, New Hampshire and 35 km of the Upper Ammonoosuc River, also in New Hampshire, with the study reaches on both rivers extending upstream from the confluence with the Connecticut River (Field Geology Services 2006).

The assessment of the Connecticut River reach between Murphy and Gilman dams found that channel migration has ceased in the last 80 years, likely due to channel incision (more than 1m compared with abandoned channel segments) resulting from channelization (i.e., straightening of the river channel so that it flows through a restricted path) and decreased sediment supply below dams (Field Geology Services 2004). Although not identified in the assessment, lack of large floods has likely also contributed to the lack of channel migration (Hill et al. 1991; Magilligan et al. 2003). No significant channel meandering has occurred in the upper Connecticut since 1925, although significant migration did occur between 1861 and 1925 (Field Geology Services 2004). Over 30% of the upper river may have been channelized prior to
Although sinuosity has been reestablished in some reaches. Sinuosity (channel distance divided by length of the valley) varied between 1.0 (a straight, channelized reach) and 2.0 (meandering, with total channel length twice that of valley length), depending on degree of channelization and valley geology. Sinuosity determines stream gradient and river morphology; confined and straightened reaches of the river are generally high gradient with a plane bed morphology, whereas unconfined reaches are lower gradient with a pool-riffle morphology. In general, channelization leads to increased channel slope and greatly increases the sediment transport capacity of the river, resulting in bed and bank erosion that creates wider channels with greater bankfull depths. Bank erosion was also identified, with 66% of the banks of the upper Connecticut eroding, sensitive to erosion, or rip-rapped to prevent further erosion.

The assessment of the Mohawk River and the Upper Ammonoosuc reveal similar processes occurring in the tributaries as on the mainstem (Field Geology Services 2006). However, hydrologic alteration and total water storage in impoundments in the tributaries surveyed in this assessment are low relative to other tributaries to the Connecticut River. Therefore, effects of changes in river flows on fluvial geomorphology will likely be greater in other tributary basins than the reaches surveyed in this study. Field Geology Services (2006) found that at least 50% of the Mohawk River reach (8 out of 16km) and 33% of the Upper Ammonoosuc reach (12 out of 35km) have been channelized, creating channels with a plane bed morphology and lack of point bars, whereas unchannelized reaches typically have riffle-pool morphology and sand and gravel bars. Similar to the mainstem, bankfull depth and area of straightened reaches in the two tributaries are greater than in meandering reaches. The Mohawk River has five small earthen dams with limited capacity for water storage. The Upper Ammonoosuc River has four dams also with low water storage capacity (US Army Corps of Engineers 2006), although the dams impound a total area of 5 km² (Field Geology Services 2006). Sediment accumulation behind one of the dams on the Upper Ammonoosuc has created a delta at the upstream end of the impoundment, resulting in channel migration and braiding. Sand and gravel bars were observed upstream of other current or breached dams. Bank erosion below dams was attributed to sediment storage behind the dam and channel straightening.
Table 1. Potential relationships between effective discharge (the discharge with the greatest impact on the process of interest over time) and selected ecological processes in streams and rivers. Many relationships between ecological processes and effective discharge will vary by site. Data are from Doyle et al. (2005).

<table>
<thead>
<tr>
<th>Ecological process</th>
<th>Effective discharge</th>
<th>Study location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phosphorus budget</td>
<td>Frequent, low flows for P retention; moderate floods for P output as FPP. Absence of floods may lead to P accumulation.</td>
<td>Bear Brook, New Hampshire</td>
</tr>
<tr>
<td>PO$_4$ transport</td>
<td>Large, infrequent floods</td>
<td>Gwynns Falls, Maryland</td>
</tr>
<tr>
<td>NO$_3$ and SO$_4$ transport</td>
<td>Modal daily discharge</td>
<td>Gwynns Falls</td>
</tr>
<tr>
<td>Annual organic matter (POM) loads</td>
<td>Flow slightly larger than mean daily discharge (varies by season, availability and size of organic matter)</td>
<td>Ichawaynochaway Creek, Georgia</td>
</tr>
<tr>
<td>Coarse and fine particulate organic matter (CPOM and FPOM) export</td>
<td>Moderate, frequent floods (but likely site- or season-specific)</td>
<td>Bear Brook</td>
</tr>
<tr>
<td>Dissolved organic carbon (DOC)</td>
<td>Moderate, frequent floods</td>
<td>Bear Brook; effective discharge may be large, infrequent floods in arid environments</td>
</tr>
<tr>
<td>Periphyton accumulation</td>
<td>Mean daily discharge</td>
<td>Sycamore Creek, Arizona</td>
</tr>
<tr>
<td>Pool availability</td>
<td>Base flows (site-specific, depends on hydraulic geometry)</td>
<td>Bear Brook</td>
</tr>
<tr>
<td>Riffle availability</td>
<td>Moderate, frequent floods (site-specific, depends on hydraulic geometry)</td>
<td>Bear Brook</td>
</tr>
<tr>
<td>Macroinvertebrate mobilization</td>
<td>Moderate, frequent floods</td>
<td>Wilson Creek, Manitoba</td>
</tr>
</tbody>
</table>
Table 2. Physical responses to altered flow regimes. Table adapted from Poff et al. (1997).

<table>
<thead>
<tr>
<th>Source of alteration</th>
<th>Hydrologic change</th>
<th>Typical geomorphic response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dam</td>
<td>Capture of sediment moving downstream</td>
<td>Downstream channel erosion and tributary headcutting</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bed armoring (coarsening)</td>
</tr>
<tr>
<td>Dam, diversion</td>
<td>Reduced magnitude and frequency of high flows</td>
<td>Deposition of fines in gravel</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Channel stabilization and narrowing</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Reduced formation of point bars, secondary channels, oxbows, and changes in channel planform</td>
</tr>
<tr>
<td>Urbanization, drainage</td>
<td>Increased magnitude and frequency of high flows</td>
<td>Bank erosion and channel widening</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Downward incision and floodplain disconnection</td>
</tr>
<tr>
<td></td>
<td>Reduced infiltration into soil</td>
<td>Reduced baseflows</td>
</tr>
<tr>
<td>Levees and channelization</td>
<td>Reduced overbank flows</td>
<td>Channel restriction causing downcutting</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Prevention of floodplain deposition and erosion</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Reduced channel migration and formation of secondary channels</td>
</tr>
<tr>
<td>Groundwater pumping</td>
<td>Lowered water table levels</td>
<td>Streambank erosion and channel downcutting after loss of vegetation stability</td>
</tr>
</tbody>
</table>
Table 3. General relationships between physical processes and flow recurrence intervals. Data are from Hill et al. (1991), Magilligan et al. (2003).

<table>
<thead>
<tr>
<th>Geomorphic process</th>
<th>Physical response</th>
<th>Flow type</th>
<th>Recurrence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Channel maintenance</td>
<td>Prevent vegetation growth in the channel</td>
<td>Bankfull discharge</td>
<td>2 years on average, although site-specific variation occurs; fall rates (rates of flow reduction on the receding limb) should be within natural variability</td>
</tr>
<tr>
<td></td>
<td>Transport sediment</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Define and maintain channel shape</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Floodplain maintenance</td>
<td>Inundate riparian vegetation and reduce competitors</td>
<td>Overbank flows</td>
<td>Depends on site; Hill et al. (1991) found 1.5-10 years for Salmon River, Idaho; Magilligan et al. (2003) defined recurrence interval as 5 years for lower floodplain and &gt; 5 years for upper floodplains and terraces</td>
</tr>
<tr>
<td></td>
<td>Maintain floodplain landforms (side channels, oxbow lakes, wetlands, swamps, ponds)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Transport seeds and nutrients</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Valley Maintenance</td>
<td>Maintain valley form, condition, slope</td>
<td>Infrequent overbank flows that reach valley sides</td>
<td>&gt; 25 years</td>
</tr>
<tr>
<td></td>
<td>Channel flow that induces meandering, scouring, filling</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Temperature

Thermal stratification often occurs in deep reservoirs behind large dams. Density of water is highest around 4°C; thus, cold water sinks to the bottom of reservoirs in the summer, whereas in the winter water deep in the reservoir may be warmer than water at the surface. Dams that release water from the bottom of these reservoirs create thermal conditions downstream that may be much colder in summer and warmer in winter than the natural thermal regime of the river (Ward and Stanford 1979; Poff and Hart 2002). In contrast, surface-release dams have effects on downstream temperatures similar to natural lakes, usually resulting in elevated summer water temperatures (Ward and Stanford 1979). Most studies of thermal effects of impoundments have focused on large dams that release cold, hypolimnetic water. However, most impoundments in the Connecticut Basin are not deep enough for thermal stratification, and most dams release water at the surface. A study of the effects of a shallow impoundment with a surface-release dam in Michigan on thermal regimes found that water temperature below the dam increased as much as 5°C (Lessard and Hayes 2003). Increased water temperature was related to decreased densities of cold-water (stenothermic) fish, including brook trout (Salvelinus fontinalis), brown trout (Salmo trutta), and slimy sculpin (Cottus cognatus), and increased fish species richness. Shifts in community composition of macroinvertebrates were also related to changes in thermal regime.

Some tributaries in the Connecticut Basin may have summer water temperatures near the thermal maximum for cold- or cool-water species such as Atlantic salmon (Salmo salar). The addition of even small surface-release impoundments may increase water temperature enough to create conditions unsuitable for species that were already near the upper limit of their thermal range. For example, impoundments created by Ball Mountain and Townshend dams have contributed to increases in water temperature in the West River, Vermont. This thermal shift may have created unsuitable conditions for migrating salmon downstream from Townshend dam (Jay McMenemy, Vermont Agency of Natural Resources, personal communication). Increased summer water temperatures below dams usually extend downstream, and temperatures may even continue to increase, unless groundwater recharge or some other cooling factor is available (Fraley 1979; Lessard and Hayes 2003). Thus, the location, density, and storage capacity of impoundments in a basin may have effects on water temperature that ultimately alter fish and invertebrate assemblages.

Response of ecological targets

Conservation targets (components of biological diversity, i.e., species, natural communities, or ecosystems) for The Nature Conservancy’s Connecticut River Program include floodplain forest communities, migratory fish, and freshwater mussel assemblages. To determine effects of hydrologic alteration on these targets, I attempted to examine relationships between hydrology and response of floodplain plants, diadromous and resident fish, and aquatic and riparian invertebrates at both the population and community level. I searched published literature and unpublished sources for data that specifically linked components of the flow regime (magnitude, frequency, duration, timing, and rate of change of low flow, median flow, and high flow events) with species or community response, including links between flow and life
history stages, species occurrence, population dynamics, or shifts in community structure. I also examined data that linked habitats or ecological processes that are dependent on specific components of the flow regime with species or community response. Because prevalent types of hydrologic alteration in the basin include reduction in overbank flows and increased short-term flow fluctuations (Zimmerman 2006), and the potential for reduced low flows, I particularly focused on species that required inundated floodplain habitat (e.g., fish that spawn on floodplains) and species found in the varial zone of rivers (i.e. the area of the channel inundated during high flows and exposed at low flows, primarily shallow water habitats near stream banks).

**Floodplain vegetation**

Floodplain communities are adapted to periodic flooding; thus, they are particularly sensitive to hydrologic alteration and are good indicators of the effects of dams and water withdrawals on high flow events (Nilsson and Berggren 2000). Floodplain forests and other riparian vegetative communities depend on seasonal floods for seed dispersal, scour of debris and potential competitors from germination sites, deposition of sediment to maintain floodplain surfaces and enrich soils, and to provide adequate moisture conditions for germination and growth (Dixon 2003). Reservoirs upstream from dams inundate riparian areas, and new or different communities may form on shorelines depending on new patterns of flooding controlled by reservoir levels (Nilsson and Berggren 2000). Changes in hydrology and connectivity between the floodplain and channel downstream from dams may result in disconnected riparian populations, invasions of exotic species, and loss of physical processes that control riparian regeneration and succession. Patterns of flood inundation, erosion, and sediment deposition determine fluvial landforms (i.e., deposition bars, active-channel shelf, floodplain, and terrace). Flood duration and frequency associated with different fluvial landforms was the most important factor determining riparian vegetation communities along a river in Virginia (Hupp and Osterkamp 1985), and species richness of riparian trees was found to be positively correlated with topographic complexity of the floodplain (Everson and Boucher 1998).

Many floodplain species in the Connecticut Basin have periods of seed dispersal and germination that coincide with recession of annual spring floods (Table 4). Spring floods remove debris and vegetation from floodplain surfaces and deliver sediment and moisture, leaving moist, mineral soils available for seed germination (Dixon 2003). Floodplain species in the Connecticut River Basin generally have highest rates of germination on sites that were recently inundated by floodwaters; however, germination may be delayed when flooding is coincident with germination period. Therefore, good conditions for germination occur when fruitfall and seed dispersal coincides with receding spring floods. The length of a species’ dispersal period is likely related to its sensitivity to the timing and duration of floods. Maples generally have shorter dispersal periods than cottonwood and willow. Thus, timing of flows with respect to seed dispersal is more critical for maple recruitment. High flows that occur after seed germination may cause erosion or anoxic conditions, leading to reductions in seedling densities.

Seedling survival is highest if flooding during the remainder of the growing season is infrequent and of short duration, although seedlings develop increased flood tolerance with age (Dixon 2003). Only floods that occur after the start of the growing season will affect growth of deciduous trees. Floods that occur in the dormant season will not affect growth but may cause
seedling mortality due to burial, erosion, or ice scour (Peterson and Bazzaz 1984; Dixon 2003). Floods occurring during the growing season will also decrease vegetation density (including tree seedlings and herbaceous species) and provide space and light for surviving individuals. Flooding combined with suspended sediment and mechanical damage will increase seedling mortality. Thus, riparian communities in areas that receive mechanical damage tend to be dominated by seedlings and herbaceous species, whereas higher floodplain sites are dominated by mature trees (Metzler and Damman 1985; Table 5). On the upper Connecticut River, herbaceous community types (e.g., cobble barren, riverside meadow, and riverside thicket) were found on lower elevation floodplains where floods occurred every 1-2 years, whereas floodplain forests occurred at higher elevations where flooding was less frequent (Nislow et al. 2002). Duration of flooding also affects species composition and community type (Table 5). Generally, in floodplain forest communities of the eastern U.S., wetter sites will be dominated by silver maple and green ash, drier sites (or with less frequent flooding) will be suitable for sugar maple, and recently disturbed sites (bare soil) will be suitable for eastern cottonwood (Dixon 2003). Overall, species composition is determined by interactions between flow patterns and seed dispersal, flood and drought tolerance, tolerance to burial, rooting depth, and shade tolerance.

A study predicting responses of riparian vegetation to changes in flood regimes found that flooding determined the composition and distribution of riparian communities along a tributary to Lake Champlain in Vermont (Hughes and Cass 1997). The authors predicted that flood control would likely decrease diversity of species and community types. Species most tolerant of inundation, such as silver maple (*Acer saccharinum*) and swamp white oak (*Quercus bicolor*), would likely disappear from riparian forests over time and species adapted to more mesic conditions (e.g., sugar maple, *Acer saccharum*) would gradually replace current floodplain species. In addition, exotic species may increase, as exotics were more abundant at greater distances from the stream where flood disturbance was less frequent and of shorter duration. Examination of seeds in flood debris found that the species richness of seeds transported by flood waters was much higher than seeds available from species found in local riparian communities. This suggests that floods ensure a diverse pool of species is available to match annual variation in germination conditions, and flood control may limit seed availability to seed drop from standing riparian species and the soil seed bank. Analysis of seed germination in relation to flood magnitude indicated that recruitment of most individuals occurred in a single year as a result of a major overbank flood, suggesting that large floods are crucial for recruitment of floodplain species whereas smaller floods (e.g., 2-year recurrence interval) are important for maintenance of existing communities. Hydrologic analyses indicate substantial changes in post-dam flood frequencies for the Connecticut River (Nislow et al. 2002) and its tributaries (Zimmerman 2006). However, I am not aware of any studies that have examined changes in riparian species and community types in the Connecticut Basin as a result of decreasing frequency and magnitude of floods.

Changes in geomorphology in the Connecticut River mainstem and tributaries, such as channel incision and lack of lateral channel movements, likely also have an effect on floodplain community structure. A study relating channel migration with riparian communities along rivers in the coastal plain of the southeastern U.S. found that development of young floodplain forest communities depends on formation of new floodplain surfaces and shallow swamps (Shankman 1993). New surfaces are created by point-bar deposition and filling-in of abandoned channels.
These surfaces are initially colonized by early-successional species tolerant to flooding, but additional sediment deposition by repeated annual floods increases site elevation and eventually creates suitable habitat for less flood-tolerant species.

Floodplain communities common along the upper Connecticut River and tributaries include silver maple-sensitive fern, silver maple-ostrich fern, and sugar maple-ostrich fern (Sorenson et al. 2004). The silver maple-sensitive fern riverine floodplain forest is the wettest floodplain forest type along the upper Connecticut River and occurs in areas with fine soils that have relatively poor drainage. This community likely floods every year, and in areas with large floodplains water may be held for a portion of most years, with inundation lasting into June (Eric Sorenson, Vermont Agency of Natural Resources, personal communication). The silver maple-ostrich fern riverine floodplain forest has more sandy soils with better drainage. These communities may only flood once every few years, or for shorter periods each year. Soils are alluvial deposition with no surface organics, confirming frequent flooding events. The sugar maple-ostrich fern riverine floodplain forest is located in areas with well drained soils, often with cobbles mixed in, and is associated with high-energy rivers. It is flooded infrequently, possibly once every few years or more. This community may be found on former floodplains that are now cut off from river flooding because of channel incision. Most of the species associated with this community, with the exception of ostrich fern, are not adapted to frequent or extended flooding. Metzler and Damman (1985) associated floodplain community types along the lower Connecticut River mainstem with flood duration (Table 5). Kearsley (1999) examined soil characteristics and general relationships with flood frequency for floodplain community types along streams in Massachusetts (Table 6).

Silver maple is the tree species that is most common in floodplain forests of the Connecticut River and tributaries. Specific relationships between flood regime and silver maple are not well documented, although inundation tolerance and duration of flooding associated with silver maple forests provide useful information (Tables 4 and 5). Soil conditions necessary for silver maple germination typically result from a receding flood, and these conditions must occur soon after spring fruitfall (Peterson and Bazzaz 1984). Although adult trees are tolerant of inundation, increased duration of flooding has a strong negative effect on growth and competitive ability of seedlings. Recovery rates of seedlings after flooding increase as seedlings age, suggesting that seedlings with higher recovery rates of photosynthetic ability have a competitive advantage.

Species of concern (federally threatened or endangered or state listed species) associated with floodplain communities in a reach of the Connecticut River mainstem below Wilder dam include bladdernut (Staphylea tridentata), Jessup’s milk vetch (Astragalus robbinsii var. jessupi), cobblestone tiger beetle (Cincindela marginipennis), and obedience plant (Physostegia virginiana) (Nislow et al. 2002). Bladdernut is found in sugar maple floodplain forests and river terrace floodplain forests that are flooded infrequently (once every 10 to 100 years). One of four known occurrences (globally) of Jessup’s milk vetch is on a rocky rivershore outcrop on Hart Island in the upper Connecticut mainstem. The elevation of this community is similar to that of the silver maple floodplain forest community that floods every 5 to 10 years under natural conditions. Cobblestone tiger beetle and obedience plant are associated with herbaceous riverside communities, including bare cobble, riverside cobble, barren, and riverside meadow,
that are usually flooded annually (see section on freshwater and riparian invertebrates, below, for more information on cobblestone tiger beetle). Nislow et al. (2002) found that hydrologic alteration in the upper Connecticut River has resulted in a lack of flooding of sugar maple and river terrace floodplain forests. Flood frequency of silver maple floodplain forests has only been reduced for higher elevations within the range of this community type, although flood duration has decreased from 4 to 7 days before impoundment to 1 to 3 days after impoundment and the total area flooded has been substantially reduced. Both silver maple and sugar maple floodplain forests examined in this study were significantly older that the date of upstream impoundment, suggesting limited recruitment after Wilder dam was constructed. In the Wilder dam reach, floods with a recurrence interval of less than 2 years, corresponding with herbaceous riverside communities, did not show a change in either frequency or duration after impoundment.
Table 4. Flood-related characteristics of common tree species found on floodplains of the Connecticut River and large tributaries. Tree species are from Thompson and Sorenson (2000). Inundation tolerance: very tolerant = able to survive standing water for 1 year or more; tolerant = able to survive for 1 growing season; moderate = able to survive for 30 days; intolerant = able to survive a few days to weeks (Bratkovich et al. 1993). Other data are from Peterson and Bazzaz (1984), Burns and Honkala (1990), Cosgriff et al. (1999), Thompson and Sorenson (2000), and Sorenson et al. (2004).

<table>
<thead>
<tr>
<th>Species</th>
<th>Period of seed dispersal</th>
<th>Soil conditions for germination</th>
<th>Shade tolerance (seedlings)</th>
<th>Inundation tolerance (adults)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silver maple (Acer saccharinum)</td>
<td>April – June (production high in most years)</td>
<td>Receding flood, soils with organic matter</td>
<td>Moderate</td>
<td>Tolerant</td>
</tr>
<tr>
<td>Green ash (Fraxinus pennsylvanica)</td>
<td>October-February (germinate the following spring)</td>
<td>Receding flood, soils with organic matter</td>
<td>Intolerant to moderate</td>
<td>Tolerant</td>
</tr>
<tr>
<td>Sugar maple (Acer saccharum)</td>
<td>September – November (germinate the following spring)</td>
<td>Moist soils high in organic matter</td>
<td>Tolerant</td>
<td>Intolerant</td>
</tr>
<tr>
<td>White ash (Fraximun Americana)</td>
<td>September – December (germinate the following spring)</td>
<td>Wet alluvium</td>
<td>Intolerant</td>
<td>Moderate</td>
</tr>
<tr>
<td>Eastern cottonwood (Populus deltoides)</td>
<td>June – mid July</td>
<td>Receding flood, freshly exposed (bare) alluvium</td>
<td>Intolerant</td>
<td>Tolerant</td>
</tr>
<tr>
<td>Sycamore (Plantanus occidentalis)</td>
<td>February - May</td>
<td>Wet alluvium</td>
<td>Moderate</td>
<td>Intolerant</td>
</tr>
</tbody>
</table>
Table 5. Relationship between flood duration, frequency and timing, and riparian community types for the lower Connecticut River. Peak flows typically occur between March 15 and May 15; thus, flood duration is longest during this period. Inundation period depends on flood duration and drainage at a site. Riverbanks generally have more mechanical disturbance than floodplains; thus, community types are often different between the two habitats and riverbank communities usually have a sparser herb layer. Data are from Metzler and Damman (1985).

<table>
<thead>
<tr>
<th>Flood duration (days)</th>
<th>Flood frequency and timing</th>
<th>Habitat description</th>
<th>Community type</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;8</td>
<td>Recurrence interval of spring floods &gt; 2 years, summer floods &gt; 25 years</td>
<td>High flood plain</td>
<td>Sugar maple-green ash (<em>Acer saccharum</em>-Fraxinus pennsylvanica)</td>
</tr>
<tr>
<td>8-39</td>
<td>8-39</td>
<td>Low flood plain</td>
<td>Silver maple-sensitive fern (<em>Acer saccharinum</em>-Onoclea sensibilis)</td>
</tr>
<tr>
<td>39-194</td>
<td>Annual spring floods, summer floods every 2-7 years</td>
<td>Silver maple-white snakeroot (<em>Acer saccharinum</em>-Eupatorium rugosum)</td>
<td></td>
</tr>
<tr>
<td>194-241</td>
<td>Annual spring floods, summer floods every 2-7 years</td>
<td>Silver maple-cottonwood (<em>Acer saccharinum</em>-Populus deltoides)</td>
<td></td>
</tr>
<tr>
<td>241-273</td>
<td>241-273</td>
<td>Broadleaf arrowhead (<em>Sagittaria latifolia</em>)</td>
<td></td>
</tr>
<tr>
<td>273-336</td>
<td>273-336</td>
<td>Arrow arum-strawcolored flatsedge (<em>Peltandra virginica</em>-Cyperus strigosus)</td>
<td></td>
</tr>
<tr>
<td>336-360</td>
<td>336-360</td>
<td>Rough barnyardgrass-fall panicgrass (<em>Echinochloa muricata</em>-Panicum dichotomiflorum)</td>
<td></td>
</tr>
<tr>
<td>&gt;360</td>
<td>&gt;360</td>
<td>Broadleaf arrowhead (<em>Sagittaria latifolia</em>)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bare zone</td>
<td></td>
</tr>
</tbody>
</table>
Table 6. Floodplain forest communities along the Connecticut River and tributaries in Massachusetts in relation to flood frequency and soils. Data are from Kearsley (1999).

<table>
<thead>
<tr>
<th>Community type</th>
<th>Dominant species</th>
<th>Flood frequency</th>
<th>Soils</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riverine island floodplain forests</td>
<td><em>Acer saccharinum</em></td>
<td>Annual</td>
<td>Nonhydric, well-drained sandy loams, some cobbles, no soil mottles, no surface organic layer</td>
<td>Connecticut River mainstem and Deerfield River</td>
</tr>
<tr>
<td></td>
<td><em>Populus deltoides</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Acer negundo</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Matteuccia struthiopteris</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Major river floodplain forests</td>
<td><em>Acer saccharinum</em></td>
<td>Annual</td>
<td>Well-drained sandy loam, no soil mottles, no surface organic layer</td>
<td>Connecticut River mainstem and Deerfield River</td>
</tr>
<tr>
<td></td>
<td><em>Populus deltoides</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Laportea Canadensis</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transitional floodplain forests</td>
<td><em>Acer saccharinum</em></td>
<td>Annual</td>
<td>Silt loam or very fine sandy loam, intermediate drainage, some soil mottling, no surface organic layer</td>
<td>Third-order or smaller tributaries of the Connecticut and depressions within mainstem floodplain forests</td>
</tr>
<tr>
<td></td>
<td><em>Arisaema dracontium</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small river floodplain forests</td>
<td><em>Acer saccharinum</em></td>
<td>Less frequent flooding, possibly every few years</td>
<td>Mixture of silt loams and fine sandy loams, some soils hydric, most with soil mottles, some with surface organic layer</td>
<td>Third-order or smaller tributaries of the Connecticut</td>
</tr>
<tr>
<td></td>
<td><em>Fraxinus pennsylvanica</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Quercus palustris</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alluvial terrace forests</td>
<td><em>Acer rubrum</em></td>
<td>Very infrequent, several times per century</td>
<td>Silt loams, most with soil mottles and a surface organic layer</td>
<td>High terraces above the active flood zone throughout the basin</td>
</tr>
<tr>
<td></td>
<td><em>Carya ovata</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Prunus serotina</em></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Diadromous and resident fish

Dams can affect fish populations through changes in flow regime, habitat quality (e.g., temperature, sediment dynamics) and lateral (i.e., river-floodplain), longitudinal (i.e., upstream-downstream), and vertical (i.e., surface-groundwater) connectivity. Extensive research investigating effects of dams on movement of diadromous fish species has been conducted in the Connecticut River, primarily focusing on dams as barriers to fish movement. However, comparatively few data are available on the effects of hydrologic alteration on diadromous and resident fishes. This report is not focused on habitat fragmentation due to dams; therefore, I have not reviewed the literature on fish movement and dam passage. I have used the body of literature on fishes of the Connecticut Basin to compile data on timing of life history stages of diadromous fishes (Table 7), habitat preferences, and environmental cues of adult and juvenile migration of diadromous species. Overall, 11 diadromous fish species are found in the Connecticut Basin (Table 7), with one of the 11 (gizzard shad, Dorosoma cepedianum) likely present as a result of recent range expansion. Not much information is available on native fish communities prior to European settlement because of the early human alteration of rivers in the region (Apse 2000). However, approximately 25% of fish species in southern New England are introduced (Bain and Meixler 2000).

Environmental factors such as temperature, photoperiod, and discharge are important triggers for life history stages of all fish species, particularly as cues to spawning. Environmental cues also regulate many migratory behaviors and physiological changes of diadromous species. Although water temperature is a factor in migration and spawning of many species (Table 7), flow is also indicated as important to life history stages. Temperature windows for migration and spawning are relatively simple to determine for most species compared with discharge, which is much more variable in space and time. Therefore, more detailed knowledge of relationships between temperature and life history stages is available than relationships with discharge. Flow relationships may also be complex and interact with other environmental factors. For example, adult Atlantic salmon (Salmo salar) that migrate into the Connecticut River to spawn respond to both temperature and flow. Increased flow may trigger movement from the estuary to the river, whereas salmon already in the river may respond to decreasing flow (Juanes et al. 2004). Pre-spawning migration of shortnose sturgeon (Acipenser brevirostrum) is initiated by temperature; however, temperature, photoperiod, and river discharge are all important for successful spawning (M. Kieffer and B. Kynard, unpublished data). Under a natural hydrograph, high spring flows usually occur before the spawning window set by photoperiod and temperature. Flood control dams often cause a delay in peak spring flows to the extent that high discharge may occur within the sturgeon’s spawning window, potentially resulting in delay or cessation of spawning (M. Kieffer and B. Kynard, unpublished data). Dams have blocked migration of diadromous species in the Connecticut River, forcing fish to spawn directly downstream of dams. Thus, patterns of discharge and water velocity immediately downstream from dams will affect spawning success of many species.

A study examining the influence of abiotic factors on juvenile American shad in the Connecticut River found that year class strength could be predicted by riverine conditions in the month of June, when larval fish are emerging (Crecco and Savoy 1984). Year-class strength was negatively correlated with mean June river discharge and total June precipitation, and positively
correlated with mean June river temperatures. The strongest year-class during the study was
recorded for a year with mean June discharge and total precipitation well below normal. High
river flows and low temperatures during emergence may reduce larval feeding success and
survival (Crecco and Savoy 1984; Crecco et al. 1985). High discharge in May was positively
correlated with American shad recruitment, possibly because high rainfall and discharge in May
depress water temperatures, postponing shad spawning and larval emergence until mid-June
when conditions are more favorable for larval survival (Crecco et al. 1985).

Floodplains provide habitat, organic matter, and nutrients to aquatic biota, and the extent
of available floodplains is associated with fish production (Junk et al. 1989). However, use of
floodplains by fish depends on life history characteristics of species present in the river and the
timing, duration, and predictability of floods (King et al. 2003). Little data are available that link
fish species present in the Connecticut Basin to inundated floodplains, either as spawning and
rearing sites or for sources of energy. Inundated floodplains are used for spawning and larval
habitat by river herring (alewife and blueback herring) in the Lower Roanoke River, North
Carolina (Walsh et al. 2005), suggesting that river herring in the Connecticut may also use
floodplains for recruitment. However, duration of flooding must be long enough to allow eggs to
hatch and for larvae to grow and be slowly exported to the river (King et al. 2003; Walsh et al.
2005).

Bain et al. (1988) examined fish community structure in the West River, Vermont and
related species with habitat variables. Water depth and flow velocity were the most important
habitat variables structuring fish distribution, and the habitat type used by most fishes in the
West was found along the river margin, suggesting vulnerability to short-term flow fluctuations.
Fifteen common species and size classes were identified, nine of which (>90% of all fish
captured) used similar habitat: small smallmouth bass (Micropterus dolomieu), small rock bass
(Ambloplites rupestris), bluegill (Lepomis macrochirus), pumpkinseed (Lepomis gibbosus),
small white sucker, blacknose dace (Rhinichthys atratulus), fallfish, mimic shiner (Notropis
volucellus), and tessellated darter all used habitat at the river’s edge, characterized by very
shallow and slow water with boulder and cobble substrate. Four species, large white sucker,
large rock bass, longnose dace (Rhinichthys cataractae), and largemouth bass (Micropterus
salmoides), used some combination of deep or fast habitat types (midstream riffles or pools).
For example, large white suckers used deep and swift water habitat with fine substrate, typically
found at the upstream end of pools. The remaining two species, American eel (Anguilla
rostrata) and smallmouth bass, were considered habitat generalists.

Fish communities in the Deerfield River, Massachusetts were found to be significantly
different than the West River, and the differences were related to the magnitude and frequency of
within-day flow variation below a hydropower dam on the Deerfield (Bain et al. 1988).
Abundance of species found in shallow- and slow- water habitats on the West River was greatly
reduced in the Deerfield, and these species were absent from sites with the greatest flow
variability. Rapid changes in flow in the Deerfield eliminated river shorelines as functional
habitat for the species that used these areas, which made up the majority of the fish community
in the West River. Species that used habitat along the river’s edge were often seen stranded in
small, isolated pools after rapid decreases in discharge. Flow increases may have also increased
the threat of predation for these small species because increased water depth along stream
margins created habitat suitable for large piscivores. In contrast to the species that used habitat along the river’s edge, habitat generalists and species that used deep or fast habitat types had higher abundance in areas with increased variability of flow. The overall effects of flow variability below the hydropower dam on the Deerfield River were reduced diversity and abundance of fishes.

Similar to the study by Bain et al. (1988), a study in the Ipswich River, Massachusetts found the river margin to be the most important habitat type for fishes (Armstrong et al. 2001). The Ipswich River has surface- and ground-water withdrawals that substantially decrease or even eliminate flows in the upper third of the basin. During periods of sustained flow, important habitat features included undercut banks, exposed roots, overhanging vegetation, and woody debris, which were only available to aquatic biota when discharge was sufficient for streamflows to reach the banks. The Ipswich also had proportions of fluvial dependent and fluvial specialist species that were lower than expected based on a reference fish community developed for inland streams of New England, and comparatively high proportions of macrohabitat generalists tolerant of low flows, warm water, and ponded conditions. Although the Ipswich is not in the Connecticut River Basin, similar changes to the fish community may potentially be found in tributaries to the Connecticut with severe hydrologic alteration or water withdrawals. Piedmont streams in northern Georgia that had mean water withdrawals greater than 0.5 to 1.0 times the magnitude of the 7Q10 (the seven-day low flow with a recurrence interval of 10 years) were shown to have fewer fluvial specialist fish species than reference streams (Freeman and Marcinek 2006). The effects of water withdrawals on fish assemblages were similar whether water was taken from unimpounded streams or from water supply reservoirs, and the effect of water withdrawals on species richness was greater than effects of land use or mean streambed sediment size.

Water quantity and temperature may be more strongly correlated with fish species richness than habitat fragmentation from dams (Cumming 2004), particularly for fishes that are not diadromous. Bain and Meixler (2000) developed the Target Fish Community (TFC) approach for defining fish communities and relative abundance of species appropriate for natural streams in southern New England. Although fish communities were not specifically related to flow regimes, the determination of habitat requirements (generalists, fluvial dependents, and fluvial specialists) and pollution tolerance for each species allows this method to be used to associate fish communities with lotic (flowing water) or lentic (ponded water, typical of altered streams) conditions. Fish community and abundance targets were developed for the Quinebaug River in Massachusetts and Connecticut using data from reference rivers (recommended by biologists as rivers in good condition) in the same major river basin as the Quinebaug (the Thames River) or other coastal drainages in southern New England. Comparison of the fish community of a river with the target community for quality rivers in the region provides a biological goal for river restoration and may indicate potential factors associated with shifts in fish community composition and species richness (i.e., replacement of fluvial dependent species with generalists suggests a biological response to hydrologic alteration).

Within the Connecticut River Basin, reference fish communities have been developed for the Mill River, Hatfield, Massachusetts (Parasiewicz et al. 2003b) and the Eightmile River, Connecticut (Walden and Parasiewicz 2005) using Bain and Meixler’s (2000) approach. Neither
study found a distinct shift from fluvial dependent species to habitat generalists. The study conducted in the Mill River combined the TFC approach with habitat modeling, using MesoHABitator SIMulator (MESOHABSIM) to relate changes in physical habitat with variations in discharge to habitat suitability requirements of selected species. The amount of suitable habitat for different species varied with discharge; however, the relationships between habitat and discharge were site-specific (Parasiewicz et al. 2003b).
Table 7. Timing and cues for life history stages of diadromous fish in the Connecticut River and tributaries. Landscape impact is based on species distribution throughout the basin and impact on other aquatic biota (1=low, 2=moderate, 3=high). Data are from personal communication with Boyd Kynard (S.O. Conte Anadromous Fish Research Center) and sources listed below.

<table>
<thead>
<tr>
<th>Species</th>
<th>Landscape impact</th>
<th>Adult migration</th>
<th>Spawning</th>
<th>Juvenile migration</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Current</td>
<td>Period</td>
<td>Period</td>
<td>Habitat</td>
</tr>
<tr>
<td><strong>Alewife (Alosa pseudoharengus)¹,²</strong></td>
<td>1</td>
<td>March-June</td>
<td>April-June</td>
<td>Temperature</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>American eel (Anguilla rostrata)³</strong></td>
<td>2</td>
<td>August-November</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>American shad (Alosa sapidissima)⁴,⁵,⁶</strong></td>
<td>2</td>
<td>April-May</td>
<td>May-June</td>
<td>Temperature</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Temperature</td>
<td>(13-18°C)</td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Landscape impact</td>
<td>Adult migration</td>
<td>Spawning</td>
<td>Juvenile migration</td>
</tr>
<tr>
<td>---------------------------------</td>
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<td>-------------------</td>
</tr>
<tr>
<td></td>
<td>Current</td>
<td>Potential</td>
<td>Period</td>
<td>Cue</td>
</tr>
<tr>
<td>Atlantic salmon <em>(Salmo salar)</em></td>
<td>1 3</td>
<td>7, 8, 9</td>
<td>April-July; some in fall</td>
<td>Temperature, flow</td>
</tr>
<tr>
<td>Atlantic sturgeon <em>(Acipenser oxyrinchus)</em></td>
<td>1 2</td>
<td>10</td>
<td>Have been extirpated from the Connecticut Basin and no longer spawn in the basin, some individuals from the Hudson River and other natal streams enter the Connecticut River estuary and may be found in the salt water wedge from June to September</td>
<td></td>
</tr>
<tr>
<td>Blueback herring <em>(Alosa aestivalis)</em></td>
<td>2 2</td>
<td>1, 2, 4</td>
<td>April-September (as low as 5°C)</td>
<td>April-September (peak late May-mid-July)</td>
</tr>
<tr>
<td>Gizzard shad <em>(Dorosoma cepedianum)</em></td>
<td>2 ?</td>
<td>11</td>
<td>Spring</td>
<td>Temperature</td>
</tr>
<tr>
<td>Hickory shad <em>(Alosa mediocris)</em></td>
<td>1 1</td>
<td>12</td>
<td>April-May; some in September-October (spawn in spring)</td>
<td>Temperature</td>
</tr>
<tr>
<td>Species</td>
<td>Landscape impact</td>
<td>Adult migration</td>
<td>Spawning</td>
<td>Juvenile migration</td>
</tr>
<tr>
<td>-------------------------------</td>
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</tr>
<tr>
<td></td>
<td>Current</td>
<td>Period</td>
<td>Period</td>
<td>Period</td>
</tr>
<tr>
<td></td>
<td>Potential</td>
<td>Cue</td>
<td>Cue</td>
<td>Cue</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sea lamprey (Petromyzon marinus)</td>
<td>3</td>
<td>3</td>
<td>April-June</td>
<td>Temperature, timing varies with distance from estuary</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shortnose sturgeon (Acipenser brevirostrum)</td>
<td>1</td>
<td>2</td>
<td>Late winter-early spring</td>
<td>Temperature, migration distance</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Striped bass (Morone saxatilis)</td>
<td>3</td>
<td>3</td>
<td>Enter in April, depart in early July</td>
<td>No spawning reported in the Connecticut Basin, found in the mainstem below Turners Falls with very high densities near river mouth; predator of most other diadromous species</td>
</tr>
</tbody>
</table>

1Lower Roanoke River, North Carolina (Walsh et al. 2005); 2Connecticut River (Loesch and Lund, Jr. 1977); 3Atlantic coast, not specific to Connecticut River (Facey and Van Den Avyle 1987; Atlantic States Marine Fisheries Commission 2000); 4Holyoke dam (O’Leary and Kynard 1986); 5Connecticut River (Leggett 2006); 6Connecticut River (Marcy, Jr. 2004); 7Holyoke dam on the Connecticut and Rainbow dam on the Farmington (Juanes et al. 2004); 8West River, VT (Whalen et al. 1999); 9Connecticut River (Nislow et al. 1999); 10Connecticut River (Gephard and McMenemey 2004); 11Connecticut River (O’Leary and Smith 1987); 12Chesapeake Bay (Mansueti 1962); 13Connecticut River (Steir and Kynard 1986); 14Atlantic Coast (Beamish 1980); 15Lower Connecticut River (Kynard 1997; M. Kieffer and B. Kynard, unpublished data).
Freshwater and riparian invertebrates

Freshwater mussels are one of the world’s most imperiled species groups (Strayer et al. 2004) and twelve species of mussels are found in the Connecticut Basin (Table 8), including the federally endangered dwarf wedgemussel (*Alasmidonta heterodon*). Mussel species richness and abundance has been shown to decline below impoundments, likely from changes in temperature, physical habitat, food availability, and abundance of host fish (Vaughn and Taylor 1999). Mussels are generally found in shallow water habitats, such as stream margins. Increased flow variability may lead to stranding or high water temperatures near the river’s edge, decreasing mussel abundance or reproductive potential. Host fish species are also usually found in these shallow water zones, and abundance of fishes using shallow water habitats was greatly decreased below a hydropower dam on the Deerfield River, a tributary to the Connecticut (Bain et al. 1988).

Freshwater mussels usually occur in habitats with low shear stress and sediments that are stable during high flows (Layzer and Madison 1995; Strayer 1999). Changes in habitat, such as shifts from coarse to fine substrate, may lead to shifts in relative dominance of mussel species (Vannote and Minshall 1982). However, a study conducted in streams of the Mobile Bay Basin in Alabama found that mussel community composition was associated with densities of host fish rather than physical habitat (Haag and Warren, Jr. 1998). Densities of host generalist mussels and host specialists with elaborate mechanisms for attracting hosts were not correlated with either habitat or fish densities. However, densities of host specialist mussels without host-attracting mechanisms were positively correlated with densities of host fishes, and were largely absent from headwater and midreach streams that tended to have more variable fish abundances. In the Connecticut River, an example of this relationship may be the range expansion of Alewife floater (*Anodonta implicata*), which has been associated with shad (*Alosa sapidissima*) restoration in the basin (Smith 1985). Variations in flow regime and habitat stability may influence mussel densities and community composition in headwater streams, whereas more stable conditions in larger rivers lead to tighter relationships between mussel densities and host fish abundance (Haag and Warren, Jr. 1998).

Many instream flow studies examine habitat suitability for freshwater mussels at varying levels of discharge for specific stream reaches. However, mussels prefer different hydraulic conditions at different levels of stream discharge; thus, habitat suitably indices are of limited value for determining instream flow needs (Layzer and Madison 1995). A study conducted in the Mill River, Hatfield, Massachusetts, examined the relationship between discharge and habitat suitability for dwarf wedgemussel, and found that the association between flow and habitat depended on the reach surveyed (Parasiewicz et al. 2003a). Overall, dwarf wedgemussel preferred moderate flows and stable habitat conditions. Because mussels are relatively immobile, habitat that is isolated or unavailable at certain discharge levels will be unsuitable.

Although instream flow studies have been conducted for fish and freshwater mussels in tributaries in the Connecticut River Basin, I am not aware of any studies that have focused on other freshwater invertebrates. Benthic invertebrates are particularly sensitive to changes in flow, because changes in hydrology affect physical variables such as substrate composition, sediment dynamics, and water depth and velocity. A study conducted in North Carolina found...
that flows required to support the benthic macroinvertebrate community were substantially higher than flows required for target fish species (Gore et al. 2001). Underestimation of flows needed for benthic macroinvertebrates may lead to reductions in invertebrate production, ultimately resulting in decreased food availability for fish.

Physical disturbance is a major factor determining invertebrate community composition and abundance in streams. Flow variation and high flows leading to substrate instability often result in low species diversity and abundance, whereas artificially stable flows and changes in water temperature can lead to lower species richness and increased abundance of remaining taxa (Vinson 2001; Bunn and Arthington 2002). Bankfull and overbank flows may be important for invertebrate community composition and production in floodplain rivers. A study conducted in the Ogeechee River, Georgia, found that tree snags along streambanks had higher arthropod biomass than the main channel or floodplain, although the floodplain was the most important source of invertebrate biomass after adjusting for habitat area, even during a dry year (Benke et al. 2000). Thus, inundated areas along the river margin and floodplain are not only important habitat for macroinvertebrates, but are also the main source of secondary production for many rivers. However, we currently have limited understanding of the relative importance of floodplain habitat for invertebrate production in the Connecticut Basin.

Dragonflies (Odonata) have been used extensively in biomonitoring, and resident breeding species can be useful indicators of the ecological integrity of rivers and floodplains (Chovanec and Waringer 2001; Chovanec et al. 2004). Lentic species of dragonflies that use floodplain wetlands are often used as indicators for connectivity between a river and its floodplain (Chovanec and Waringer 2001; Chovanec et al. 2004). Less is known about species that are lotic specialists; however, these species may be useful indicators for flow conditions within the river channel (Hofman and Mason 2005). Adult dragonflies may travel some distance from breeding sites; thus, larvae or emerging adults are more useful indicators of habitat conditions (Hofman and Mason 2005). Currently, I am not aware of any completed studies relating dragonfly assemblages to altered hydrology or floodplain connectivity in the Connecticut River Basin. However, dragonfly emergence or larval abundance data are currently being collected for some portions of the Connecticut River (the New England Institute for Landscape Ecology is currently conducting a dragonfly survey for three sites along the Connecticut River - Haverhill/Wells River, Lebanon/Plainfield, and Charlestown/Walpole), and additional analyses may be able to link these data with flow conditions or floodplain inundation.

Two species of rare tiger beetles, puritan tiger beetle (Cicindela puritana) and cobblestone tiger beetle (Cicindela marginipennis) are found in shoreline habitats along the Connecticut River. The puritan tiger beetle is listed as a federally threatened species, and is listed as endangered in Massachusetts and Connecticut. Habitat for this species is sandy shoreline at the river’s edge, including sand bars and beaches, and larval abundance is more strongly associated with sand texture than other environmental variables such as moisture, cover, or prey availability (Omland 2002). Historical records indicate that several (at least 12) populations existed along the Connecticut River between Claremont, New Hampshire and Cromwell, Connecticut (U.S.Fish and Wildlife Service 1993; Omland 2002). Only two known populations exist today, on sandy beaches near Hadley, Massachusetts and Cromwell, Connecticut. Both sites are areas of sediment deposits along large bends in the river. Loss of
populations and reduced abundance of this species has been associated with construction of flood control dams in tributaries to the Connecticut River and hydropower dams along the mainstem (U.S. Fish and Wildlife Service 1993; Leonard and Bell 1999). Flood control dams have reduced or eliminated floods that deposit sediment, remove shoreline vegetation, and maintain sandy beaches. Hydropower dams increase short-term flow fluctuations, reducing the availability of stable beach habitat for foraging adults. In addition, impoundments upstream of dams may flood potential beach habitat. Urbanization, bank stabilization, poor water quality, and recreational use of beaches also likely led to reduced abundance of puritan tiger beetle in the watershed, although flow regulation has been implicated as the primary threat to this species (U.S. Fish and Wildlife Service 1993).

The cobblestone tiger beetle is found on cobble shoreline along the mainstem of the Connecticut River in Vermont, New Hampshire, and Massachusetts and the White and West Rivers in Vermont, tributaries to the Connecticut. This species is listed as endangered in Massachusetts and threatened in Vermont and New Hampshire. Habitat for the cobblestone tiger beetle is primarily cobble and sand beaches on the upstream side of islands (New Hampshire Fish and Game Department 2005). Similar to the puritan tiger beetle, habitat for the cobblestone tiger beetle is flooded regularly, with floods and ice scour maintaining substrate texture on beaches and removing encroaching vegetation. Thus, a primary threat to cobblestone tiger beetles is flow regulation. Flood control dams have inundated potential habitat, and decreased the frequency and duration of floods that scour vegetation and maintain cobble beaches (Leonard and Bell 1999; New Hampshire Fish and Game Department 2005). Hydropower dams increase short-term flow fluctuations, periodically inundating beaches during natural low-flow periods and likely decreasing survival of adults and larvae (New Hampshire Fish and Game Department 2005). Potential elimination of ice jams from the Connecticut River by the Army Corps of Engineers is another potential threat, because ice jams also scour vegetation from cobble shores (New Hampshire Fish and Game Department 2005).
Table 8. Habitat requirements and life history information for freshwater mussels in the Connecticut Basin. Most data are from Nedeau and Victoria (2003) and Ortmann (1919), other sources are listed below.

<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
<th>Habitat preference</th>
<th>Glochidia release</th>
<th>Host fish species</th>
<th>Population status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern pearlshell1</td>
<td><em>Margaritifera margaritifera</em></td>
<td>Coldwater streams, small rivers</td>
<td>Mid August-late October</td>
<td>Atlantic salmon, brown trout</td>
<td>Species of special concern (Connecticut)</td>
</tr>
<tr>
<td>Dwarf wedgemussel2,3,4</td>
<td><em>Alasmidonta heterodon</em></td>
<td>Streams and rivers</td>
<td>March-June</td>
<td>Tessellated darter, slimy sculpin, Atlantic salmon</td>
<td>Endangered (federal)</td>
</tr>
<tr>
<td>Triangle floater3</td>
<td><em>Alasmidonta undulata</em></td>
<td>Small to medium-sized rivers, also lakes</td>
<td>Late April-June</td>
<td>Broad range of host fish, primarily blacknose dace</td>
<td>Widespread (Connecticut), special concern (Massachusetts)</td>
</tr>
<tr>
<td>brook floater4</td>
<td><em>Alasmidonta varicosa</em></td>
<td>Small to medium-sized rivers</td>
<td>Mid April-May</td>
<td>Longnose dace, golden shiner, pumpkinseed, slimy sculpin</td>
<td>Endangered (Connecticut, Massachusetts, New Hampshire), threatened (Vermont)</td>
</tr>
<tr>
<td>Creeper5</td>
<td><em>Strophitus undulatus</em></td>
<td>Streams and rivers</td>
<td>Late April-early June</td>
<td>Broad range of host fish, including creek chub, largemouth bass, common shiner, longnose dace, yellow perch</td>
<td>Widespread but not abundant (Connecticut), special concern (Massachusetts)</td>
</tr>
<tr>
<td>Eastern elliptio6</td>
<td><em>Elliptio complanata</em></td>
<td>Streams, rivers, ponds and lakes</td>
<td>July-August</td>
<td>Broad range of host fish</td>
<td>Widespread and abundant</td>
</tr>
<tr>
<td>Species</td>
<td>Scientific name</td>
<td>Stream type</td>
<td>Substrate</td>
<td>Velocity</td>
<td>Glochidia release</td>
</tr>
<tr>
<td>--------------------------</td>
<td>-----------------------------</td>
<td>--------------------------------------------------</td>
<td>-----------------------------------------------</td>
<td>-----------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>Eastern floater</td>
<td>Pyganodon cataracta</td>
<td>Streams, rivers, ponds and lakes</td>
<td>Various substrate types, including deep silt and mud</td>
<td>Slow to moderate</td>
<td>April</td>
</tr>
<tr>
<td>Alewife floater</td>
<td>Anodonta implicata</td>
<td>Streams, rivers, ponds and lakes</td>
<td>Various</td>
<td>Slow to moderate</td>
<td>Spring</td>
</tr>
<tr>
<td>Eastern pondmussel</td>
<td>Ligumia nasuta</td>
<td>Streams, rivers, coastal ponds</td>
<td>Various, prefers silty riverbanks</td>
<td>Slow to moderate</td>
<td>June-July</td>
</tr>
<tr>
<td>Tidewater mucket</td>
<td>Leptodea ochracea</td>
<td>Medium to large rivers, coastal ponds</td>
<td>Various</td>
<td>Slow to moderate</td>
<td>Spring</td>
</tr>
<tr>
<td>Yellow lampmussel</td>
<td>Lampsilis cariosa</td>
<td>Medium to large rivers and lakes</td>
<td>Various</td>
<td>Slow to moderate</td>
<td>Spring to early summer</td>
</tr>
<tr>
<td>Eastern lampmussel</td>
<td>Lampsilis radiata radiata</td>
<td>Streams, rivers, ponds, and lakes</td>
<td>Sand and gravel</td>
<td>Slow to moderate</td>
<td>July-August</td>
</tr>
</tbody>
</table>

1Connecticut River Basin (Smith 1976); 2Neversink River, New York (Strayer and Ralley 1993); 3Connecticut River (Wicklow 2004); 4Mill River, Hatfield, MA (Parasiewicz et al. 2003a); 5Pennsylvania (Gray et al. 2002); 6Quebec (Downing et al. 1993)
Estuarine communities

River regulation has often resulted in reductions of freshwater reaching estuaries, causing the mixing zone of fresh and salt water to move farther inland into habitat that may be less suitable for estuarine species (Pringle et al. 2000). Reductions in freshwater may also increase salinity content in brackish tidal marshes. Effects of hydrologic alteration and sediment transport because of dams on tidal freshwater wetlands in the northeast U.S. have not been examined (Roman et al. 2000). However, patterns of hydrologic alteration in the Connecticut River Basin suggest that annual freshwater discharge has not been greatly reduced. Rather, changes in the frequency, magnitude, and duration of flood flows are the main hydrologic alterations that may impact tidal wetlands.

The Connecticut River is significant in that is the only major river in the northeast U.S. without a major urban center or harbor at the estuary. Designated as The Connecticut River Estuary and Tidal River Wetlands Complex, tidal wetlands in the lower river (58 kilometers extending upriver from Long Island Sound) were selected as Wetlands of International Importance under the Ramsar convention (Jacobson et al. 2004). The saline estuary is defined as the extent of the salt water wedge, whereas the tidal freshwater estuary encompasses the area of the river between the salt water wedge and the upstream extent of tidal flooding. Tidal flooding in the Connecticut River extends to Windsor locks, Connecticut, 85 kilometers upriver, whereas the salt water wedge only extends about 13 kilometers (Barrett 1989). The distribution of salinity in the area of the salt water wedge depends on river discharge and tidal fluctuations. During spring floods (discharge > 2000m/s) there is very little salinity in the lower reaches of the river, whereas during late summer low flow periods (discharge <100m/s) low salinity concentrations have been detected as far as 25 km upriver (Meade 1966).

Salinity concentrations determine three major classes of tidal wetlands in the lower Connecticut River, extending from East Haddam, Connecticut to Long Island Sound: freshwater tidal wetlands, brackish tidal wetlands, and salt marshes (Barrett 1989). Barrett (1989) described plant community types for each of these wetland classes. In general, community composition of each wetland class shifts with changes in salinity and duration of flooding. Salinity gradients are controlled by both river discharge and tidal flooding. Flood duration is largely controlled by tides, although river discharge also has an effect on flood duration of freshwater tidal wetlands (Barrett 1989). Changes in magnitude, frequency, and duration of river discharge may alter salinity concentrations in tidal wetlands, leading to shifts in plant community composition (Barrett 1989). Storm water runoff may degrade salt marshes by diluting salinity levels and depositing sediment, although specific effect of storm water runoff on salt marshes in the Connecticut River estuary are unknown (Connecticut Department of Environmental Protection 1994). Overall, few data are available relating specific effects of dams on freshwater hydrology and response of Connecticut River tidal wetlands.

Vegetation patterns in freshwater tidal wetlands are determined by flood stress and flood disturbance (Barrett 1994; Table 9). Flood stress is determined by flood depth and duration resulting from regular tidal influences, elevation, and soil drainage. Flood disturbance is measured by stream power, and is determined by mechanical damage from episodic river flooding. Although Barrett (1994) did not discuss the potential effects of hydrologic alterations
on freshwater tidal wetlands, the patterns outlined in Table 9 suggest that changes in riverine flood frequency and magnitude would alter plant composition and vegetation structure in these habitats.

Reductions in tidal flooding from dikes and drainage ditches may be the main cause for changes in species composition and ecology in salt marshes in New England estuaries (Portnoy 1999; Roman et al. 2000), rather than changes to river hydrology. For example, a study conducted in tidal estuaries of the Housatonic River, Connecticut found tidal hydrology and salinity gradients to be significant factors determining the relative dominance of native *Spartina alterniflora* and invasive *Phragmites australis* in tidal marshes (Chambers et al. 2002). Growth of *Phragmites* could be controlled by increased depth and frequency of tidal flooding and/or higher salinity or sulfide concentrations. Wetlands dominated by *Phragmites* are lower in plant and animal diversity and may lose the ability to function as spawning and nursery habitat for fish and crustaceans.
Table 9. Relationship between vegetation patterns in freshwater tidal wetlands, flood stress (tidal influence), and flood disturbance (riverine influence). Data are from Barrett (1994).

<table>
<thead>
<tr>
<th>Riverine influence</th>
<th>Tidal influence</th>
<th>Vegetation characteristics</th>
<th>Characteristic species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequent inundation, strong currents</td>
<td>Frequent inundation, long duration</td>
<td>Small and rosulate</td>
<td>Eriocaulon parkeri</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Creeping, prostrate Heterophyllous</td>
<td>Limosella subulata</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Slow growing and depauperate</td>
<td>Eleocharis parvula</td>
</tr>
<tr>
<td></td>
<td>Less frequent inundation, strong currents</td>
<td>Range from small and leafy to erect annuals, subperennials and perennials</td>
<td>Elatine minima</td>
</tr>
<tr>
<td></td>
<td>Frequent inundation, short duration of flooding</td>
<td></td>
<td>Callitriche heterophylla</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tufted graminoids</td>
<td>Sium suave</td>
</tr>
<tr>
<td></td>
<td>Frequent inundation, long duration</td>
<td>Small and rosulate</td>
<td>Bidens eatonii var. simulans</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Coarse perennials</td>
<td>Polygonum hydropiperoides</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Leafy annuals</td>
<td>Gratiola aurea</td>
</tr>
<tr>
<td>Frequent inundation, quiet water</td>
<td>Frequent inundation, long duration</td>
<td>Spongy, leafy emergents possessing lacuna or arenchyma with thick rhizomes</td>
<td>Ludwigia palustris</td>
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<tr>
<td></td>
<td></td>
<td>Junciform</td>
<td>Lindernia dubia</td>
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<td></td>
<td></td>
<td></td>
<td>Mimulus alatus</td>
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<td></td>
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<td></td>
<td>Hypericum mutlum</td>
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<td></td>
<td></td>
<td></td>
<td>Lycopus virginicus</td>
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<td></td>
<td></td>
<td></td>
<td>Panicum virginicum</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Eulalia vimea</td>
</tr>
<tr>
<td>Infrequent inundation, quiet water</td>
<td>Infrequent inundation, short duration</td>
<td>Tall, coarse perennials and herbs</td>
<td>Eupatorium dubium</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Coarse perennial grasses</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Leafy annuals</td>
<td>Phalaris arundinacea</td>
</tr>
<tr>
<td></td>
<td>Tussock forming</td>
<td>Coarse perennial grasses</td>
<td>Calamagrostis canadensis</td>
</tr>
<tr>
<td></td>
<td>Strongly rhizomatous</td>
<td>Phragmites australis</td>
<td>Cinna arundinacea</td>
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<td></td>
<td></td>
<td></td>
<td>Carex stricta</td>
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<td></td>
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<td>Carex lacusris</td>
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<td>Typha latifolia</td>
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<td></td>
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<td></td>
<td>Scirpus fluviatilis</td>
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<td></td>
<td></td>
<td></td>
<td>Phragmites australis</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Acorus calamus</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Iris pseudacorus</td>
</tr>
</tbody>
</table>

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Conclusions

Specific data linking hydrologic alteration to physical and ecological processes and ecological targets are scarce for the Connecticut Basin. Most studies in ecohydrology have been conducted in areas with dams that have the potential to store greater volumes of water and shift both the magnitude and shape of the hydrograph. However, the number of dams on the Connecticut River and tributaries and cumulative effects of water storage, withdrawals, and flow fluctuations from hydropower generation appear to be altering the structure and function of riparian and aquatic communities. Studies conducted in the Connecticut Basin and in rivers of the eastern U.S. have determined some links between hydrology and response of physical processes, ecological processes, species and communities. However, more research is needed to determine specific links between altered hydrology and ecological response (see research needs, below).

Based on the most prevalent patterns of hydrologic alteration in the Connecticut River Basin and available information linking hydrology with physical and ecological process and biota, I recommend to focus flow restoration efforts on reintroducing small floods that link rivers with their floodplains in tributaries to the Connecticut River, and reduce diurnal (short-term) flow fluctuations below dams, both in the mainstem and in tributary rivers. Additional hydrologic analyses should be performed to determine the extent of water withdrawals throughout the basin and potential effects of water withdrawals on the magnitude and duration of low flows. Flow restoration plans should include a research component, to examine links between flows and physical and ecological response specific to the Connecticut River and its tributaries, and provide the opportunity for adaptive management.

Research needs

In addition to hydrologic alteration, streams in the Connecticut Basin tend to have a high degree of fragmentation, due in part to historical construction of mill dams that are still present in many streams but may not have a current function. In addition to fragmentation from dams, the large number of road crossings in the basin has resulted in fragmentation from culverts in many small streams. Preliminary analyses of hydrologic alteration and fragmentation in tributaries of the Connecticut River have identified the lack of overbank flows and high number of stream culverts as prevalent stressors. Therefore, research on floodplains and stream connectivity is needed to understand effects of these stressors on aquatic and riparian processes and communities. For example, although hydrologic analyses indicate decreased frequency and magnitude of overbank flows in the Connecticut River and its tributaries, I am not aware of any research that examines the effects of the decrease in flood events on changes in species composition or age structure of riparian forests. I have outlined priority areas for research on floodplains and connectivity (first two points, below). In addition, I have summarized additional areas for research needed to address other types of hydrologic alteration and additional aquatic stressors in the Connecticut River and tributaries (remaining points, below).

Implications of decreased flood frequency for stream geomorphology, riparian communities, and nutrient dynamics – Examine response of geomorphic and ecological processes and riparian
communities in New England to reductions in overbank flows, using experimental floods or taking advantage of natural flood events. Specific research objectives include the following: (1) examine geomorphic change resulting from changes in flood frequency, duration, and rate of change (rise and fall rates), including changes in sediment dynamics (instream sediment, floodplain deposition, and areas of scour), channel geometry, and habitat diversity. (2) Investigate and define functional attributes of mainstem and tributary floodplain sites with the potential for floodplain reforestation/restoration. In addition to connectivity with the river relative to current hydrologic regime, these attributes might include specifics related to site land use history, seed bank, site topography, etc. (3) Determine availability and distance of seed sources for floodplain species from potential sites for floodplain restoration. Examine relationship between timing, magnitude, and duration of floods and local seed dispersal. (4) Determine current status and monitor regeneration patterns of silver maple and other floodplain species, as well as distributions of floodplain community types, after experimental or non-experimental flood events. (5) Examine relationship between floods and stream nutrient dynamics.

Importance of river connectivity for fish population dynamics – Examine spatial scale and ecological attributes of connected habitat necessary to sustain fish populations and genetic diversity. Specific research objectives include the following: (1) examine metapopulation dynamics of target fish species, and determine the spatial scale and ecological attributes of connected habitat necessary to support metapopulation structure. (2) Investigate habitat needs for source populations in different seasons and life stages. Explore relationships between habitat needed for spawning, feeding, cover, etc. and spatial configurations of connected habitat. Determine whether habitat needs can be easily defined to focus protection efforts. (3) Determine degree of movement, and variation in movement, of target fish species, seasonally and at different life stages.

Effects of increased flow stability in tributaries – Examine potential shifts in community composition, including increased abundance of species with low disturbance tolerance (such as aquatic macrophytes, some mussel species) and decreased species richness of macroinvertebrates.

Increased short-term flow variability below hydropower dams and some flood control dams – Assess effects of short-term (within-day) flow variability on bank stability, sediment dynamics, and species found along river margins (riparian areas and shallow water zones).

Detailed life history information for target species, specifically related to hydrology – Identify aspects of the hydrograph that are triggers for spawning, migration, or other life stages of aquatic and riparian species. Determine frequency, magnitude, duration, timing, and rate of change of flow types necessary for species during various life stages. Describe use of habitats that are affected by hydrologic alteration (e.g., use of floodplains) or the interaction between hydrologic and physical alteration (e.g., movement between habitats that may be blocked by culverts at low flows).

Importance of intact headwaters for ecological processes and community composition throughout the Connecticut Basin – Examine land use gradients in the Connecticut Basin to
determine the relative importance of ecological functions in headwater streams for ecological processes and species in the mainstem.

*Assessment of multiple stressors (land use, hydrologic alteration, fragmentation)* – Investigate relative effects of impervious surfaces and other land use, hydrologic alteration from dams and water withdrawals, and habitat fragmentation from dams and culverts on aquatic ecosystem structure and function. Examine potential spatial patterns in the relative importance of each stressor on ecosystem processes and ecological targets.

*Hydrologic effects of cumulative water withdrawals* – For a subset of streams in the basin, assess hydrologic alteration from cumulative groundwater pumping and surface water withdrawals. Examine hydrologic impact of water withdrawals relative to surface water storage in reservoirs in streams that have both impacts.

*Estimate stressor-response functions for flow alteration* – Using existing biological data and/or a mechanistic modeling approach, examine how particular parameters of flow alteration are likely to impact the structure of biological communities. This might take the form of a generalized stressor-response function developed using fish and/or macroinvertebrate data from rivers where flow alteration is the primary stressor.

*Develop multi-metric indices of flow alteration* – Based on existing Connecticut Basin fish and macroinvertebrate data, develop multi-metric biological indices that are sensitive to flow alteration.
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