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Marine-Derived Nutrient Cycling in the St. Croix River, Maine

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**MARINE-DERIVED NUTRIENT CYCLING IN THE ST. CROIX RIVER,
MAINE**

By

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A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Wildlife Ecology)

The Graduate School

The University of Maine

May 2018

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Dissertation Advisor: Dr. Joseph Zydlewski

An Abstract of the Dissertation Presented
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Anadromous species can boost freshwater productivity through nutrient subsidies. Along the Maine coast of the northeast United States, several alewife populations are recovering after freshwater connectivity is restored. Iteroparity in this part of their range may reduce their role as nutrient subsidies. Stable isotope analysis was used to detect marine-derived nutrient input. Spatial and temporal trends were characterized in the St. Croix as a baseline before alewife recovery, and nutrient-diffusing substrates indicated nutrient co-limitation. A reference watershed was used to compare nutrient dynamics when alewives were present versus absent. Results indicated isotope shifts within particular functional feeding groups, but not in the freshwater community as a whole. In addition, potential alleviation of nutrient limitation during the peak of the alewife run was seen.

A deterministic model was developed to explore the theoretical nitrogen and phosphorus dynamics of Alewife migrations under a range of scenarios. At low escapement levels, the number of recruits produced per spawner was high and juvenile nutrient export dominated. At high escapement levels, fewer recruits were produced per

spawner, and so adult nutrient import dominated. These trends persisted regardless of scenario, though the magnitude of endpoints changed. When dams were present, the reduction in upstream passage determined adult abundances. Downstream juvenile rates determined recruitment, as well as nutrient export. The effect of poor passage at sequential dams or an in-river fishery depended on their location in relation to spawning habitat. The St. Croix River, which is located between Maine and New Brunswick, has the majority of spawning habitat upstream. When passage in the lower river was varied, phosphorus difference was insignificant at low passage levels. When varied in the upper river, import dominated at a wide range of upstream passage rates when downstream passage was high. This led to a combined effect of more surviving juveniles per spawner, but a narrower range of passage rates that resulted in phosphorus import. Spawner abundance was higher when a fishery was located upstream than at the estuary, highlighting the need to consider dam and fisheries locations in relation to spawning habitat when estimating population recovery and nutrient dynamics.

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CHAPTER 1

ALEWIFE IN THE ST. CROIX RIVER: A SERIES OF UNFORTUNATE EVENTS

1.1 Industrial Use and Fisheries Exploitation in the St. Croix River

Anadromous fish migrate from the ocean into freshwater to reproduce. Species historically present along the northeast coast of North America included Atlantic salmon (*Salmo salar*), American shad (*Alosa sapidissima*), alewife (*A. pseudoharengus*), blueback herring (*A. aestivalis*), and sea lamprey (*Petromyzon marinus*). Populations of anadromous fish species in Maine have been in decline for centuries, primarily due to inaccessible spawning habitat, fisheries exploitation, and degraded water quality (Saunders et al. 2006). The St. Croix River, in Maine, has a unique and complex past associated with conflicts that developed around the exploitation of anadromous fish species. The St. Croix, which forms the border between northeastern Maine, USA and southern New Brunswick, Canada (Figure 1.1), has a watershed of approximately 1,649 miles² (4,271 km²) with 61 lakes and 183 tributaries (Dill et al. 2010).

The St. Croix watershed has been occupied for tens of thousands of years by native peoples, some of whom used the river to travel between inland settlements along the Penobscot and Saint John rivers and coastal settlements (Caron et al. 2012). The Passamaquoddy Tribe has deep ties with the St. Croix River, with families typically spending the winter inland and gathering along the coast in the spring to harvest migratory fish (Spiess & Cranmer 2005). Today, this tribe continues to live along the St. Croix River and Passamaquoddy Bay. In 1604 French explorers founded the first

European colony, the capital of Acadia, on St. Croix Island. After the 1780s, following the American Revolutionary War, a boom in settlement occurred along the St. Croix, and in 1798 the river was designated as the official boundary between the United States and Canada (FB Environmental 2008; Caron et al. 2012).

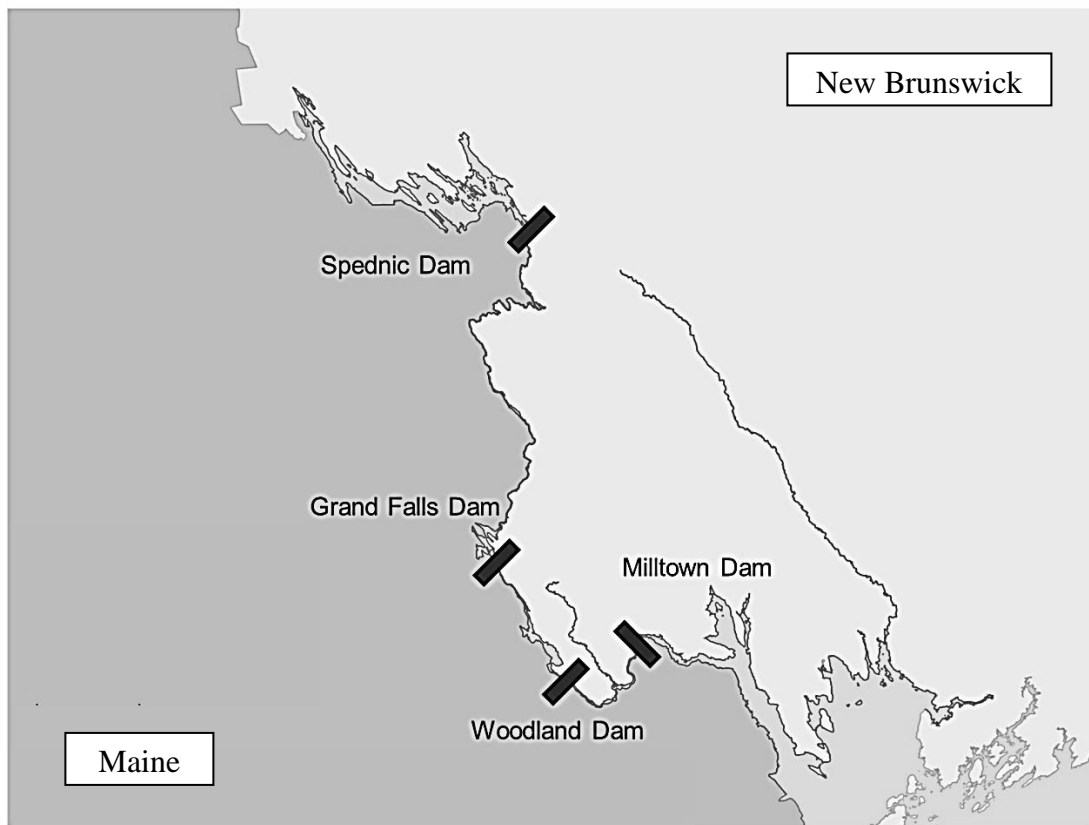


Figure 1.1. The St. Croix River, located between Maine and New Brunswick. Locations of dams are indicated by rectangles, and labeled by name.

The St. Croix River was initially settled because of the area's vast timber resources, and became a logging and ship-building hub in New England (Forkey 1993). The St. Croix River was used to move logs from inland areas to the coast, and as a consequence many dams were constructed in the 1880s to create flowages. While

initially built to control water levels, many of these dams were maintained to produce power for lumber mills (Caron et al. 2012). This intense industrial use led to poor water quality, as both solid and chemical wastes were poured into the river from tanneries as well as from pulp, lumber, and textile mills (FB Environmental 2008). Unchecked pollution from urban centers, four of which were developed close to the head of tide, led to pollution that became concentrated in the lower part of the river and the estuary (Forkey 1993). One major problem associated with lumber mills was the dumping of large quantities of sawdust into the river that subsequently washed down to the estuary (FB Environmental 2008). At the height of industrial production, sawdust was so thick it often prevented large cargo ships from moving through the estuary. Even larger steamships had a hard time navigating the sawdust islands that formed (Forkey 1993).

At the same time the region was developing a thriving timber economy, it was also becoming known for its exceptional sport fishery (Fletcher & Meister 1982). During the era of the industrial revolution, outdoor recreation was encouraged as a means for the wealthy to escape the endless bustle of city life. This led to the development of a major tourist industry in the St. Croix River Valley, with railways and steamboats bringing sportsmen and visitors from throughout the east coast to the flourishing coastal communities along the river (Forkey 1993). Between the visiting anglers and the local subsistence and commercial fisheries, fishing pressure was high for species such as Atlantic salmon, alewife, and American shad.

1.2. Dams, Fish Passage, and the IJC

The combination of fishing, dams, ocean mortality, and water pollution led to a precipitous decline in anadromous fish populations (Flagg 2007). Actions were taken on

both sides of the border starting in the late 1840s to require fish passage and prohibit mills from dumping waste, but the power to enforce these laws did not exist and so they were ineffective (Forkey 1993). From the late 1860s to early 1870s, the State of Maine appointed commissioners to determine which dams needed fishways and gave wardens the power to fine those mills that did not build them (Maine 1867) or continued to deposit waste into the river (Maine 1871). Similar laws were passed in Canada, but the specifics of these laws differed enough between Maine and New Brunswick that enforcement was often a moot point as it only applied to one side of the river (Fisheries 1870). In 1909, the International Joint Commission was established to address disputes between the United States and Canada regarding border waters and ensure equitable laws were passed related to water quality and fisheries regulations (FB Environmental 2008).

The economic and political influence of recreational fishing soon outweighed that of the commercial fisheries present in the watershed. Eventually the latter group was edged out of access to the resource, favoring visiting anglers over commercial harvest (Forkey 1993). Fishing laws and regulations reflected this shift, as well as the decision to develop hatchery programs for Atlantic salmon in the early 1870s. Three hatcheries, one in Maine and two in New Brunswick, were operated until the 1920s. In Maine, the Grand Lake Stream hatchery still operates, rearing and stocking landlocked Atlantic salmon into the west branch of the St. Croix. Sea-run Atlantic salmon, however, have disappeared from the river, despite stocking both adults and juveniles for several decades. In 2010 the Committee on the Status of Endangered Wildlife in Canada listed St. Croix salmon as endangered as part of the Outer Bay of Fundy Designated Unit (USASAC 2015).

However, because the St. Croix is an international boundary water its salmon population is not considered in the United States' federal Endangered Species Act.

Declines in anadromous fish populations in the St. Croix were primarily caused by dams with no fish passage. Though Europeans started building small mill dams on the St. Croix River in the late 1700s, the first to span the entire river was built at the head of tide in 1836 (Fletcher & Meister 1982). This run of the river dam, located at what is now Milltown (Figure 1.1), had no fishway, and anadromous fish runs in the St. Croix River sharply declined after it was built (Atkins 1889; Decker 1967; Fletcher & Meister 1982). Although a fishway was installed in 1960 (pool and weir, height = 7.3 m), it was thought to be ineffective. Effective passage was provided in 1981 when an improved pool-and-weir fishway with resting pools was constructed (Flagg 2007), revising the over century long decline of the historically large anadromous fish runs in the St. Croix River.

Three other dams were built on the main stem of this river and are currently owned by the United States company Woodland Pulp, LLC. Woodland Dam was originally built in 1905, Grand Falls Dam in 1912, and Vanceboro Dam in 1836 (Flagg 2007). Neither Woodland nor Grand Falls dams were built with a fishway. It wasn't until 1964 that denil fishways were constructed at both Woodland Dam (227 m) and Grand Falls Dam (183 m) (Decker 1967). When the fishway at Woodland Dam was constructed, it was the longest denil in the eastern United States (Decker 1967). Vanceboro Dam was constructed at the outlet of Spednic Lake, and it raised the water level of this natural lake. The fishway at Vanceboro Dam is a vertical slot, which likely has the highest passage rate of the four main-stem dams (Decker 1967).

1.3. Alewives in the St. Croix River

Alewives are native to the east coast of North America and range from South Carolina to Newfoundland (Durbin et al. 1979). It is thought that alewives live in the ocean over the continental shelf until they reach sexual maturity after 3-5 years, when they migrate to freshwater to spawn (Davis & Schultz 2009). Adults prefer to spawn in slow moving water such as lakes or flowages (Bozeman & Van Den Avyle 1989). In the northern part of their range they are iteroparous, meaning that adults return to the ocean after spawning (Bozeman & Van Den Avyle 1989). Juvenile alewives spend 2-7 months in freshwater, and at 23-100 mm total length they migrate to the ocean (Richkus 1975).

Alewife have been of particular interest in fisheries recovery plans along the East Coast of the United States because their remarkably high reproductive potential lends itself to success stories after fishway improvements or dam removals. Alewife were historically numerous throughout New England, but populations have been in decline for decades thanks to water quality issues, the construction of dams, high rates of ocean mortality, changes in offshore food availability, and myriad of other influences (Hall et al. 2012). However, populations in many rivers in Maine have recently demonstrated increasing abundance, including the Penobscot and Kennebec Rivers which saw a rise from tens of thousands to 1.3 million and 3.5 million returning adults in 2017, respectively (DMR 2017).

Alewife historically had a large spawning population in the St. Croix River (Havey 1963). If allowed access to the entire St. Croix watershed, alewife production has been estimated at between 12-24 million individuals (based on the potential of 118-235 adult returns per acre of spawning habitat; Flagg 2007). Archeological evidence suggests

that alewives were present above the head of tide as far back as 4,000 years ago (Deal 1985), and waste from middens indicates they were an important food source to native peoples (Brigham 2005; Spiess & Cranmer 2005). After fishway improvements in the St. Croix in the 1980's the alewife population reached over two million individuals (Figure 1.2).

At the same time the alewife population was increasing the smallmouth bass (*Micropterus dolomieu*) population was perceived to be declining (IJC 2005). This species was introduced into LaCoute Lake near Vanceboro, Maine in 1877 (Warner 2005). Once established, fishing guides and outfitters began to rely on a recreational smallmouth bass industry as a source of income (Watson 1965). When smallmouth bass populations began to decrease in the mid-1980s, the guides who worked in the St. Croix watershed put pressure on the State of Maine to combat this decline and pointed to alewife as a cause (Willis 2009). One of the major stated concerns involving alewife in the St. Croix River was the possibility of resource competition with smallmouth bass. Juveniles of both species feed on plankton, and a study conducted in Oromocto Lake and Mactaquac Arm noted the potential for overlap in food resources (Hanson & Curry 2005).

In response to the concern voiced by Maine guides, in 1987 the St. Croix River Fisheries Steering Committee blocked the Vanceboro Dam fishway that had allowed anadromous fish species access to Spednic Lake (Figure 1.1). The committee also asked the Georgia Pacific Company who owned this dam to modify its water management plan in an effort to minimize the effects of lake drawdown on bass spawning and fry survival (Flagg 2007). In addition, the St. Croix River Fisheries Steering Committee started an

alewife production assessment for the lower part of the St. Croix that involved temporarily closing the fishway at Grand Falls Dam in 1991 (St. Croix International Waterway Commission 1990). A five-year management plan was developed in 1993, and the fishway was to be reopened in 1995 at the end of the assessment (Diadromous Fisheries Steering Committee 1993). However, Maine freshwater fishing guides and recreational outfitters located along the river remained concerned that there was a negative interaction between smallmouth bass and alewives in other areas of the watershed besides Spednic Lake (Flagg, 2007; Dill et al., 2010). As a result, they supported the passing of LD 520 (An Act to Stop the Alewives Restoration Program on the St. Croix River) in 1995 that resulted in the permanent closure of the fishways at both Grand Falls Dam and Woodland Dam.

After these closures the alewife population declined, with a run as low as 900 individuals at Milltown Dam in 2002 (Figure 1.2). In 2001, there was an attempt to repeal the law that prohibited alewife from accessing the river above Woodland Dam (Dill et al. 2010). When this failed, the Department of Fisheries and Oceans in New Brunswick began a trapping and trucking program for alewives caught at Milltown Dam and released upstream of Woodland Dam (Flagg 2007).

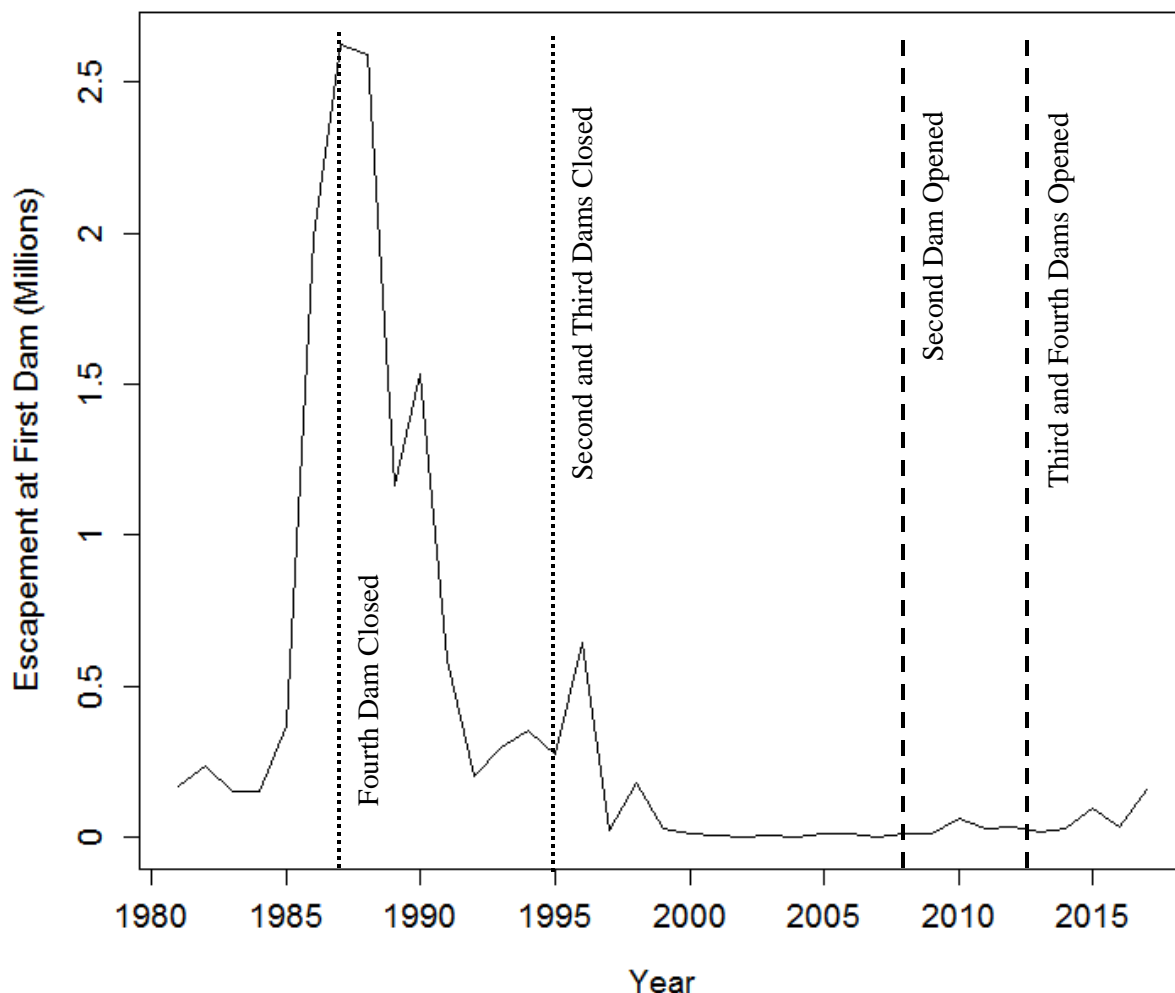


Figure 1.2. Alewife Count at Milltown Dam, NB, at the head of tide from 1981-2017. Count data provided by the Atlantic Salmon Federation. Dotted black lines indicate years where fishways were closed, and dashed lines represent years they were re-opened.

In 2006, Maine Rivers published a collaborative report that included two studies conducted by researchers at the University of Southern Maine and Dalhousie University in Nova Scotia, as well as contributions of scientific data from federal and state agencies on both sides of the border. One of the conclusions from this report was that there was no substantial evidence indicating a negative effect of alewives on the SMB populations

downstream of Spednic Lake and bass fry were losing protective habitat because of lake drawdown (2.7-4.3 m; Willis et al. 2006). These studies concluded that poor bass fry survival over several years had led to a general decrease in the bass population in Spednic Lake, though recent studies have indicated cold temperatures in 1986 likely reduced smallmouth bass egg and fry survival, affecting year-class strength (Dudley & Trial 2014). It was also postulated that lake drawdown may have forced smallmouth bass, alewife, and perch fry to compete more than usual for food and habitat, and that this competition could have been intensified as the alewife population was increasing. Though diet overlap likely occurs when fry are smaller, size differences quickly lead to resource partitioning between these species (Hanson & Curry 2005). These findings helped incite a second and successful attempt in 2008 to change LD 520, resulting in the re-opening of the fishway at Woodland Dam (Dill et al., 2010). In 2013 fishways at both Grand Falls Dam and Vanceboro Dam were re-opened, and alewife once again had access to the St. Croix watershed from the head of tide to Spednic Lake.

1.4. Current and Future Alewife Management in the St. Croix River

The dynamics of reintroduction and passage efficiency are important issues to address. In the 1980's before the fishways were closed, improvements to their construction led to an increase in the alewife population from 100,000 to two million individuals in a relatively short time period. Alewife counts have been conducted from 1981-2017 at Milltown Dam, located at the head of tide, by the St. Croix Waterway Commission and the Atlantic Salmon Federation, among other organizations. Escapement levels were also recorded at Woodland Dam and Grand Falls Dam from 1984-1988 before the fishways were closed when the population was at its highest run

size. These records indicated that on average 40% of the fish that passed Milltown also passed Woodland, and of those 30% continued up past Grand Falls (St. Croix Milltown Trap, 1981-2017). Escapement was not recorded at Vanceboro Dam at any point. The St. Croix watershed has the potential to support an alewife run of 20 million individuals, an order of magnitude higher than what was seen in the 1980's (Dill et al. 2010). Passage issues at any one of the four dams on the main stem could limit the recovery of alewife and prevent this level of re-introduction.

After fishways were re-opened, the alewife population counted passing the first dam in the St. Croix increased from 16,677 spawners in 2013 to 157,750 spawners in 2017 (Figure 1.2). From 2015 to 2016 the population decreased from 93,503 to 33,016 spawners. This was likely due to problems associated with attraction flow at the first dam at Milltown, and has since been partially alleviated by turning off the turbine(s) closest to the fishway during the peak of migration (Lee Sochasky, Atlantic Salmon Federation, personal communication).

While the growth in population abundance since 2013 is promising, there are still challenges that must be addressed for the alewife population to realize its potential. Each upstream passage facility has problems, from infrastructure that is literally crumbling to the usual difficulties associated with attraction flow and variable water velocities through a denil fishway (Bunt et al. 2012). The upstream fishways currently in use at the second and third dam in the system were built in the mid-1960s, and their foundations are beginning to fail. Currently, there are many questions regarding whether or not these dams need to be relicensed under the Federal Energy Regulatory Commission, which could result in requirements involving replacing or repairing existing fishway

infrastructure. This could be an expensive undertaking for Woodland Pulp LLC, as two of the fishways they own would likely need extensive repairs (FB Environmental 2008).

To determine recovery trajectory, both upstream and downstream passage efficiency needs to be determined for each dam on the main stem of the river. Dams commonly delay or prevent downstream passage as well as upstream passage (Roscoe & Hinch 2010). For the population in the St. Croix to recover, the majority of juveniles need to pass several dams. In addition, adult downstream survival is important to maintain the iteroparous life history seen in northern alewife populations (Leggett & Carscadden 1978). Adult cohorts can contribute to multiple spawning runs, and older fish tend to be more fecund, so repeat spawners could contribute to more rapid population recovery (Leggett et al. 2004; Oldani et al. 2007).

In the St. Croix, downstream passage structures exist at the first and second dams, but no specific structure was built at the third dam and fourth dams. There are no screens in place to prevent alewives from entering the turbines at any of the hydroelectric dams, though trash racks may exclude larger adults. At the head of tide downstream passage is through a sluiceway, and at the second dam through a pipe located close to the water intake for the mill. The third dam has a pulp sluice that is dry at low water levels, and there is evidence that fish primarily move downstream through the turbines (Rizzo et al. 1989). At the fourth dam, whose jurisdiction is in the US but whose fishway is in Canada, downstream passage likely occurs either when the water is spilling or potentially through the vertical slot fishway built for upstream passage.

Even though upstream passage, and downstream in some form, exists at all four dams, current estimates of passage efficiency would help produce a reasonable operating

plan for each fishway. Several groups have performed recent tagging studies on alewife, however, more information is needed to accurately estimate escapement. In 2014 and 2015, the Atlantic Salmon Federation acoustically tagged and released alewives directly upstream of Milltown dam. In both years, the majority of tagged fish remained between the first two dams. Only two alewives successfully passed the third dam, but these fish did not move upstream to the fourth dam and did not successfully exit the river (Chafe & Carr 2016). In 2015, receivers were also placed in Passamaquoddy Bay and alewives were released below the first dam, but none were detected moving upstream into the river. In 2016 and 2017, tagging studies were conducted at both the second and third dams using Passive Integrated Transponder (PIT) tags, but there were issues associated with the stationary receivers located at the top and bottom of the fishways (Ajmani et al. 2016). Counting tubes are expected to be placed within each fishway in 2018 to collect escapement data to extrapolate some measure of passage probability.

As of 2017, several local groups were still interested in overturning the legislation that allowed the fishways to be re-opened, and the political turmoil surrounding alewife in the St. Croix continues. The Sipayik Environmental Department (SED) plans to develop an alewife trapping and trucking program to boost productivity in certain lakes and alleviate poor upstream passage success (Edward Bassett, Sipayik Environmental Department, personal communication), but this idea is not widely supported. Actions are being taken to mediate potential problems to population recovery such as delays in fishway improvements. The Next Steps Working Group has been effectively opening up spawning areas downstream of Woodland Flowage by removing small, privately owned dams that were impassable by alewife (International St. Croix River Watershed Board

2017). These types of actions will serve as a contingency plan so that population recovery will likely continue even if the fishway at the second dam collapses. However, it will not allow alewife to approach the production potential of the St. Croix River.

1.5. Alewives as an Ecological Force

The return of a large spawning population to the St. Croix River is expected to provide subsistence fishing to Passamaquoddy tribal members, a potential commercial fishery to local townships, and a myriad of environmental benefits. Juvenile alewife can help protect Atlantic salmon smolts during out-migration by providing an alternative prey source for predators (Saunders et al. 2006). Juvenile and adult alewife provide a substantial forage base for piscivorous fish, as well as birds and mammals (Jaecks & Quinn 2014; Dalton et al. 2009).

One role that alewife can play is that of nutrient delivery, where migrating adults provide a pulse of marine-derived nitrogen (N) and phosphorus (P) to freshwater systems at the beginning of the spring growing period (Durbin et al. 1979). In addition to light availability, nutrient accessibility can be a major determinant of primary production rates, which provides a critical basal resource for the freshwater community (Vanni 2002; Durand et al. 2011). Anadromous species that migrate from the ocean into freshwater to spawn can affect resident communities by supplying pulsed inputs marine-derived nutrients (MDN) that enter the food web through direct consumption of carcasses and gametes or indirectly through excretion (Bauer & Hoyer 2014; Childress et al. 2014). This can be particularly important in temperate regions where marine habitats are more productive than freshwater habitats and anadromous fish exhibit rapid growth in the ocean (Gross et al. 1988).

Previous studies have explored the role of anadromous fish in freshwater productivity. Spawning Pacific salmon have been shown to supply MDN, causing an increase in primary production (Richey et al. 1975; Cederholm et al. 1999), biofilm growth (Wipfli et al. 1998), macroinvertebrate density (Piorkowski 1995; Wipfli et al. 1998; Minakawa et al. 2002) and fish growth (Bilby et al. 1996). The net MDN balance of established alewife populations has been modelled, suggesting substantial import into freshwater systems (Durbin et al. 1979; Walters et al. 2009; West et al. 2010). Alewives providenutrient subsidies in the spring coincident with increased freshwater aquatic community metabolism (Samways & Cunjak 2015). Alewives have a high reproductive potential, and a small number of returning adults can produce a large number of offspring (Gibson & Myers 2003). Freshwater-reared juvenile fish can potentially remove nutrients as they migrate back to the ocean (Moore & Schindler 2004). This fluctuation of nutrients between marine and freshwater systems is part of the natural functioning of intact coastal ecosystems that in the past century has been reduced by structures that block fish passage (Twining et al. 2017). As the alewife population in the St. Croix River recovers and the spawning run increases, MDN input could potentially boost the productivity of freshwater lakes and streams.

1.6. Linking Alewife Recovery to Nutrient Delivery

Two broad objectives were used to link alewife recovery to nutrient dynamics in the St. Croix River. First, we explored MDN dynamics within freshwater communities. This involved characterizing community structure in the St. Croix River, and exploring MDN incorporation as would be expected after alewife population recovery using a reference watershed with an established spawning run. Stable isotope analysis was used

to explore community structure among sites through time in the St. Croix, as well as to make comparisons in a reference watershed between sites where alewife were present and absent. We also characterized baseline nutrient limitation before alewife population recovery in the St. Croix River using nutrient diffusing substrates (NDS). This same approach was used to explore the alleviation of nutrient limitation related to alewife presence in a reference watershed.

1.6.1. Food Web Stable Isotope Analyses

Baseline information about the freshwater food web in the St. Croix River before population recovery was collected that can be used in future assessments. The reintroduction of alewife into this river provides a novel opportunity to sample the population and provide data that can be compared in a before/after sampling regiment. The food web was characterized using stable isotope analysis, which traces nutrients as they move up the food web from autotrophs to predators (Garman & Macko 1998; Kline et al. 1990; Cederholm et al. 1999; Chaloner et al. 2002; Post 2002; Schindler et al. 2003; Fry 2006; Layman et al. 2007; Hocking & Reimchen 2009). Isotopes are forms of an element that are heavier or lighter than the more typical form. Heavy isotopes are more likely to be retained in the tissues of an organism during fractionation, a process that separates light and heavy isotopes because the former reacts faster than the latter (Fry 2006). These heavier isotopes are therefore accumulated as nutrients move up the food web through consumption of prey tissue, and so predators are generally enriched compared to the prey they ingest, which can be used to infer trophic level (Jardine et al. 2003; Fry 2006).

The ratio of the heavier to the lighter form of an element can be measured and compared among individuals, sites, and habitats. Stable isotope results are most often represented as δ values, calculated as follows:

$$\delta = \left(\frac{R_{Sample}}{R_{Standard}} - 1 \right) * 1000,$$

where R_{Sample} and $R_{Standard}$ represent the ratio of the fractional abundance of heavy isotopes to the fractional abundance of light isotopes. Samples are compared to standards in order to make associations between studies and sites (Jardine et al. 2003).

Many food web studies focus on ^{13}C and ^{15}N because these provide information on the isotopic niche of the community being studied, based on the Hutchinsonian definition of an n-dimensional hypervolume whose axes are defined using scenopoetic (environmental) and bionomic (trophic) components (Hutchinson 1978). Newsome et al. (2007) suggested quantifying an isotopic niche by determining an area whose axes are defined using isotopic values, as $\delta^{15}\text{N}$ is used to explore trophic and $\delta^{13}\text{C}$ environmental components within a food web (Deniro & Epstein 1978; Fry 2006; Atkinson et al. 2014; France 2012). The isotopic niche is often used as a proxy for trophic niche, and while they are correlated they may not be directly comparable (Layman et al. 2007; Jackson et al. 2011). Typically, $\delta^{13}\text{C}$ is used to address questions about basal C sources for a community as its isotope ratio remains relatively constant moving up through a food chain (Deniro & Epstein 1978; Hicks 1997; Post 2002). Depending on the primary carbon source for the food web being studied, the value of $\delta^{13}\text{C}$ can vary both along a latitudinal gradient and on a smaller scale among sites within the same area (Finlay et al. 2002).

1.6.2. Measuring Marine-Derived Nutrient Input Using Stable Isotope

Analysis

Stable isotope analysis was used to investigate how marine-derived nutrients are delivered by alewife and incorporated into a freshwater community. Nutrient input was compared between a site where alewife were present and one where they were absent. Samples were collected seasonally over several years. Stable isotopes can be used to infer nutrient delivery by anadromous species because individuals from a marine habitat are generally enriched in both ^{15}N and ^{13}C compared to those from a freshwater habitat (Fry 2006). As marine-derived nutrients become incorporated into a food web, the isotopic values of freshwater species should shift to reflect that enrichment (MacAvoy et al. 2001; Kohler et al. 2012). The presence of marine-derived nutrients should become pronounced as they work their way up the food web and become more concentrated (Richardson et al. 2017). This process imposes a time lag between when nutrients are available in the system and when they are detected within the tissues of organisms at higher trophic levels (Fry 2006; Sato et al. 2016). Eventually the marine-derived nutrients added to a system will exit the food web in an inorganic form through excretion and egestion and their effect will no longer be seen within the food web, though it is less clear how long this takes (Fry, 2006).

While isotopes are used extensively in studies of anadromous fish, there are limitations to interpreting the data. There are also differences in isotope fractionation rates among species within a community as well as variability within a species given a range of environmental conditions (Fry 2006). Also, tissues (i.e. muscle, liver) may differ in the amount of heavy isotope they store because of various rates of turnover or

tissue-specific fractionation, and so the sampling period needs to match this rate (Jardine et al. 2005). Metabolic processes could also affect turnover rates, potentially leading to variability between slow-growing species and ephemeral species.

Interpretation can also be affected by how the data is organized. Sampled species are often divided into functional feeding groups in order to explore food web components. However, omnivory is also a problem when dividing a community by functional feeding group for statistical analyses (McIntyre & Flecker 2006; Layman et al. 2007). While this type of division is generally informative, it comes with the assumption that all individuals of a species feed similarly and could result in some food sources not being accounted for (Lauridsen et al. 2014). To be certain of a species' functional feeding group, a detailed diet study needs to be performed and this has not been done for every aquatic invertebrate species (Layman et al. 2012). Despite these limitations, stable isotope analysis is frequently used as a tool to infer MDN input in freshwater systems (Bilby et al. 1996; Chaloner et al. 2002; Walters et al. 2009; Weaver et al. 2016a).

1.6.3. Nutrient Limitation

Freshwater systems have site-specific nutrient availability, which can determine the rate of primary productivity (Welch and Cooke 1995). In the northeastern United States, streams are generally oligotrophic and many have a measured N:P around 70:1, indicating P limitation (Allan 1995), though studies have also found many instances of co-limitation. Oligotrophic systems may demonstrate greater boosts in freshwater productivity due to MDN input than eutrophic systems. Baseline nutrient limitation was characterized at each site to put into context the magnitude of potential alewife subsidies. Nutrient diffusing substrates (NDS) were used to determine site-specific limitation by

comparing algal growth among nutrient treatments. Higher chlorophyll *a* biomass associated with a particular treatment inferred the alleviation of baseline limitation. The presence of a large alewife spawning run can also alleviate baseline nutrient limitation within a site. To explore this, results of NDS were compared between sites with and without alewife present throughout the course of the spawning run.

1.6.4. Alewife Population and Nutrient Modeling

For the second broad objective, we modeled the potential MDN dynamics within the St. Croix River based on a variety of scenarios related to habitat connectivity, freshwater productivity, and the presence and location of an in-river fishery. Potential MDN input was estimated for alewife in the St. Croix River by developing a population model and linking it to net nitrogen (N) and phosphorus (P) balance as determined by adult import and juvenile export. This deterministic model was developed to explore how changes in Alewife population levels could theoretically affect nitrogen and phosphorus dynamics related to adult import and juvenile, or young of the year (YOY), export. We used this model to explore how theoretical nutrient dynamics change through the process of population growth and eventual stabilization, then applied it specifically to the St. Croix River. This involved exploring the influence of dams on the main stem of the river and the presence and location of fisheries mortality as constraints to population growth

If connectivity issues in the St. Croix River are addressed and alewives have access to large areas of spawning habitat, this highly productive species has the potential to experience extensive population growth. The objectives of this study allow us to characterize baseline freshwater community structure in the St. Croix River before the

recovery of the alewife population, explore potential shifts related to MDN incorporation as may occur with population growth, and estimate potential net nutrient balance within the watershed related to habitat connectivity. Assessing anadromous alewife subsidies allows us to characterize the ecological role this species may play in Maine ecosystems and throughout their geographic range.

CHAPTER 2

MEASURING MARINE-DERIVED NUTRIENT INPUT USING STABLE ISOTOPE ANALYSIS

2.1. Chapter Abstract

Anadromous species can boost freshwater productivity through nutrient subsidies, especially in oligotrophic habitats. Along the Maine coast of the northeast United States, several anadromous alewife populations are recovering after freshwater connectivity was restored. Alewives have higher rates of iteroparity in this part of their range than further south, and the extent that spawning populations contribute substantial marine-derived nutrient subsidies to freshwater communities is unknown. Stable isotope analysis was used to detect marine-derived nutrient input by comparing results from a site where alewife were present in moderate to high abundance and one where they were effectively absent. Isotope shifts reflecting marine nutrients within particular invertebrate functional feeding groups were detected, however these shifts did not occur within the freshwater community as a whole. In addition, baseline information was collected for a watershed where alewife population growth is expected, allowing long term monitoring of marine-derived nutrient input over the course of recovery. Spatial and temporal trends in isotopic signatures were characterized for a range of organisms. Fish and invertebrate communities sampled at lake sites had a larger standard ellipse area than those sampled at in-river sites. There was a relatively narrow range in $\delta^{13}\text{C}$ values among sites.

2.2. Introduction

Anadromous species migrate from the ocean into rivers to spawn, providing nutrient subsidies that are important for productivity in temperate regions where marine habitats are more productive than freshwater habitats (Gross et al. 1988; Bilby et al. 1996). These marine-derived nutrients (MDN) enter a freshwater food web both directly through the consumption of fish carcasses or gametes and indirectly through excretion (Childress et al. 2014; Weaver et al. 2016a). Freshwater-reared juvenile fish remove nutrients as they migrate back to the ocean (Moore & Schindler 2004). This movement of nutrients between marine and freshwater systems is part of the natural functioning of intact coastal ecosystems that has been reduced by manmade structures that block fish passage (Twining et al. 2017).

A wide range of diadromous fish can bring marine nutrients into freshwater. The magnitude of nutrient delivery is dependent on the size of the spawning run, the number of fish that die, and the flushing rate of that site (Hocking & Reimchen 2009; Naiman et al. 2002; Schindler et al. 2003). Pacific salmon (*Oncorhynchus* spp.) are a well-documented vector of marine-derived nutrients (for review, see Naiman et al. 2002; Cederholm et al. 1999; Schindler et al. 2003). Their semelparous life history, use of small streams as spawning habitat, and large body size results in a substantial contribution of nutrients to the freshwater environment (Schindler et al. 2003). Other semelparous species such as sea lamprey (*Petromyzon marinus*) deliver nutrients into freshwater systems that are rapidly incorporated into stream macroinvertebrate and algal communities (Weaver et al. 2016a).

The delivery mechanisms of nutrients differ significantly with life history strategy. While carcasses of semelparous species are a major component of nutrient delivery, marine-derived nutrient influences have also been ascribed to iteroparous fish species (Twining et al. 2017). Although Atlantic salmon (*Salmo salar*) abundance on the northeast coast of the United States has declined, Alosines remain the dominant anadromous species by number and biomass, though populations are low compared to historic numbers (Limburg & Waldman 2009). Life history strategies for Alosines exhibit a north to south gradient in magnitude of repeat spawning (Davis & Schultz 2009). In the northern part of their range, Alosines have a dominantly iteroparous life history, suggesting that carcasses may not be the major delivery mechanism as for populations in the south that are semelparous (Leggett & Carscadden 1978; Bozeman & Van Den Avyle 1989). Despite being repeat spawners, northern populations can still experience high mortality rates during their migration, with estimates of 39-57% for Alewife (*Alosa pseudoharengus*; Yako et al. 2000; Taylor & Kissil 1974). Excretion is likely an important pathway for Alosines such as alewife and blueback herring (*A. aestivalis*) as smaller fish have a higher mass-specific nutrient excretion rate, though ecosystem retention will depend on site-specific flow rates (Twining et al. 2017). Also, direct consumption of adult Alosines by predators is likely a dominant pathway for nutrient uptake (Garman & Macko 1998).

Seasonal dynamics will determine the relative influence a nutrient input has on a freshwater community. Resource pulses are defined as having a short duration, extreme magnitude, and relatively infrequent timing (Yang et al. 2008). A pulse in nutrient availability may not greatly affect the lifetime growth of a longer-lived species or a

migratory species, but can provide the resources necessary for shorter-lived individuals to grow within a season (Yang et al. 2008). Alosines represent a relatively frequent resource input that is available at the beginning of the growing period in temperate regions (Durbin et al. 1979). There are multiple pathways for nutrient import into freshwater systems. Excretion is immediately bioavailable, while carcass tissue decomposes over a period of weeks (Weaver et al. 2016a). Thus the temporal delivery, and the mode, of marine-derived nutrient supplementation can determine its role (Post & Walters 2009; S. M. Collins et al. 2016; García et al. 2017). In freshwater systems, environmental factors such as temperature, hydrology, and baseline nutrient levels will also affect nutrient use and availability within a particular site (Flecker et al. 2010; Wheeler et al. 2015).

Marine-derived nutrients can affect multiple trophic levels in systems with a large anadromous run (Chaloner et al. 2002; Kline et al. 1990; Cederholm et al. 1999; Schindler et al. 2003). Nutrient delivery from Pacific salmon, increase primary production (Richey et al. 1975; Cederholm et al. 1999), biofilm growth (Wipfli et al. 1998), macroinvertebrate density (Piorkowski 1995; Minakawa et al. 2002; Wipfli et al. 1998) and fish growth (Bilby et al. 1996). In the Columbia River watershed, Pacific salmon deliver roughly 3 million kg of nitrogen (N) and 0.36 million kg of phosphorus (P) a year based on the nutrient content of carcasses and the average biomass of the run (Moore & Schindler 2004). Alaskan lakes with sockeye salmon (*O. nerka*) have 30% more P compared to lakes without a spawning run (Kyle 1996). Lakes with subsidies from a salmon run have standing stock of phytoplankton twice that of lakes with no run (Kyle 1996; Naiman et al. 2002).

2.2.1. Alewife as Nutrient Vectors

Alewives, when present, tend to be the most numerically abundant of the Alosines. Alewives have a high reproductive potential, and a small number of adults can produce a large number of offspring (Gibson & Myers 2003). Nutrient modelling suggests that at low spawner numbers alewife will be net exporters (Walters et al. 2009; Barber et al. in press). However, as the population grows net nutrient dynamics can transition to considerable import of N and P into freshwater systems (Durbin et al. 1979; Walters et al. 2009; West et al. 2010).

Delivery is not the same as retention, however, and whether these nutrients are incorporated into the freshwater food web in the spring is unknown. This knowledge gap was addressed by considering three aspects: i) patterns of nutrient uptake within freshwater communities; ii) the availability of MDN; and iii) uptake of MDN within a site. Within a watershed the most likely location of alewife MDN input would be the lakes and ponds the species use as spawning habitat. In these areas, carcass, gamete, and excretion inputs would be available for freshwater production. Areas where spawners are delayed in their passage (e.g. below dams), are also likely places where excretion and carcass inputs could become available to freshwater food webs.

One challenge in exploring nutrient dynamics is the inherent spatial and temporal variability associated with their availability and detection. Hydrology is a major determinant of nutrient retention, and therefore availability (Wheeler et al. 2015; Sagouis et al. 2015; Vander Zanden & Fetzer 2007). The first objective of this study was to characterize this variability within the freshwater community. To do this, baseline information was collected for the freshwater community at both lentic and lotic sites.

These included spawning habitat, as well as areas where delays were likely to occur. Sites were also sampled throughout time to classify seasonal trends in freshwater communities.

After characterizing baseline community structure, the second objective was to detect the influence of MDN within a freshwater community where alewives were present in a sufficient abundance to result in a nutrient input. To address this, we sampled sites with and without an established, large spawning run. In addition, N and P have to be taken up by freshwater organisms at high enough rates to be detectable in body tissues. Longer-lived freshwater consumers may exhibit different temporal trends associated with MDN input than their shorter-lived counterparts (Yang et al. 2008). Moreover, each potential source of MDN input could be incorporated by particular feeding guilds but not by others due to either top-down or bottom-up incorporation into the food web (Minakawa et al. 2002). Sites were therefore characterized both by focusing on the community as a whole as well as determining the presence of MDN input within different functional feeding groups. Sites were sampled at short-term (seasonal) and long-term (annual) scales within the time period associated with the spring spawning run of Alewife to characterize temporal trends in nutrient incorporation.

2.3. Methods

2.3.1. Sample Sites

We chose to characterize variability in baseline community structure in the St. Croix River (Figure 2.1). Alewives were historically abundant in this river, but logging practices, ecological misconceptions, and political polarity in the past century and a half nearly led to their extirpation (Willis 2009). Since the 1980's alewife passage in the

watershed has been part of a fisheries management conflict in Maine and New Brunswick (Dill et al. 2008). In the 1960s, improved fishways were constructed and by the early 1980s the alewife spawning run increased to 2.5 million individuals (St. Croix Milltown Trap 1981-2016). At the same time the alewife population was recovering, year-class failures were affecting an introduced smallmouth bass population in the river, leading to the conclusion that these two events were cause and effect (Willis et al. 2006; Flagg 2007). As no information on alewife-smallmouth bass interactions specific to the St. Croix was available to refute this perceived interaction, the fishway at Vanceboro was closed in 1987. This was followed by the Maine Legislative closing fishways at Grand Falls and Woodland dams in 1995 (Dill et al. 2010; Figure 2.1). The dam at the head of tide, with the fishway in New Brunswick, remained open. Following these closure the alewife spawning run in the St. Croix declined dramatically. After a series of events, mediated in part by the International Joint Commission St. Croix Watershed Board, the Maine law blocking fish passage was repealed allowing alewife passage at Woodland in 2008 and the other two dams in 2013. As the population in the St. Croix recovers, the baseline information collected can be compared to future sampling to determine the extent MDN from alewife are incorporated into freshwater communities. When samples were collected (2013-2015) the St. Croix River had a small alewife population, and MDN values were not expected to be detectable (Figure 1.2 in Chapter 1).

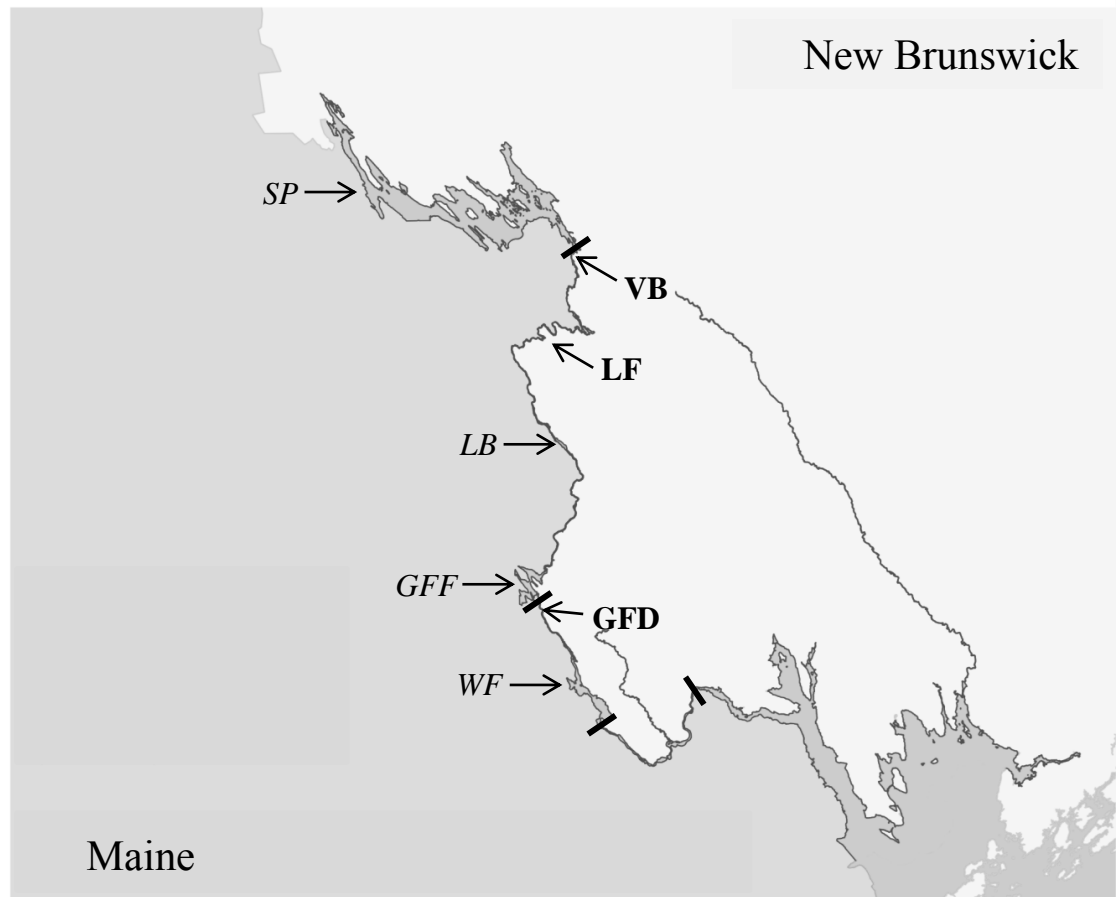


Figure 2.1. Map of the St. Croix River. Study sites are indicated with arrows. Lotic sites are bolded and labeled to the right, lentic sites are italicized and labeled to the left. Black bars indicate main-stem dams.

Lentic and lotic sites in the St. Croix River, which forms part of the border between Maine and New Brunswick (Figure 2.1), were sampled to characterize variability in baseline community structure. Within the St. Croix River, samples were collected from seven sites spanning from the head of tide to Spednic Lake (*SP*; 6968 hectares; max depth 16 m), covering roughly 80km (Figure 2.1). These sites were specifically chosen

as either likely spawning habitat or places where alewife could be delayed in their migration. Samples came from four lentic sites at lakes or flowages and three lotic sites on the main stem of the river. On the main stem, sites were sampled immediately downstream of Grand Falls (GFD) and Vanceboro dams (VB), where water levels fluctuated within a season (Figure 2.1). Little Falls (LF) was located immediately below a small natural falls that was likely passable at all flows by alewife, but may have delayed upstream movement. Loon Bay (LB) was a section of the river that was wide and flat with low flow where alewife could potentially spawn. Grand Falls Flowage (GFF; 2708 hectares; max depth 9 m) and Woodland Flowage (WF; 486 hectares; max depth 10 m) were both created when dams were built. Within all three lake or flowage sites, the same area was sampled each year, near the outlet of the respective waterbody.

The East Machias watershed, which is located nearby to the southwest of the St. Croix and has a large, established alewife run, was selected to address the second objective of detecting MDN within the freshwater community. This river, which is 3,600 hectares and has no dams on the main stem, has an estimated run between 2-4.5 million river herring (ME ASMFC River Herring Sustainable Fishing Plan Update 2015). Two sites were chosen, one at Chase Mill Stream (44°45'22"N, 67°21'37"W) which is the outlet of Gardiner Lake, and a tributary to the main stem of the river. The second site at the East Machias is Clifford Stream (44°51'58"N, 67°20'35"W), which is one of the inlets of Gardiner Lake.

Precise alewife counts at the Chase Mill Stream site on the East Machias are not available for the years it was sampled (2014-2015), but rough estimates ranged from 350,000 to 400,000 spawners, of which approximately 70-80% were harvested

(MEDMR 2016). Harvest occurred directly upstream of the sampling site, and on days when harvest is allowed, fish are delayed in a trap pen until they are removed from the river. Excretion rates are likely high at this site, but carcass input is likely below natural levels because of the fishery. The Clifford Stream site is within the same watershed and was selected because there is no spawning habitat available upstream and thus it had very few to no alewife present.

2.3.2. Stable Isotope Sampling Regiment

To estimate baseline community structure in the St. Croix watershed, each site was sampled multiple time periods for three consecutive years (2013-2015). These time periods corresponded with the beginning, peak, and after the end of the alewife run in Maine so that future comparisons can be made once population abundance increases. Sampling also needed to account for the time lag associated with the shift of consumer tissue to reflect a new diet source (Hertz et al. 2016). Fish have a longer time lag than invertebrates, with the former on a timescale of months and latter of weeks (Abrantes et al. 2014). In 2013, sites were sampled in late May at the peak of migration, in July several weeks after the majority of alewife had completed their run, and in September well after adults had exited the watershed. The sampling in September was intended to collect juvenile alewife, though this was not successful. Dates were shifted slightly in 2014-2015 to include early May, mid-June, and late July to ensure that sampling captured the expected time lag for the entire freshwater community.

Sampling was performed to maximize the number of species collected, but not to estimate species abundance within a site. All samples were placed on dry ice after collection and kept frozen until analysis as other techniques for preserving them would

likely affect the results of the stable isotope analysis (Jardine et al. 2003). Fish were sampled using boat electrofishing (all years), and gillnets and seine nets in 2013. Electrofishing occurred during the day, with 2-3 sites sampled in a day. Sites were fished for 45-60 minutes, and no effort was made to measure catch per unit effort (CPUE). Mass and total length were measured for each fish sampled. Large fish were identified to species in the field, and roughly 1x1 cm of dorsal muscle tissue was taken from each individual. Smaller shiners and juveniles were brought into the lab for identification and, when possible, muscle tissue was dissected for stable isotope analysis. Sample processing required roughly 5 mg of dry tissue, and so a 0.5 x 0.5 cm of dorsal muscle was generally sufficient for these smaller fish. However, several juveniles were too small to extract a muscle plug and so these fish were analyzed whole. Scales were removed from both muscle samples and whole fish before drying in the lab. In addition to sampling freshwater fish, adult alewives were collected at the head of tide from the counting facility at Milltown Dam. Adults are lethally sampled every year through a collaboration of the Atlantic Salmon Federation (ASF), the Department of Fisheries and Oceans Canada (DFO), and the US Fish and Wildlife Service (USFWS) to provide a long-term record of morphometric and life history traits for the population. Dorsal muscle tissue was taken from 30 adult alewives and frozen for processing.

Macroinvertebrates were primarily collected by kick sampling with a D-net in wadeable areas along the shore, and secondarily by removing individuals directly from rocky substrate. Mussels and snails were collected by hand. This sampling encompassed all habitat types present at each site. There was no attempt to quantify abundance during this study, and so collection continued until a sufficient biomass from each species was

obtained for stable isotope analysis. Samples were placed on dry ice after collection, and in the lab macroinvertebrates were identified to family when possible. Most individuals were analyzed separately, but very small individuals (i.e. early instars of nymphs) had to be pooled to reach target biomass of at least 5 mg of dry tissue. When possible, multiple samples of each family were analyzed at each site, either as individuals or as pooled samples.

Zooplankton was sampled during the day at lake sites using a Wisconsin net towed along approximately 400 m transect. A net with 156 μm mesh size was used in 2013, but this did not collect all species and so a 50 μm mesh was used in 2014-2015. As all sampled sites were fairly shallow ($< 5\text{m}$), the net was towed along the surface. Zooplankton were subsampled in the laboratory. Samples were gently agitated to produce a homogenous mixture and subsamples were collected with a Hensen-Stempel Pipette (2 mL syringe). Sub-sampling was repeated until there was a minimum of 200 individuals counted for each time and site combination, or until 10 subsamples were completed. Subsampling was conducted without replacement of individuals. Each subsample was analyzed under a dissecting microscope and all individuals were divided into dominant taxonomic groupings, including *Cladocera*, *Laevicaudata*, *Copepoda*, *Ostracoda*, *Chironomidae* and “other”. After identification, zooplankton samples were collected on a 4.7 cm diameter glass fiber filter (MilliporeSigma, Burlington, Massachusetts, USA).

To explore MDN influence and temporal shifts related to nutrient input, the East Machias watershed was sampled from 2014-2015. Samples were collected mid-May (before the run), late May (the peak of the run), mid-June (as the run slows), and July

(after the run). Fish were collected using backpack electrofishing in collaboration with the Maine Department of Marine Resources using power settings recommended to avoid damage to endangered Atlantic salmon that could potentially be encountered. Sites were sampled for 45-60 minutes, with no effort to calculate CPUE. Invertebrates were collected using the same methods as the St. Croix River. Organisms were identified and grouped in the lab for stable isotope analysis as described above.

2.3.3. Preparation and Processing for Stable Isotope Analysis

For stable isotope analysis, all samples were dried at 60°C for 24-28 hours, and then fish and macroinvertebrates were ground to a fine powder using a mortar and pestle sterilized with ethanol to avoid contamination. There was no attempt to remove gut contents from macroinvertebrate samples. Lipids were not chemically extracted prior to processing, but after running samples, normalization was applied using recorded C:N values as described in Post et al. (2007). All sampled $\delta^{13}\text{C}$ values were normalized because the majority had measured C:N values that indicated relatively high lipid levels (>3.5 ; McConnaughey & McRoy 1979; Post et al. 2007; Logan et al. 2008). Stable isotope samples were analyzed at the Stable Isotopes in Nature Laboratory (SINLAB, Fredericton, New Brunswick, Canada). Analysis was performed with Costech 4010, NC2500, and NA1500 elemental analyzers that were interfaced with Delta XP/Conflo III, Delta Plus/Conflo II, and Delta V/Conflo IV continuous flow isotope-ratio mass spectrometers, respectively (Thermo-Finnigan, Bremen, Germany). Isotope values were recorded in δ notation relative to the international standards, including Vienna PeeDee Belemnite for C and atmospheric air for N. Secondary standards for animal tissues were lab-specific and included Nicotinamide ($\delta^{13}\text{C} = -34.52 \text{ ‰} \pm 0.13$; $\delta^{15}\text{N} = -1.71 \text{ ‰} \pm$

0.10), Bovine Liver Standard (BLS; $\delta^{13}\text{C} = -18.8 \text{ ‰} \pm 0.14$; $\delta^{15}\text{N} = 7.18 \text{ ‰} \pm 0.17$), and Smallmouth Bass (SMB; $\delta^{13}\text{C} = -23.41 \text{ ‰} \pm 0.18$; $\delta^{15}\text{N} = 12.31 \text{ ‰} \pm 0.11$).

2.3.4. Data Organization

The stable isotope data was organized before performing statistical analyses to address the objectives. This included removing outliers, making corrections, and grouping the data. Extreme outliers were visually identified using boxplots, but were only removed from the dataset if a compelling reason existed to do so (e.g. several outlier samples were identified as being dropped during processing or equipment malfunctions may have occurred). Lipid normalization corrections were applied as described above. Macroinvertebrate and fish species were then separately grouped according to their feeding type. For fish this included predators, omnivores, and detritivores (Appendix A), while macroinvertebrates included these groups as well as collector-filterers, collector-gatherers, herbivores, scraper-grazers, and shredders (Appendix B). Species were assigned to functional feeding groups (FFG) using FishBase (package `rfishbase`; Froese & Pauly 2017) and (Merritt et al. 2008).

Diet differences can exist based on ontogeny (Abrantes et al. 2014), and this could result in a correlation between size and $\delta^{15}\text{N}$ value, especially for predatory species. To address this possibility, fish species were each tested for correlation between $\delta^{15}\text{N}$ and both total length (mm) and weight (g). A statistically significant correlation ($p \leq 0.05$) was found for 4 of the 18 fish species (Appendix C). Length and $\delta^{15}\text{N}$ were correlated for *E. niger* (length: $R^2 = 0.53$, slope = -0.0254 , $p = 0.0006$; weight: $R^2 = 0.7$, slope = 0.00164 , $p = 0.0032$), *L. gibbosus* (length: $R^2 = 0.043$, slope = 0.0613 , $p = 0.0292$; weight: $R^2 = 0.1$, slope = 0.00789 , $p = 0.00676$), and *M. dolomieu* ($R^2 = 0.19$, slope =

0.0441, $p = 7.7\text{e-}06$; weight: $R^2 = 0.087$, slope = 0.00102, $p = 0.012$), and weight and $\delta^{15}\text{N}$ were correlated for these three species as well as *M. Americana* ($R^2 = 0.48$, slope = 0.0226, $p = 0.0156$). Diets were checked using FishBase to determine if differences existed based on ontogeny. *E. niger* was listed as predatory regardless of age and *L. gibbosus* was recorded as feeding on insects and fish eggs as both adults and juveniles (Froese & Pauly 2017). *M. americana* are recorded as feeding primarily on zooplankton as recruits, but also adding fish eggs/larvae and aquatic insects as juveniles and adults (FishBase). As the smallest white perch collected was 12 cm, it was safe to assume they had all transitioned to the juvenile/adult diet. With expected similar diets, juveniles and adults of these three species were not divided into size classes. *M. dolomieu* young were reported as feeding on plankton and aquatic insects, while adults were listed exclusively as predators. Juvenile size is between roughly 3 – 11 cm (Easton & Orth 1992), and the smallest smallmouth bass caught was 11.6 cm, so this species was not divided into size classes either.

We chose not to use a baseline correction. While corrections are often applied in stable isotope data, there is debate on which trophic group to use as a reference. Further, using a correction can reduce the range of isotope values, especially $\delta^{13}\text{C}$, measured at a site and affect the ability to make comparisons among sites and time periods. Corrections using primary producers can result in temporal variability (Post 2002; Matthews & Mazumder 2003), influences associated with water velocity and downstream flow (Hicks 1997; Pettit et al. 2017), and confounding $\delta^{13}\text{C}$ enrichment due to photosynthesis (Hicks 1997). In addition, biofilm consists of a matrix of primary producers, fungi, and bacteria, making it hard to sample only one component. While community centroids and primary

consumers have been successfully used as baseline values to correct for spatial and temporal variation in stable isotope analyses (Schmidt et al. 2011; Sagouis et al. 2015), we did not apply a correction factor for our analyses. When exploring diet sources for a particular species, information about potential basal resources and fractionation between trophic levels is necessary for correct inferences (Post 2002; Schmidt et al. 2011; Layman et al. 2012; Blanke et al. 2017). Spatial variability in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can occur because the isotopic ratios can vary among sites, leading to differences in availability (Layman et al. 2012).

2.3.5. Statistical Analyses

2.3.5.1. Baseline Community Structure

To explore baseline community structure in the St. Croix River, comparisons were made between individual sites and between lake sites and main-stem sites. Site differences were explored using biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values averaged by species, as well as standard ellipses that are analogous to standard deviations and were calculated to contain 95% of the data (Batschelet 1981; Jackson et al. 2011). Ellipses were calculated as described in Jackson et al. (2011) using the R package SIBER. This package calculates the bivariate means and covariance matrix for each sample grouping (i.e. site by sample type), and the eigenvalues and eigenvectors of the matrix are used to calculate the semi-major and semi-minor axes, and as well as the angle of the axes (Jackson et al. 2011). Within a site, ellipses were calculated for each sample type (fish muscle, macroinvertebrate, and plankton) because longer-lived species such as fish can exhibit less variability in their isotopic values than shorter-lived species such as aquatic insects (McIntyre & Flecker 2006). A macroinvertebrate primary consumer can display greater

variability and a lower $\delta^{15}\text{N}$ value than a fish primary consumer, despite being considered in the same trophic position (Abrantes et al. 2014).

In addition to site comparisons of the spread of the data, three metrics were calculated to explore baseline isotope trends comparing lake sites where spawning is likely to occur and main-stem sites where alewife may be delayed. The range in $\delta^{13}\text{C}$ (CR) was calculated to give an estimate of the breadth of the resource base where a higher value means there are multiple potential origins for the C source (i.e. terrestrial, freshwater, marine input) at the base of the food web (Layman et al. 2007). In addition, the range in $\delta^{15}\text{N}$ (NR) was calculated to estimate trophic diversity, where a higher value indicates a community that is more functionally heterogeneous (Layman et al. 2007). Last, the bi-variate area of the isotopic space was measured by calculating the standard ellipse area (SEA) as described in Jackson et al. (2011), which uses the center of a community's bivariate isotopic space, rather than the outside values (Sagouis et al. 2015).

To calculate these metrics, a Bayesian approach was used as described in Jackson et al. (2011, 2012) using the package SIBER. This approach was used because it allows the joint distribution of covariance matrices to be calculated when comparing bivariate samples, and it accounts for potential biases based on small sample size (Ricklefs & Nealen 1998; Jackson et al. 2011). A vague normal prior was assigned to the means and an Inverse-Wishart prior to the covariance matrix. Markov chain Monte Carlo (MCMC) simulation using the package rjags (Plummer 2016) was used to calculate posterior estimates with a multivariate normal likelihood (Jackson et al. 2011). The model was run for 20,000 iterations and thinned by 10 samples, with the first 1,000 iterations discarded.

Metrics were calculated for each grouping using the remaining iterations. A correction factor (SEA_c) was applied to the ellipse area calculated for each community using the iterative Bayesian approach (SEA_b) so that different sites and time periods could be compared regardless of differences in sample size (Jackson et al. 2011).

2.3.5.2. MDN Input

Community differences were explored between the site with alewife present and with alewife absent in the East Machias using several statistical approaches. The East Machias was sampled during four time periods representing mid-May (before the run), late May (the peak of the run), mid-June (as the run slows), and July (after the run). To explore community structure, SEA was calculated for each year, site, and season combination. In addition, NR and CR were calculated for each site and year combination. These metrics were calculated using the Bayesian approach described above.

Temporal comparisons to explore seasonal trends in stable isotope values were also analyzed using circular statistics. This method has been used in stable isotope analyses to quantify directional changes because it does not use traditional estimates of mean and deviation, which can become complicated when multiple community variables, time periods, and sites are being considered (Schmidt et al. 2007; Bartels et al. 2012; Jackson et al. 2012). As very few fish were sampled in the East Machias, only invertebrate communities were used for these analyses. Invertebrates were grouped by functional feeding groups and compared by time period. For each FFG, the pairwise difference in the mean relative $\delta^{13}C$ and $\delta^{15}N$ between each possible time period combination within each year was calculated (Schmidt et al. 2007; Bartels et al. 2012).

Bivariate data was then converted to a vector as needed for circular analysis and used to calculate both the direction and magnitude of change for each functional feeding group as well as a mean for the community for each site and season using the package circular in R (Schmidt et al. 2007; Bartels et al. 2012; Jackson et al. 2011; Agostinelli and Lund 2017).

Statistical analyses were performed using a Rayleigh's test for circular uniformity. This test was performed to determine whether the distribution of the mean angles of change was uniform and nonrandom at each site between seasons 1-2 and seasons 2-3 (Schmidt et al. 2007; Bartels et al. 2012; Jackson et al. 2016). For this test, the null hypothesis states that the angles within a treatment are uniformly distributed and are not clustered in any particular direction (Fisher 1993; Pewsey et al. 2013). This was used to see if any pattern of mean change in angle was consistently seen across sites or time periods (Schmidt et al. 2007; Pewsey et al. 2013).

2.4. Results

2.4.1. Baseline Community Structure in the St. Croix River

At each site sampled in the St. Croix River, the average range of $\delta^{13}\text{C}$ (-40 to -23) and $\delta^{15}\text{N}$ values (-0.5 to 9) were relatively similar (Figure 2.3). Several outliers did exist, ranging from -43 to -18 for $\delta^{13}\text{C}$ and -0.5 to 12 for $\delta^{15}\text{N}$, with fish and leeches constituting the higher nitrogen values. The average values for alewife was -19 for $\delta^{13}\text{C}$ and 12 for $\delta^{15}\text{N}$. Both of these values were outside of the mean range at each site sampled in the St. Croix, but were within the most extreme values for outliers. At all

three lake sites, zooplankton displayed similar $\delta^{15}\text{N}$ values and slightly depleted $\delta^{13}\text{C}$ values as compared to macroinvertebrates.

In the St. Croix River, no indication of MDN influence was seen at any site or time period. Slight differences between lake and main-stem sites reflected habitat variability rather than marine input, which were anticipated given the small alewife run relative to the habitat size. Biplots of baseline stable isotope results indicated no difference between isotope values from 2013 to 2015 (Figure 2.2). Main-stem river sites seemed to have a less obvious separation between invertebrate and fish groupings than lake sites, which was likely because the latter had a higher abundance of large predator fish than the former. SEA_c indicated that invertebrate communities had a wider bi-variate niche space than fish communities for both site groupings (Figure 2.3). This indicated a wider range of basal resources, as invertebrate communities had a larger number of functional feeding groups than fish communities. The average SEA_c and NR of fish communities at main-stem sites was also smaller than at lake sites, which was reflective of greater trophic diversity in the latter. The average CR between lake and main-stem sites was much closer and 95% confidence intervals overlapped, indicated relatively similar basal resources for their respective food webs.

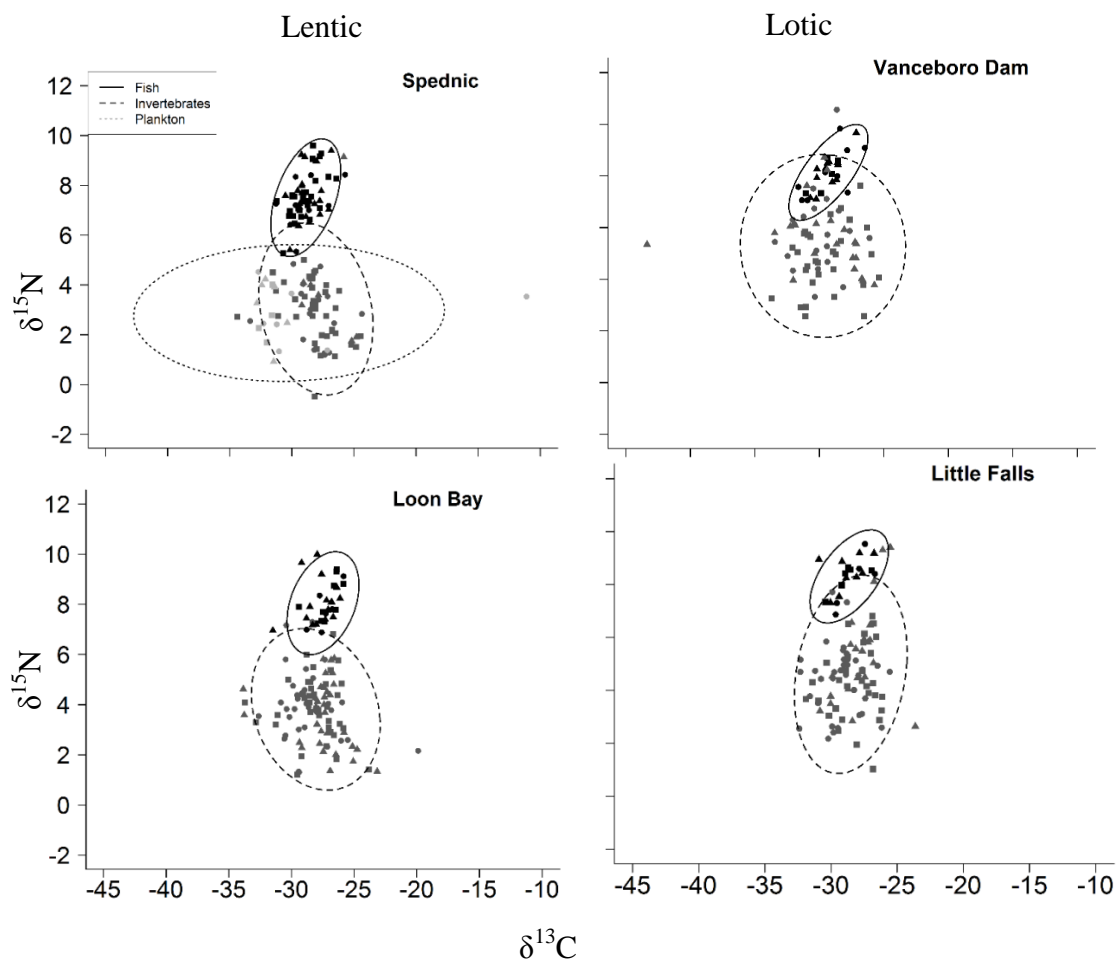
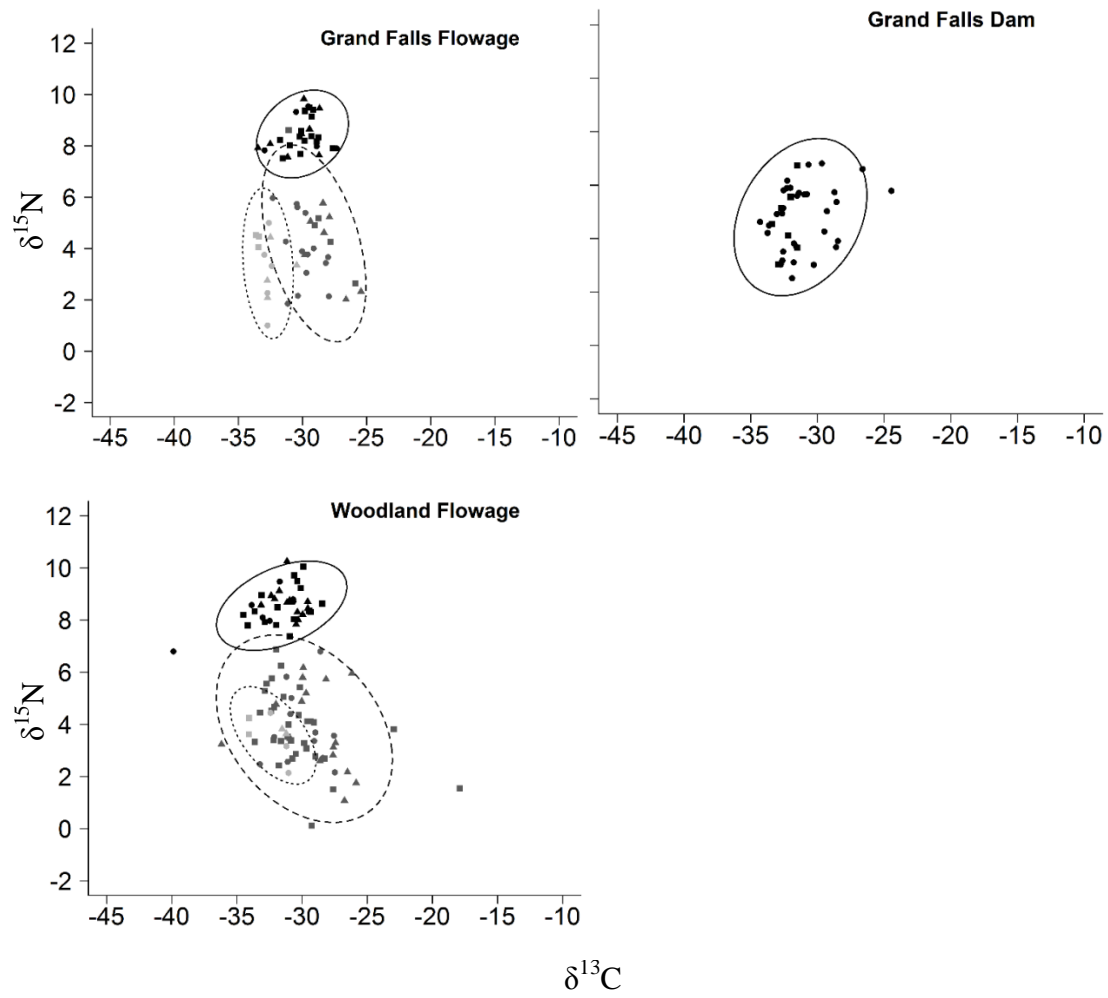


Figure 2.2. Stable isotope biplots for each site in the St. Croix River. Lentic sites are in left column, with upstream to downstream sites arranged from top to bottom. Lotic sites are in right column. Colors indicate sample types including fish (black), invertebrate (dark grey), and plankton (light grey) communities. Points are averages for functional feeding groups by year where 2013 is represented by squares, 2014 by circles, and 2015 by triangles. Standard ellipses were drawn around 95% of the data for each sample type grouping, with the center of the ellipse corresponding to the mean of that community. Average alewife values were -19 for $\delta^{13}\text{C}$ and 12 for $\delta^{15}\text{N}$.

Figure 2.2 continued



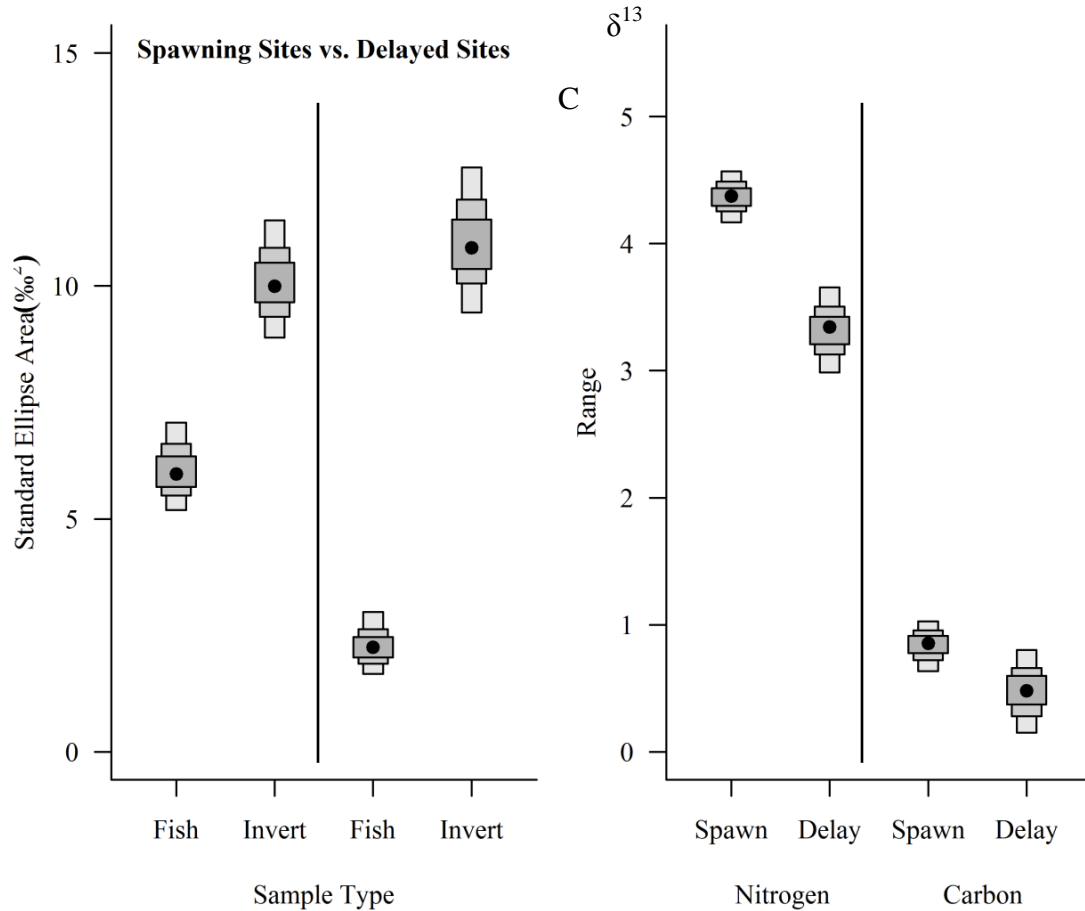


Figure 2.3. Comparison of SEA, $\delta^{15}N$ range, and $\delta^{13}C$ range for spawning habitat sites and sites where alewives are likely delayed. An SEA was calculated for both fish and invertebrate communities for each site type. Mean SEA and mean ranges were calculated after fitting Bayesian multivariate normal distributions to each grouping. Boxes around the mean represent credible intervals at 50, 75, and 95.

Seasonal trends at all sites in the St. Croix explored the shift in community structure between seasons 1-2 and seasons 2-3. Rayleigh's Test results indicated that the angle and magnitude of change was non-random for three site and season combinations, though none of these were indicative of MDN input that would have both increasing $\delta^{15}N$

and increasing $\delta^{13}\text{C}$ (Table 2.1). At Little Falls, which is a site on the that could potentially have delayed passage at low flow levels, seasons 1-2 had a high rate of increasing $\delta^{15}\text{N}$ and seasons 2-3 decreasing $\delta^{15}\text{N}$ (Figure 2.4). Both season pairs trended toward decreasing $\delta^{13}\text{C}$.

Table 2.1. Results from seasonal comparisons by site. S1-3 refer to a time series of samples taken from each site. Mean vector direction is the angle in radians of the difference between each pair of seasons. Rayleigh's Test was used to determine uniformity of the sample distributions around the circle. Bolded row indicates significant results.

Site	Season	Mean vector			Rayleigh's Test		
	Comparison	n	direction	length	circular SD	Z	P
GFD	S1 to S2	3	1.80	0.492	1.19	0.492	0.526
	S2 to S3	5	0.245	0.277	1.60	0.277	0.703
GFF	S1 to S2	3	2.21	0.433	1.29	0.433	0.612
	S2 to S3	2	0.229	0.877	0.513	0.877	0.243
SP	S1 to S2	5	2.38	0.713	0.823	0.713	0.072
	S2 to S3	5	2.76	0.651	0.926	0.651	0.119
LF	S1 to S2	7	2.92	0.970	0.245	0.970	*0.00
	S2 to S3	6	0.556	0.835	0.600	0.836	*0.009
LB	S1 to S2	5	0.642	0.346	1.457	0.346	0.575
	S2 to S3	5	-1.52	.0322	1.50	0.322	0.620
VB	S1 to S2	6	3.01	0.909	0.436	0.909	*0.002
	S2 to S3	4	-0.298	0.478	1.215	0.478	0.429
WF	S1 to S2	4	0.697	0.772	0.719	0.772	0.086
	S2 to S3	7	2.51	0.139	1.99	0.139	0.881

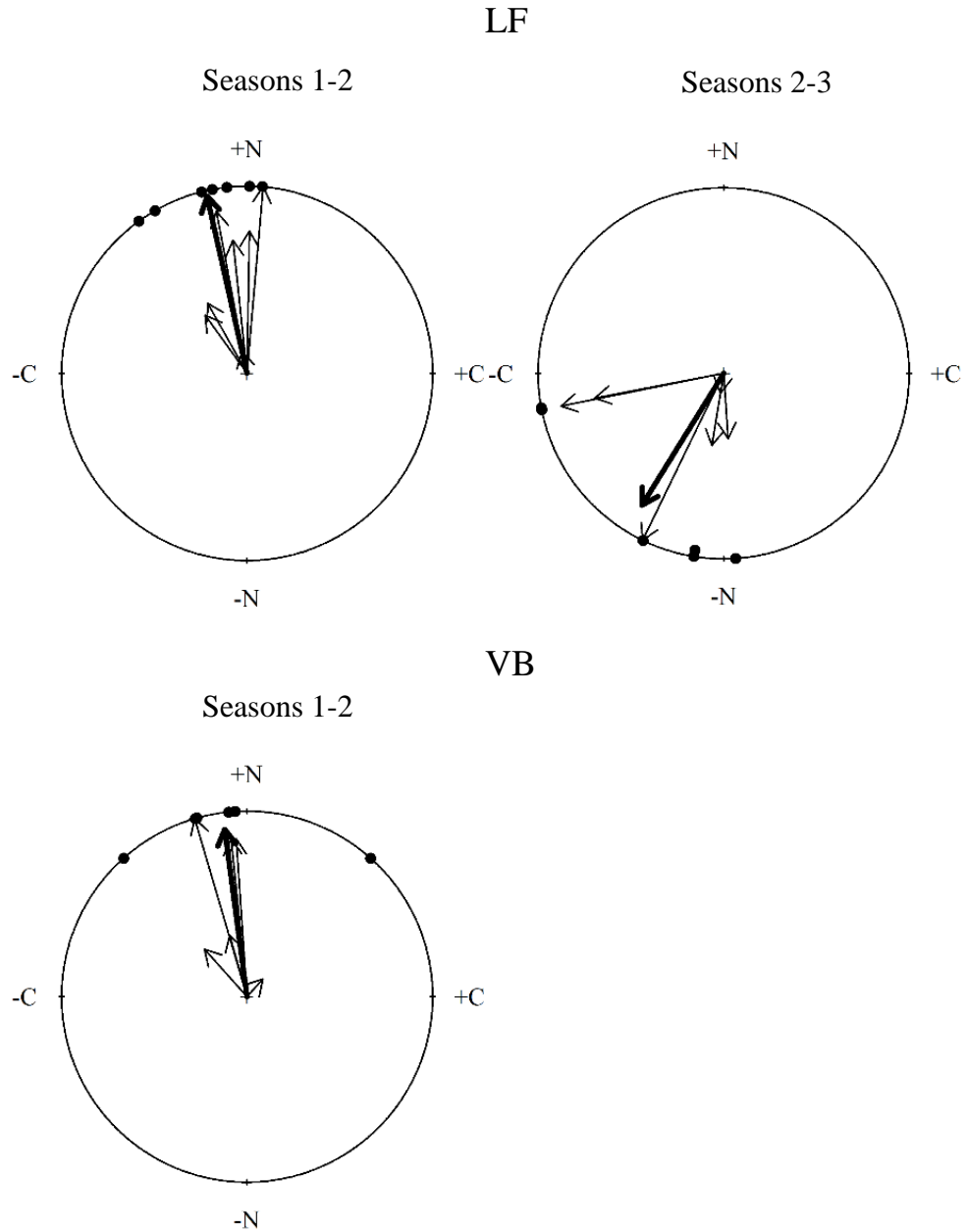


Figure 2.4. Arrow diagrams for seasonal time series comparisons between significantly non-random sites in the St. Croix River. Points around the circle correspond to the pairwise difference in the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between each sampling season. Arrow direction indicates shift among seasons, and magnitude of that shift is represented by the length. Bold arrow indicates vector mean of all arrows displayed.

2.4.2. MDN Input Comparing Alewife Presence and Absence

2.4.2.1. Community Trends

There was no strong indication of MDN incorporation at the community level in the East Machias River at the coarsest temporal scale. A consistent difference in $\delta^{13}\text{C}$ was seen where the alewife site was more enriched than the reference site during every season in both years (Figure 2.5). Bayesian distributions indicated that in 2014 the non-alewife site had a wider C range than the alewife site; in 2015 the opposite pattern was seen. The $\delta^{15}\text{N}$ values between the two sites were relatively similar; in 2014 the N range was almost identical and in 2015, the N range was higher for the alewife site, though the confidence interval was wide (Figure 2.5; Appendix C). As site differences were only seen in the C values and not the N values, it's more likely these were due to differences in basal resources rather than MDN input.

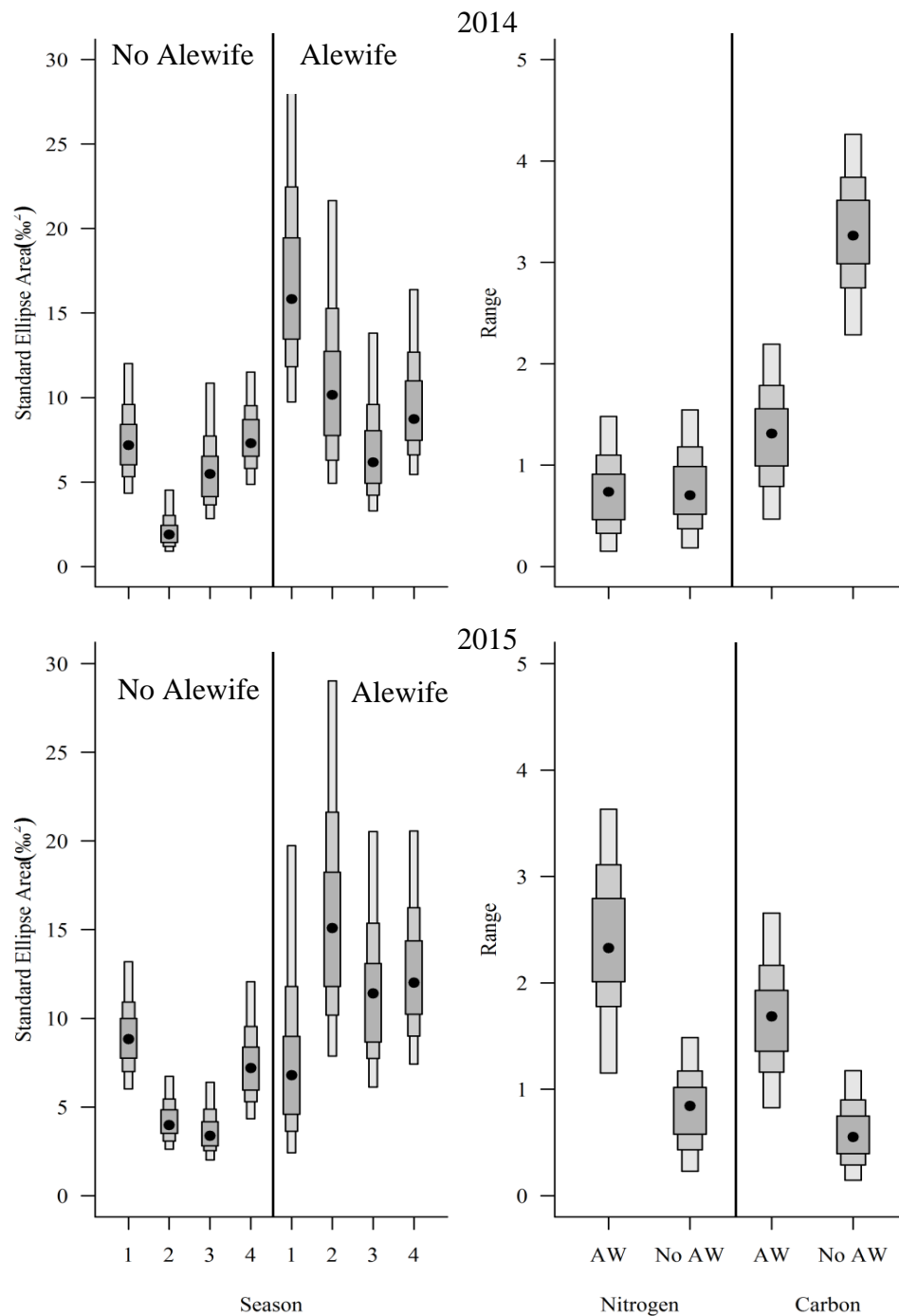


Figure 2.5. Community SEA, $\delta^{15}\text{N}$ range, and $\delta^{13}\text{C}$ range. Comparisons made by year and season between a site with alewife present (AW) and one with alewife absent (No AW). Mean SEA and mean ranges were calculated after fitting Bayesian multivariate normal distributions to each grouping. Boxes around the mean represent credible intervals at 50, 75, and 95.

Several seasonal trends that may indicate MDN influence were identified at a finer time scale within each year at both sites. In 2014, seasons 1 and 2 at the alewife site had the widest confidence intervals, indicating the community occupied a large bivariate space. The SEA in season 2 (both years) and season 3 (2015) was so wide for the alewife site that it encompassed the non-alewife site, which had very similar, albeit small, confidence intervals during the respective season (Figure 2.5). This indicated a much higher trophic diversity and potentially wider resource base within the invertebrate community during the peak of the alewife run when spawners were present as opposed to when they were absent. At the alewife site, the mean calculated SEA in 2014 was highest in season 1, and in 2015 it was greatest in season 2. This could indicate differences in timing associated with the peak of the alewife run, assuming that a high SEA area acts as a proxy for MDN input.

Temporal comparisons among seasons indicated a shift in the community bivariate space at the alewife site from season 1 to season 2 that was indicative of MDN input (Figure 2.6; Table 2.2). The mean community angle indicated a shift toward increasing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and the magnitude was large. Rayleigh's Test indicated a non-uniform distribution for this site and pair of seasons. This was seen in 2014 but not 2015 for the same site and time period (Figure 2.6). At the non-alewife site, Rayleigh's Test indicated a marginally significant non-uniform distribution in 2014 moving from season 3 to season 4. This community had a mean angle that was indicative of both increasing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, but had a much wider circular standard deviation (Table 2.2, Figure 2.6). In 2015, none of the site and season combinations resulted in a significantly non-uniform mean vector angle. However, the mean vector angles for the shift from seasons 1-2 and

2-3 were both in the direction of MDN input. Circular standard deviation between the angles for each FFG in those communities was wide.

Table 2.2. Results from seasonal comparisons by site and year in the East Machias. S1-4 refer to a time series of samples taken from each site. Mean vector direction is the angle in radians of the difference between each pair of seasons. Rayleigh's Test was performed to test uniformity of the sample distributions around the circle. Bolded rows indicate significant results, and italicized rows indicate comparisons that approached significance.

		Mean vector				Rayleigh's Test	
Site (Year)	Comparison	n	direction	length	circular SD	Z	P
No Alewife							
2014	S2 to S3	7	2.51	0.139	1.99	0.139	0.881
	S1 to S2	4	-0.586	0.627	0.966	0.627	0.218
	<i>S2 to S3</i>	<i>3</i>	<i>2.66</i>	<i>0.921</i>	<i>0.406</i>	<i>0.921</i>	<i>0.0669</i>
	<i>S3 to S4</i>	<i>6</i>	<i>-2.50</i>	<i>0.688</i>	<i>0.866</i>	<i>0.688</i>	<i>0.052</i>
2015	S1 to S2	6	-2.85	0.261	1.64	0.261	0.683
	S2 to S3	6	1.20	0.484	1.204	0.484	0.255
	S3 to S4	5	-2.31	0.331	1.488	0.331	0.603
Alewife							
2014	S1 to S2	4	-2.67	0.901	0.456	0.901	*0.027
	S2 to S3	4	2.32	0.379	1.39	0.379	0.594
	S3 to S4	5	-3.14	0.486	1.20	0.486	0.324
2015	S1 to S2	3	-1.97	0.772	0.719	0.772	0.175
	S2 to S3	5	-2.22	0.269	1.62	0.269	0.718
	S3 to S4	5	2.37	0.546	1.10	0.546	0.236

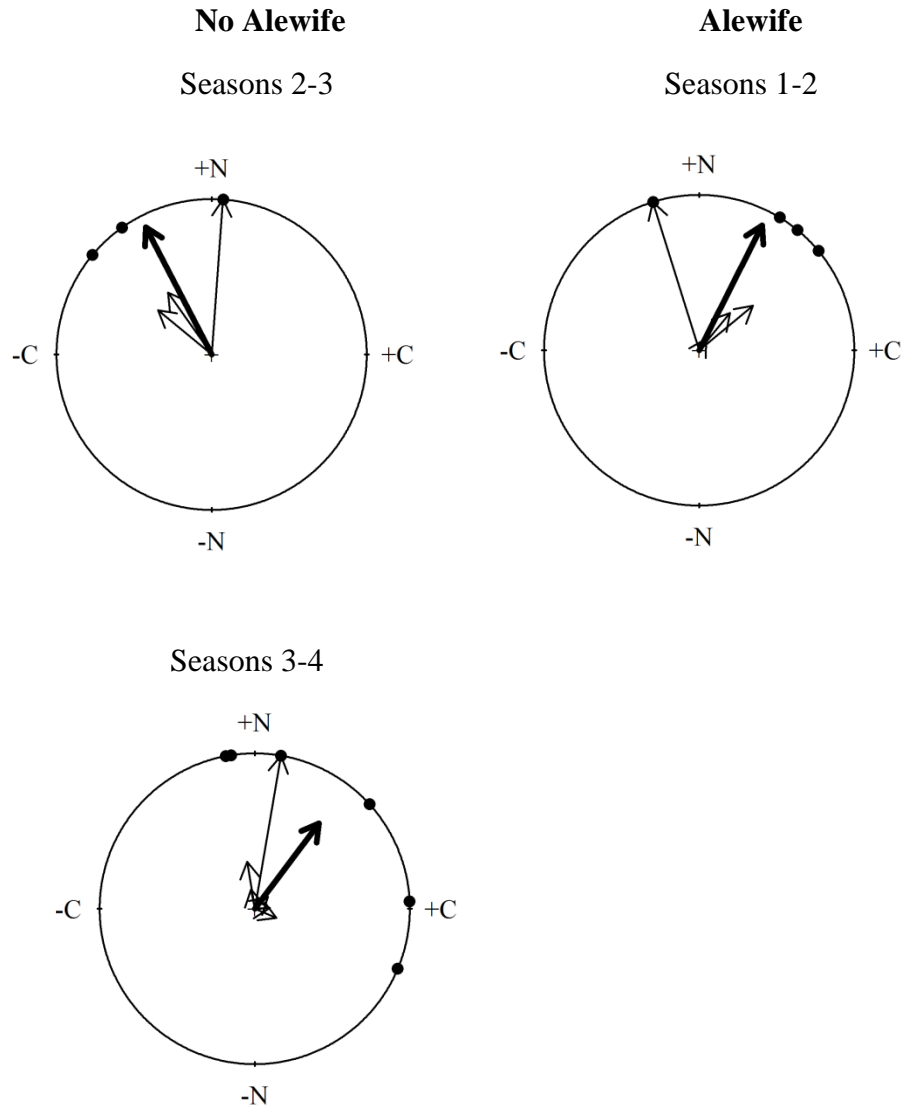


Figure 2.6. Arrow diagrams for seasonal time series comparisons of invertebrate communities between sites in the East Machias River in 2014. Points around the circle correspond to the pairwise difference in the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between each sampling season. Arrow direction indicates shift among seasons, and magnitude of that shift is represented by the length. Bold arrow indicates vector mean of all arrows displayed.

2.4.3. MDN Input and Invertebrate Functional Feeding Groups

While a MDN influence was not observed for all FFGs within the invertebrate community, several groups displayed temporal trends indicating alewife influence. In 2015, shredders had enriched isotope values for seasons 2-4 compared to season 1 at the alewife site. This was especially pronounced in $\delta^{15}\text{N}$, which at the non-alewife site had a much smaller range and did not display the same seasonal pattern. However, in 2014 shredders did not display the same seasonal pattern and had wide standard errors associated with N at both sites. Scraper-grazers also displayed a temporal trend in both years, with season 1 having a lower average $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than the other three seasons. In 2014 the trend was less pronounced, with similar N values between sites but a wider range in C at the alewife site (-28 to -24) than the non-alewife site (-34 to -35). In 2015 this temporal trend was much more pronounced at the alewife site, with a wide C (-29 to -23) and N (2.1 to 4.5) range. At the non-alewife site, all four seasons were tightly clustered and standard errors overlapped, indicating no significant difference.

In both years, temporal trends were less pronounced for collector-filterers, collector-gatherers, predators, and fish. These functional groups were more variable between seasons, though in both years the total bivariate niche space was generally wider for samples from the alewife site than the non-alewife site. In 2014 and 2015, both collector-filterers and collector-gatherers had a wider range in N at the alewife site than the non-alewife site, though several of the seasons had very small sample sizes and so inferences should be carefully considered. Invertebrate predators and fish both had tight clusters between seasons, with very similar $\delta^{15}\text{N}$ values at both sites.

For the four functional groups with potential temporal trends at the alewife site, the increase in isotope value through time was more pronounced for $\delta^{13}\text{C}$ than $\delta^{15}\text{N}$ (Figures 2.7 and 2.8; Appendix C). While C values were elevated at the alewife site compared to the non-alewife site for all feeding groups, the temporal trend was an increase from the first season throughout the other three seasons for collector-filterers in 2014, shredders in 2015, and scraper-grazers in both years. For these groups, error bars indicated that there was separation in the mean isotope value indicative of enrichment through time. However, low sample sizes meant that not all means were associated with error bars, making inferences more difficult.

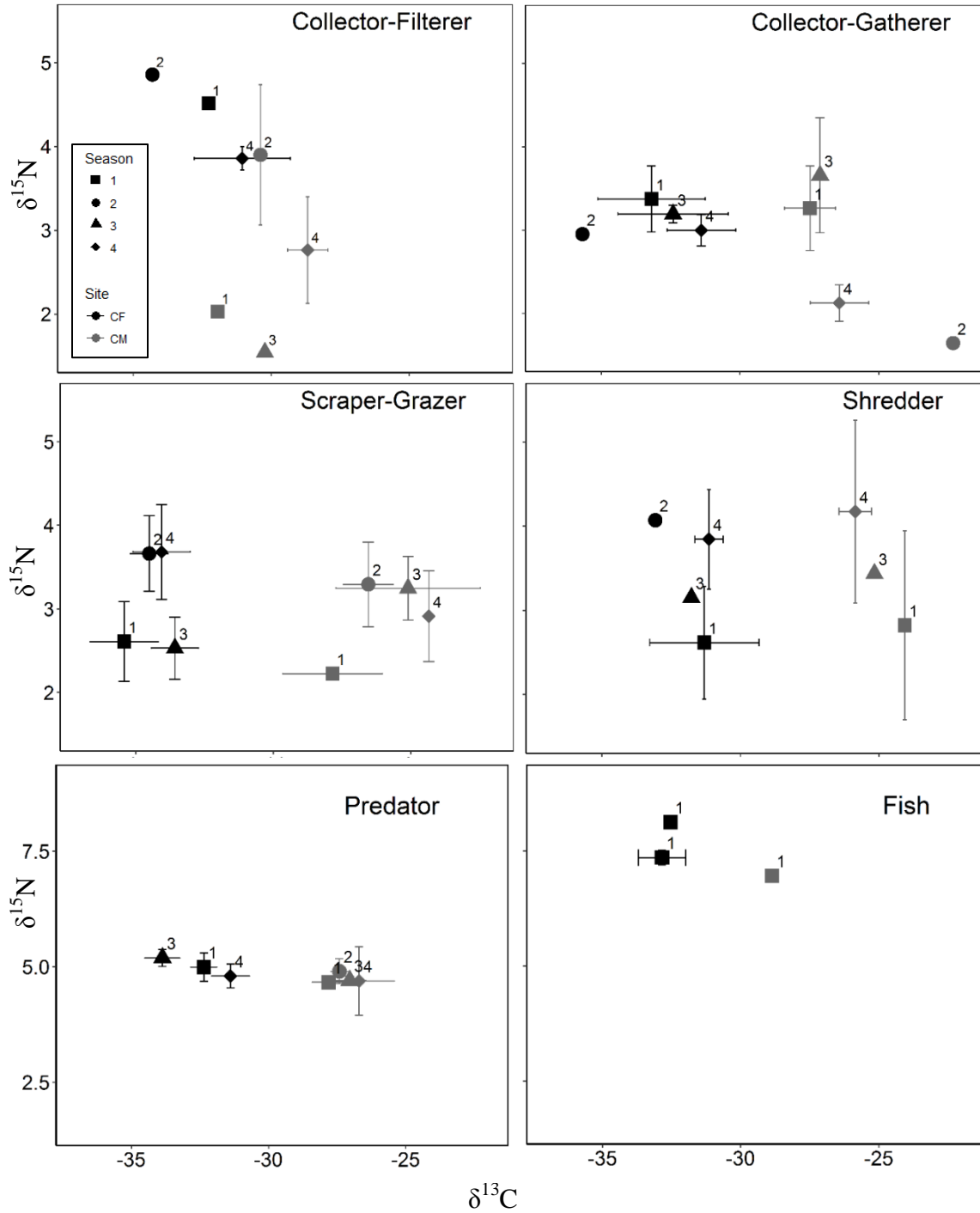


Figure 2.7. Biplots for each functional feeding group sampling in 2014 in the East Machias River. Points are averages with standard errors. Seasons are indicated by shapes and numbers, and sites are indicated by color. Note difference in y-axis on last two plots. Average alewife values were -19 for $\delta^{13}\text{C}$ and 12 for $\delta^{15}\text{N}$.

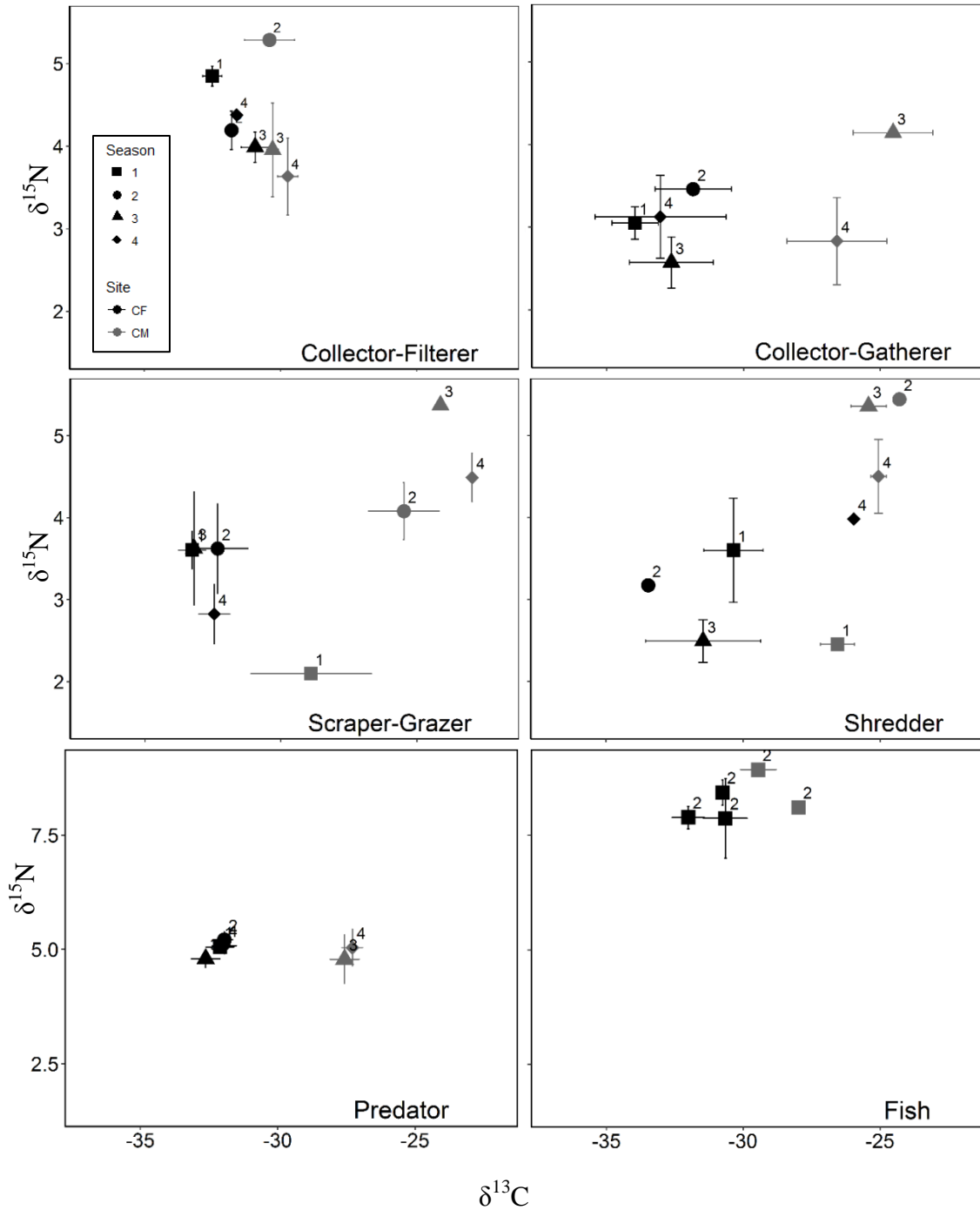


Figure 2.8. Biplots for each functional feeding group sampling in 2015 in the East Machias River. Points are averages with standard errors. Seasons are indicated by shapes and numbers, and sites are indicated by color. Note difference on y-axis on last two plots. Average alewife values were -19 for $\delta^{13}\text{C}$ and 12 for $\delta^{15}\text{N}$.

2.5. Discussion

Baseline isotope data from the St. Croix River indicated similar community structure among sites, and any differences were aligned with habitat type. Invertebrate communities at all sites in the St. Croix had similar isotopic niche space, SEAs, and C ranges. Fish communities at lake sites had a higher mean SEA and N range than at main-stem sites, indicating wider trophic diversity in lakes. The mean SEA for invertebrate communities was larger than fish communities, with no overlap between confidence intervals. This indicated that invertebrates used a wider resource base than fish, which was reflected in a larger number of FFG. Several sites in the St. Croix did have a community shift in SI values, but none reflected what would be expected due to marine-derived nutrient input. Invertebrate communities at LF and VB, both main-stem sites with the potential for delayed passage for alewife, had changes in mean $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ bivariate space on a short-term temporal scale. At LF and VB, $\delta^{15}\text{N}$ increased between seasons 1-2, which could suggest enrichment. However, paired $\delta^{13}\text{C}$ values for these comparisons decreased, which is not indicative of a marine input.

2.5.1. MDN Input

2.5.1.1. Site-Specific Carbon Variation at Community Scale

In both 2014 and 2015, $\delta^{13}\text{C}$ was higher for all four seasons in the East Machias at the site where alewives were present than the one where they were absent. This could be the result of persistent marine-derived nutrient input, but is more likely related to inherent differences between sites. It is possible that enriched isotope values are the result of anthropogenic inputs from camp properties, as the alewife site was at the outlet stream of a large lake (Wada 2009). If this were the case, however, enriched N values would likely

be seen (Bentivoglio et al. 2016). Previous studies have demonstrated that aquatic consumers may have C isotope values that more closely reflect algal than terrestrial inputs, and the former could have a wide $\delta^{13}\text{C}$ range in stream environments (-47 to -12; France 1995; Finlay 2001). When stream primary productivity is high and CO_2 values relatively low, epilithic algal $\delta^{13}\text{C}$ values become depleted as water velocity increases because of C limitation associated with a thinner water boundary layer (Keeley & Sandquist 1992; Finlay et al. 1999). The alewife site had high flows with predominantly rapid/riffle habitat, while the non-alewife site had slower flows and finer substrate. However, $\delta^{13}\text{C}$ enrichment occurred at the site with higher flow, so water velocity did not explain the difference between sites.

It is likely that differences in upstream habitat influenced the consistent distinctions in $\delta^{13}\text{C}$ between sites in the East Machias. The alewife site had a lake directly upstream, though phytoplankton and submerged freshwater macrophytes tend to be depleted in $\delta^{13}\text{C}$ (Hamilton & Lewis 1992; Beer & Wetzel 1982). Habitats with high primary productivity can also display $\delta^{13}\text{C}$ enrichment, especially in epiphytic algae (Finlay et al. 1999; Hamilton & Lewis 1992). The non-alewife site may have been less productive, and tannic water suggested a large influence of the surrounding woodland habitat. Terrestrial woody detritus is generally depleted in heavy C because trees undergo C3 carbon fixation, a process that leads to enrichment in light isotopes (Farquhar et al. 1989; Cloern et al. 2002). Last, watershed area has demonstrated a positive correlation with $\delta^{13}\text{C}$ enrichment (Finlay 2001). The alewife stream is fed by several lakes and streams, whereas the non-alewife stream is at the top of the watershed and has no large water bodies located upstream.

2.5.1.2. Nutrient Delivery and Incorporation

Despite the presence of a large alewife run, pronounced shifts in isotope values related to MDN input were not seen for the freshwater community as a whole. Previous studies focusing on MDN input due to Alosines have demonstrated isotopic enrichment when comparing spatial or temporal trends related to migration. Alewife and blueback herring presence led to C and N isotope enrichment in periphyton and collector-gatherers (Walters et al. 2009), as well as C and S enrichment in resident predatory fish (Garman & Macko 1998; Macavoy et al. 2009). There were three functional feeding groups at the alewife site in the East Machias that demonstrated an increase in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with time, which was indicative of a marine-derived nutrient input. However, these trends were not consistent between years, despite similar spawner abundance.

Given the estimated size of the alewife run (300-400,000 fish) relative to the size of the stream, enrichment of the freshwater community was expected. Studies have found that the influence of MDN input can be variable with respect to site and that not all components of the freshwater community are influenced. Twining et al. (2013) looked at historic alewife input through sediment cores and found no clear isotopic signal. Walters et al (2009) found no effect of alewife MDN input on water chemistry, terrestrial leaf decomposition rate, and periphyton abundance in a stream in Connecticut. In contrast, Norris (2012) saw a small increase in water nutrient concentration in Maine streams when alewives were present, though the same effect was not seen in lakes.

There are several reasons why site-specific variability in MDN incorporation exists. First, site variability is likely related to turnover rates in the resident freshwater community. Walters et al. (2009) found enrichment due to alewives tended to be short-

lived, with enrichment occurring until June and then either declining or remaining stable for the rest of the season. Enriched isotopes are rapidly incorporated into a food web, but turnover rates differ between ephemeral and long-lived species. Organisms with fast tissue turnover rates that rapidly incorporate MDN inputs may just as quickly revert back to a freshwater signature, making influences difficult to detect. Fish have demonstrated turnover rates after a diet change on the scale of weeks, but this is positively correlated with mass for both C and N (McIntyre & Flecker 2006; Trudel et al. 2011). These slower turnover rates could lead to a delay between nutrient input and detection of enriched isotopes. When a $\delta^{15}\text{N}$ tracer was added to a lake at low levels, it took approximately 10 days to be reflected in aquatic consumer isotope values, and this source was immediately bioavailable (Hadwen & Bunn 2005). The average decomposition rate of blueback herring in the James River, Virginia was about 10 days, though carcasses were colonized by fungus within two days (Garman 1992). Inputs that must be broken down first (i.e. carcasses and gametes), will likely represent a long-term nutrient input that would be available as temperatures increase and community productivity reaches its peak.

A second reason for variability is the timing of nutrient subsidies in relation to seasonal hydrology and freshwater productivity. By all accounts, alewives have the potential for high MDN input because they have large, abbreviated spawning runs (Post & Walters 2009). Studies focusing on MDN, particularly of Pacific salmon, have demonstrated isotope enrichment in the freshwater community, as well as increases in primary productivity and consumer abundance (Richey et al. 1975; Piorkowski 1995; Welch et al. 1998; Wipfli et al. 1998; Cederholm et al. 1999). However, the timing and duration of the alewife spawning run may lead to a desynchronization of marine-derived

input with the freshwater community's ability to sequester these nutrients, leading to a comparative reduction in their influence. Alewives migrate early in the spring when precipitation, stream flows, and lake turnover rates are high. This is in contrast to many spawning runs for Pacific salmon, which occur later in the summer when nutrient retention is probably higher because of decreased water levels and flow rates (Twining et al. 2013). In addition, primary production is still low in the northeastern United States when alewives are entering a system, though passage delays could help synchronize the timing of delivery to sites further upstream. It is possible that input is flushed downstream before it can be incorporated into a particular site and boost primary productivity. In addition, colder temperatures earlier in the spring can decrease tissue turnover rates for both N and C isotopes in organisms, meaning the ability to detect MDN input may be reduced when spawner abundance is highest (Bloomfield et al. 2011). If nutrient input is retained in a system, however, the effect of a pulsed subsidy early in the growing season is likely more pronounced than the same input level available later in the season (Sato et al. 2016).

Last, the timing of nutrient availability is related to the dominant pathway of input (i.e. carcasses, gametes, and excretion), which is likely habitat-specific for alewife because they spawn in slow-moving water. Alewife input into freshwater food webs may be highest in lakes where turnover is slower and carcass input is present. Previous studies on alewife have indicated that carcasses represent the largest potential MDN input (Durbin et al. 1979; West et al. 2010; Barber et al. in review). Predators such as birds, mammals, and fish forage on alewife carcasses, and anadromous fish are an important part of the aquatic-terrestrial linkage in freshwater systems (Willson & Halupka 1995).

Life history strategies will also influence nutrient pathways. Higher rates of iteroparity in the northern part of their range could result in a decrease in input through carcasses and an increase in the importance of excretion and gametes.

In Maine, excretion is likely a large source of MDN input from alewives because smaller fish have a high mass-specific excretion rate (Twining et al. 2017). Previous studies have indicated that excretion is a dominant nutrient input for both Pacific salmon (Tiegs et al. 2011) and alewives (Post & Walters 2009). Excretion is immediately bioavailable, and so its influence could be especially high in the downstream reaches of a river, in areas where flow rates are low enough that the distance of nutrient spiraling is short, or in lakes where population abundances are high and turnover rates are low. At the alewife site sampled in the East Machias River in this study, we thought excretion had the highest potential as a nutrient input. This is partly because of the commercial fishery located immediately upstream of the site, that concentrated alewife input because spawners were held in a pen. The lack of pronounced MDN input is likely due to high spring flows that washed excretion inputs downstream and diluted the signal before they could be sequestered by invertebrates. On the other hand, the presence of this fishery removed the majority of spawners that could have otherwise been available as a carcass input.

In conclusion, baseline isotope values in the St. Croix River reflected site-specific differences and seasonal trends. This information can be used to monitor changes associated with MDN input as the alewife population in the St. Croix River recovers. In the East Machias River, alewife presence resulted in shifted isotope levels within particular functional feeding groups, but not for the freshwater community as a whole.

This illustrates the variable influence of MDN inputs, which has been suggested in previous studies. Our results will also help inform future sampling endeavors focus on particular feeding groups in an effort to reduce cost and effort.

CHAPTER 3

NUTRIENT LIMITATION AND SITE-SPECIFIC PRODUCTIVITY

3.1. Chapter Abstract

Marine-derived nutrient subsidies related to anadromous alewives could alleviate nutrient limitation in oligotrophic lakes and streams. Baseline nutrient limitation was categorized in a river with a recovering alewife population to use for future monitoring efforts. Nutrient diffusing substrates were used to determine baseline limitation at potential spawning sites and areas where alewife may become delayed as the population grows. Results indicate that this watershed experiences nutrient co-limitation. Nitrogen additions led to high algal growth, but the synergistic effect of nitrogen and phosphorus led to the highest chlorophyll *a* biomass at all sites and time periods. The influence of alewife presence was also explored using nutrient diffusing substrates at sites in a neighboring watershed. Algal growth in the form of chlorophyll *a* biomass was compared between a site where alewives were present and one where they were absent. The alewife run had the potential to alleviate nutrient limitations, but algal growth was low and varied annually during the spawning migration.

3.2. Introduction

Nutrient cycling can alter the relative availability of nitrogen (N) and phosphorous (P) within a stream or lake (Rodin and Basilevich 1967; Elser and Urabe 1999; Ballantyne et al. 2008). Freshwater primary productivity is limited by light and nutrient availability (Vanni 2002; Durand et al. 2011). Biogeochemical processes and the structure of the local food web can determine site-specific nutrient availability (Welch

and Cooke 1995; Elser et al. 1988). Autotroph productivity can be limited by a single nutrient (Liebig 1842) or co-limited, depending on the species and community-scale adaptations (Ballantye et al. 2008; Gorban 2010). Whereas freshwater systems were once thought to be primarily P-limited (Schindler 1997), co-limitation has been found in many streams (Harpole et al. 2001; Francoeur 2001; Elser et al. 1990; Sanderson et al. 2009; Ruegg et al. 2011; Davidson and Howard 2007). Co-limitation comes in many forms, including 1) a synergistic effect where the single addition of N or P has no effect on growth but when added together productivity increases and 2) an independent effect where the addition of N and/or P leads to a boost in growth, and the further addition of NP increases that growth (Davidson and Howard 2007; Harpole et al. 2001). The order of additions may or may not have an effect on primary productivity (Craine 2009).

Within a freshwater community, species may adapt to local nutrient conditions (Gorban 2010). These adaptations can include efficient use of a pulsed resource such as marine-derived nutrient (MDN) input from anadromous fish species, especially in an oligotrophic system. A MDN input has been found to increase ecosystem productivity for spawning aggregations of Pacific salmon (*Oncorhynchus* spp.; Richey et al. 1975; Wipfli et al. 1998; Cederholm et al. 1999; Chaloner et al. 2002; Ruegg et al. 2011), Atlantic salmon (*Salmo salar*; Guyette et al. 2014; Samways & Cunjak 2015), Sea lamprey (*Petromyzon marinus*; Samways et al. 2015; Weaver et al. 2016), Rainbow smelt (*Osmerus mordax*; Samways et al. 2015), and Alewives (*Alosa pseudoharengus*; Walters et al. 2009).

Of the migratory species present on the East coast of the United States, Alosines are the most abundant and have the greatest potential for population restoration. In the

watersheds of the northeastern United States, these species (alewives, blueback herring, and American shad) exhibit a high rate of iteroparity (Bozeman and Van der Avyle 1989; Twining et al. 2013) thus carcasses may not be the dominant source of nutrient additions by these fish. Alewives specifically have a high N:P ratio which varies between carcass, gamete, and excretion inputs (Twining et al. 2016). Alewife can have large magnitude spawning runs and varying N:P ratios related to input source, which combined could boost primary productivity in a freshwater system. The first objective of this study, therefore, was to determine whether MDN input due to the presence of alewife led to an alleviation in nutrient limitation in freshwater habitat. This was done by comparing two watersheds, one with a sizeable established alewife run and one with a small population at the beginning of recovery. Within the watershed with an established run, sites with and without alewives were compared to explore differences in chlorophyll concentration. The second objective was to identify baseline conditions of nutrient limitation to use for future comparisons in the watershed where alewife are undergoing a population recovery.

3.3. Methods

3.3.1. Study Sites

Two watersheds were separately examined for site-specific nutrient limitation and to assess potential marine-derived nutrient (MDN) input associated with alewife (Figure 3.1). To explore alewife-related MDN input, two sites in the East Machias watershed were sampled. These two sites were streams that formed part of the inflow (44°51'44"N, 67°21'14"W) and the outflow (44°45'21"N, 67°21'40"W) of a large lake (3720 acres). The outflow stream had a large alewife run with a commercial fishery at the outlet of the lake. The inflow stream did not have any water bodies further upstream, and if alewife

were present they were very few in number (Kyle Winslow, Downeast Salmon Federation, personal communication). Comparisons were made between the two sites and seasonal trends compared between the two watersheds to determine the effect of alewife presence.

The St. Croix River has experienced low spawner abundance for most of the past century, with the current population at about 0.5% of its estimated capacity of roughly 20 million adults (Dill et al. 2010; Chapters 2 and 3). From 2013-2017, spawner abundance has grown from 16,000 to 160,000 fish, but given the watershed size (60,847 acres of habitat) this is still a relatively small run at ~3 fish/acre. Nutrient limitation in the St. Croix River was therefore assessed between habitat types and on a spatial gradient to use as a baseline for future comparisons after population recovery. Six sites were sampled in 2014 and seven sites in 2015, and were specifically chosen as areas where nutrient input would likely be high as spawner abundance increases. These were separated into two categories: sites with slower flow that constituted alewife spawning habitat, and sites on the main stem where passage delays likely occurred. Nutrient input in spawning habitat would be the result of carcasses, gametes, and excretion. However, at sites with passage delays, it's likely that excretion and carcasses are the dominant inputs.

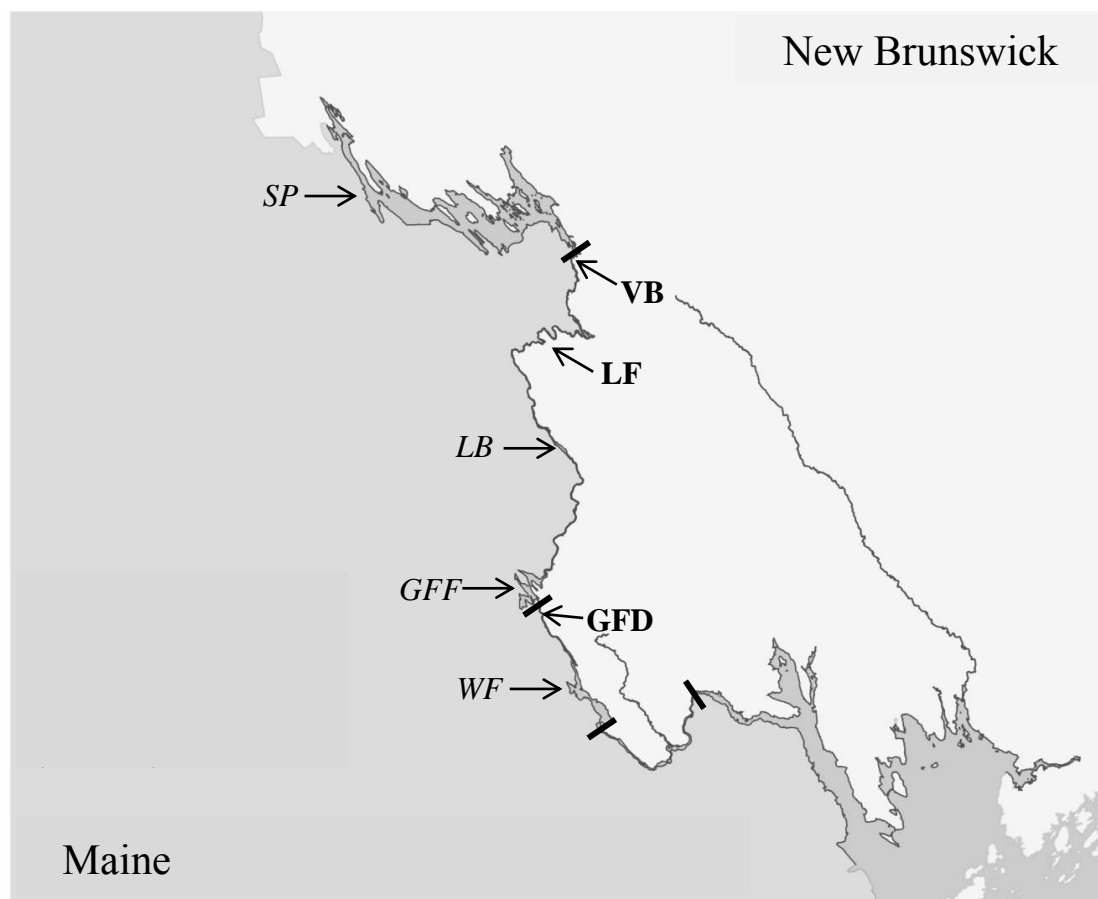


Figure 3.1. Map of the St. Croix River with study site indicated by arrows. In-river sites are bolded, lake sites are italicized.

3.3.2. Sampling Design

3.3.2.1. Nutrient Limitation

Surface water samples were collected at each site to determine baseline nutrient levels. Samples were taken either mid-river at main-stem sites or mid-lake (Jarvie et al. 2002). Water was filtered in the field through a 0.45- μ m cellulose nitrate membrane (Millipore Corp., Massachusetts, USA) using a 60 mL syringe into an acid-washed glass

bottle. Samples were preserved for long-term storage (up to 28 days) by adding 1 mL of using 4.5 N sulfuric acid (H_2SO_4) and were kept chilled until processing (Henrikson 1969). In 2013, samples were taken only from the St. Croix watershed and were analyzed for total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP). In 2015, water samples were taken from both watersheds in May. Total N was measured as $\text{NO}_3\text{-N}$ after persulfate digestion (D'Elia et al. 1977). Orthophosphate was determined colorimetrically by an ion analyzer as the detection limit (~ 0.01 mg/L) for this procedure was lower than for inductively coupled plasma mass spectrometry (~ 0.1 mg/L), and most of the samples were below the latter value (Jarvie et al. 2002).

3.3.2.2. Nutrient-Diffusing Substrate Arrays

Nutrient-diffusing substrates (NDS) were used to assess 1) baseline nutrient limitation in both watersheds and 2) alleviation in this limitation due to the spring alewife run in the East Machias River. This method of nutrient measurement involves using an artificial substrate to slowly release nutrients onto a surface where algae growth can be measured. A higher rate of biomass accumulation between nutrient additions and a control treatment indicate nutrient limitation (Rugenski et al. 2008; Tank et al. 2006). For this study, NDS consisted of periphytometers, which have been tested against other methods and used extensively (e.g. Corkum 1996; Matlock et al. 1998; Capps et al. 2011). These periphytometers were made of 60 mL polyethylene bottles filled with lab-grade agar mixed with one of four nutrient treatments that consisted of: 1) no nutrients (control), 2) 1.0 M NH_4NO_3 , 3) 0.5 M KH_2PO_4 , and 4) a combination of 1.0 M NH_4NO_3 and 0.5 M KH_2PO_4 . A hole was drilled in the lid of the bottle and a glass fiber filter (area = 2.5 cm^2) was used as a substrate for algae to grow. Bottles were placed inside an array

of PVC tubes attached to cement blocks that were deployed at each site at a constant depth of 0.5 m. Upon retrieval, filters were carefully removed from the agar using forceps, placed in separate tubes, and set on dry ice to keep frozen until processing. No attempt was made to prevent invertebrates from accessing the algae on the filters, and during collection small individuals that were occasionally found on top of the bottles were removed.

3.3.2.3. NDS Deployment

Two NDS arrays were placed at each site, each consisting of three randomly-distributed replicates of the four nutrient treatments. For each set of arrays, one was collected after two weeks in the water, and the second after three weeks. Within two days of the second set being picked up, newly made bottles of nutrient solution were deployed. This meant that during the alewife run (roughly 30 April to 15 July with peak in late May) diffusers were continually in the water at each site, allowing us to determine whether or not additional nutrients were incorporated into the site due to the run. Many individual samples and entire arrays were lost in 2014 due to variable water flows as well as human curiosity, and so in 2015 replication of each nutrient treatment was doubled. The biweekly and triweekly timing of sample collection was maintained in both years, resulting in three sets of arrays deployed in 2014 and four sets in 2015.

3.3.2.4. Chlorophyll *a* Analysis

Filters were defrosted and ground into a homogenized 14 mL solution using 90% acetone, and then refrigerated for 12-24 hours to allow time for extraction of chlorophyll *a*. Samples were centrifuged at 20° C and 5000 rpm for 15 minutes. Absorbance was measured for the five wavelengths (630 nm, 647 nm, 664 nm, 665 nm, and 750 nm) using

a digital spectrophotometer, both for untreated chlorophyll *a* and after the samples were mixed for 90 s with 100 µL of 0.1 N HCl. The acid causes chlorophyll *a* to lose a magnesium atom, thereby converting it into phaeophytin *a* (a common degradation product of chlorophyll *a*), which can then be measured using spectrophotometry (APHA 2005). This pheopigment absorbs light at the same wavelength as chlorophyll *a* and can lead to an overestimation of algal biomass, and so corrections were made as in APHA (2005).

Chlorophyll *a* biomass (µg/cm²) was measured using the following equation:

$$\text{Chlorophyll } a = \frac{26.7 * ((664 \text{ BA} - 750 \text{ BA}) - (665 \text{ AA} - 750 \text{ AA})) * \text{EV}}{\text{FA}},$$

where 664 and 750 BA was the wavelength measurement “before acid”, 665 and 750 AA was the wavelength “after acid”, EV was the extract volume (mL), and FA was the filter area (constant at 2.5 cm²). In the equation, the number 26.7 represents an absorbance correction that includes both a coefficient for chlorophyll *a* and a correction for acidification (APHA 2005).

3.3.3. Statistical Analyses

Statistical comparisons were made between the alewife and non-alewife site in the East Machias River using a multi-factor analysis of variance (ANOVA; Underwood 1997). The same test was used to compare habitat types within the St. Croix River to explore differences in baseline dynamics between spawning sites and main-stem sites where fish passage will likely be delayed. For each year, chlorophyll *a* biomass was modelled as a function of site comparison, nutrient treatment, deployment date, and retrieval date. As chlorophyll *a* data did not meet the assumption of normality (Shapiro-Wilk W test; EM 2015 p-value << 0.001; EM 2015, SC 2014 and 2015 p-value <<

0.001), data was log transformed for each watershed and year. Tukey's HSD was used for post hoc comparisons of statistically significant factors to determine which groups were different from one another (Underwood 1997).

Nutrient response ratios (NRRs) were calculated in the East Machias River for time periods where the control treatment had higher chlorophyll *a* biomass than at least one other nutrient treatment. NRRs were calculated by taking the average chlorophyll *a* biomass for each nutrient addition at each site and date combination and dividing it by the value for the control (Ruegg et al. 2011). A NRR less than one indicates that baseline nutrient levels lead to higher algal growth than nutrient additions, which can be indicative of MDN input.

3.4. Results

3.4.1. Baseline N and P

In the St. Croix River there were no differences in baseline TDN and TDP that indicated an overall effect of habitat type for either 2013 or 2015 (Figure 3.2 and 3.3). There was a lack of replication within some sampling date and site combinations, but overall N:P was consistently high (>50) at every site, indicating P limitation throughout the watershed (Allan 1995). There was variability among sites and sampling dates, but trends were not consistent between years. In 2013 the four upstream sites generally had lower dissolved nutrient concentrations when compared to the three downstream sites across the season, although there was high variability with both factors. The two downstream lake sites, GFF and WF, had similar patterns for TDN and TDP where concentrations were similar in May and July and higher in September (Figure 3.2). SP,

located the furthest upstream, had the highest TDP in July and TDN in September. The two main-stem sites furthest upstream, LF and VB, did not have large differences in TDN among dates, nor did the LB which was located close to LF. Both LF and VB had low P values in September, the month that most sites had their greatest TDP concentration. In May, the sites furthest upstream had the lowest system-wide values for TDN and TDP during the study.

In May of 2015, the three downstream sites had lower nutrient concentrations than 2013. The four upstream sites also generally had higher nutrient concentrations, but results were more variable. Variability between sites was most notable at LF and SP, where the TDN value was higher in May than all of the other sites whose error bars overlapped (Figure 3.3). Orthophosphate values in the St. Croix overlapped more between sites than TDN, though GFD and GFF were both lower than all sites except WF.

In the East Machias, baseline TDN and orthophosphate were both higher at the non-alewife site than the alewife site in 2015 (Figure 3.3). There was more variability between samples for orthophosphate than total N. The trend was the opposite of what would be expected from alewife MDN input, but it is possible that these samples were taken out of sync with the timing of nutrient delivery from the run. In addition, excess nutrient input could have been taken up quickly by biofilms.

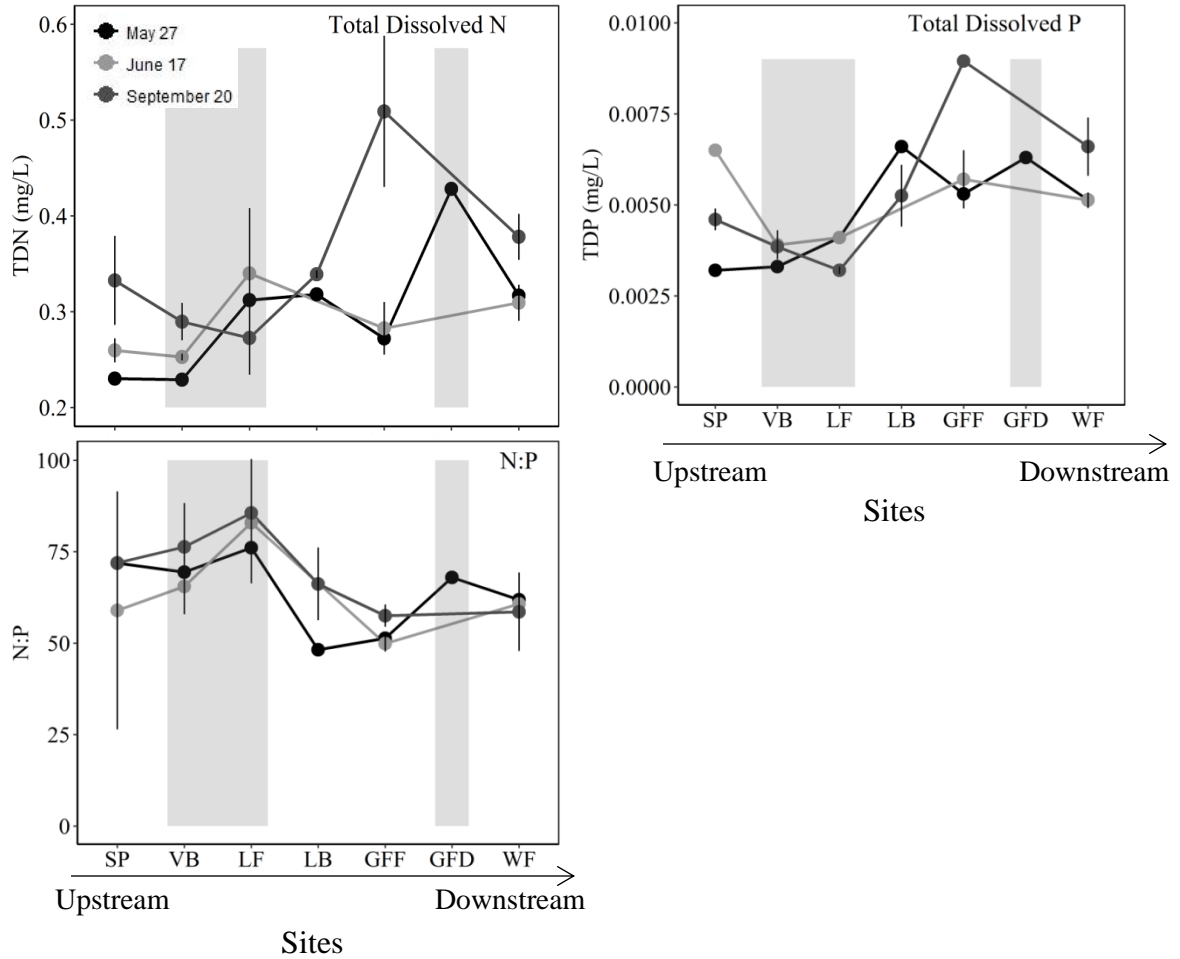


Figure 3.2. Total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), and the nitrogen to phosphorus ratio (N:P) at all sites sampled in the St. Croix River. Samples were taken in May, July, and September of 2013. Grey rectangles indicate main-stem sites, no rectangle indicates lake sites. Sites are arranged upstream to downstream from left to right. Error bars represent variability between samples collected for a site and date combination.

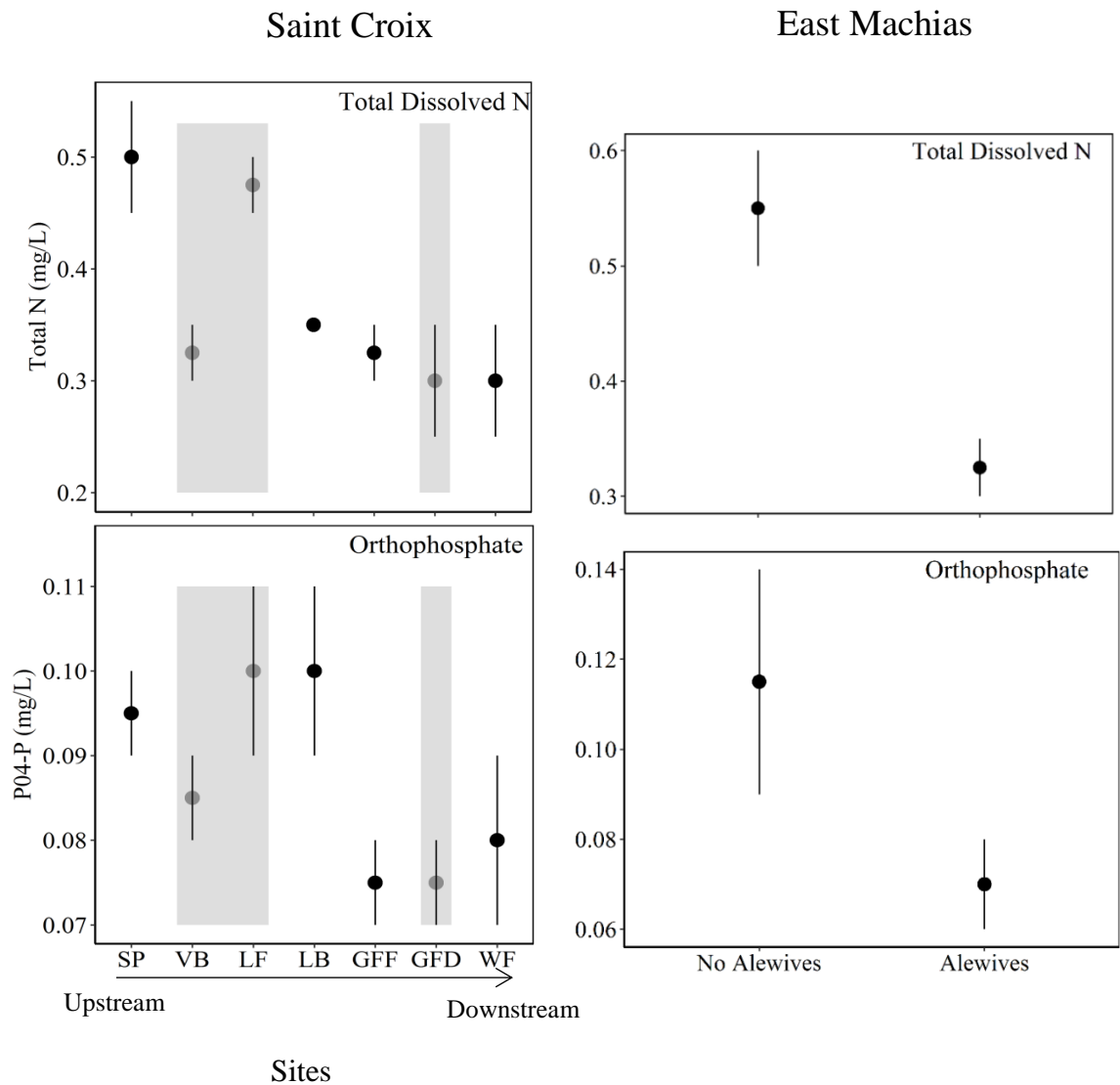


Figure 3.3. Total nitrogen and orthophosphate sampled at all sites in both watersheds on May 22, 2015. Sites in the St. Croix Grey are arranged upstream to downstream from left to right. For St. Croix sites, rectangles indicate main-stem sites, no rectangle indicates lake sites. Error bars represent variability between samples collected for a site and date combination.

3.4.2. Chlorophyll *a* Biomass

3.4.2.1. East Machias

In the East Machias, trends in chlorophyll *a* biomass differed between years (Figure 3.4). In 2014, there was a general trend of increasing chlorophyll *a* biomass through time was seen at the site with no alewife. The exception to this was a decrease in biomass for the P treatment from early June to late July. At the site with alewife, there was very little difference in chlorophyll *a* biomass for collectors left out for two weeks. Those left out for three weeks had an increase with N addition and in the control, and a decrease with NP and P additions.

There were differences based on nutrient type and set times in 2014, but not between sites or retrieval times (Table 3.1). Set time was indicative of seasonal change, with sets consisting of paired retrieval dates in May, June, and July. Both N and P were limiting at the alewife site in early June in 2014, as indicated by the wide a separation in chlorophyll *a* biomass between treatments at this time compared to the other retrievals at that site (Figure 3.4). The non-alewife site saw consistently high biomass related to NP additions indicating a strong co-limitation, though in early June the NP and P treatments had overlapping standard errors. Interactions between site and nutrient type, site and set time, and nutrient type and set time were highly significant (Table 3.1).

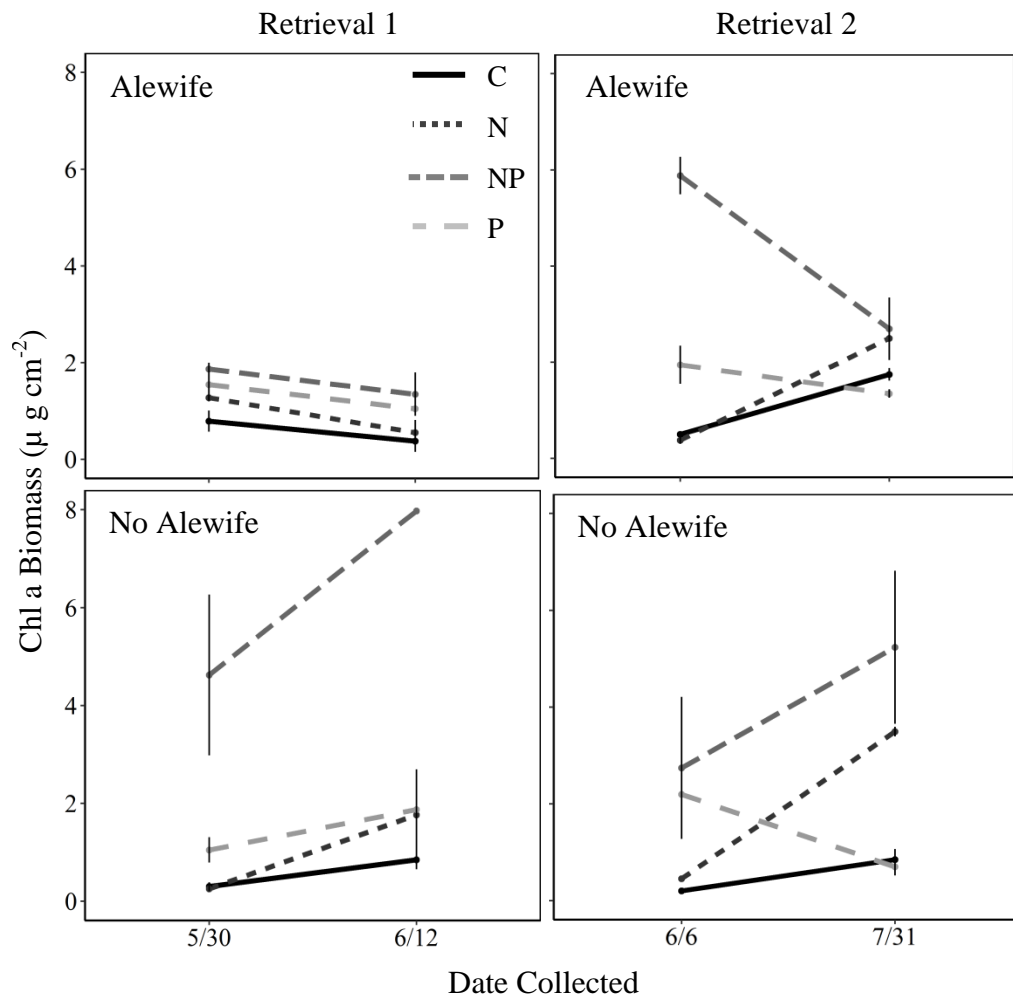


Figure 3.4. Chlorophyll a biomass for four nutrient treatments measured in the East Machias at an alewife and a non-alewife site in 2014. A set of two arrays deployed at the same time was paired by retrieval date, with Retrieval 1 collected after two weeks in the water (left panels) and Retrieval 2 after three weeks (right panels). Exact dates each array was retrieved are on x-axis. In 2014 many arrays were lost, and so not all months had paired dates analyzed.

Table 3.1. Results of multi-factorial ANOVA from nutrient-diffusing substrates placed in the East Machias River in 2014 and 2015. Two sites were tested, one with alewife present and one without. Nutrient treatments included N, P, N+P, and a control. Statistically significant p-values (< 0.05) are in bold.

East Machias	2014				2015			
	df	F	p-value		df	F	p-value	
Site	1	1.3	0.26		1	109.2	<<0.001	***
Nutrient	3	57.6	<<0.001	***	3	131.4	<<0.001	***
Set	2	12.4	<0.001	**	3	43.5	<<0.001	***
Retrieval	1	1.2	0.27		1	130.3	<<0.001	***
Site*Nutrient	3	7.8	<0.001	**	3	81.3	<<0.001	***
Site*Set	2	23.8	<<0.001	***	3	38.2	<<0.001	***
Nutrient*Set	6	11.1	<<0.001	***	9	2.0	0.04	*
Site*Retrieval	1	4.4	0.04	*	1	5.5	0.02	*
Nutrient*Retrieval	3		0.39			3.0	0.63	
Set*Retrieval	1	0.6	0.43		3	12.9	<<0.001	***
Site*Nutrient*Set	6	1.9	0.09		8	3.6	<0.001	**
Site*Nutrient*Retrieval	3	3.0	0.04	*	3	1.2	0.3	
Site*Set*Retrieval	NA	NA	NA		2	6.5	0.002	*
Nutrient*Set*Retrieval	1	19.6	<0.001	**	9	2.9	0.003	*
Site*Nutrient*Set*Retrieval	NA	NA	NA		6	3.9	<0.001	**
Residuals	56				265			

In 2015, general trends differed between sites, seasons (sets), retrieval times, and nutrient treatments (Figure 3.5; Table 3.1). Diffusers left for three weeks had higher overall biomass values than those left for two weeks, which was to be expected. At the alewife site, the 5/21, 6/6 and 6/11 retrieval dates had a higher biomass on the control compared to the other treatments, suggesting an alleviation of nutrient limitation during this time, which coincided with the peak of the alewife run in the watershed. Calculated NRR values for these dates were < 1 for all three nutrient treatments, as was used as evidence of salmon-derived alleviation by Ruegg et al. (2011; Table 3.2). This site had

consistently low chlorophyll *a* biomass for all nutrient treatments until the beginning of July, at which point biomass levels increased sharply and NP limitation was seen.

For these same retrieval dates at the non-alewife site, the NP addition produced the greatest chlorophyll *a* biomass, followed by the N addition, indicating independent nutrient co-limitation (Harpole et al. 2011). Chlorophyll *a* biomass was lowest in the control treatment, followed by the P addition. Maximum biomass accrual due to NP additions was twice as much at this site compared to the alewife site, potentially indicating greater community productivity at the alewife site. Generally, N limitation increased later in the season, demonstrated by a narrower difference between biomass accrual for the N and NP treatments. The strong growth response to the NP treatment at the non-alewife site led to greater variability among sampling periods compared to the variation seen at the alewife site. Both sites had maximum growth in July, followed by a slight decrease in August.

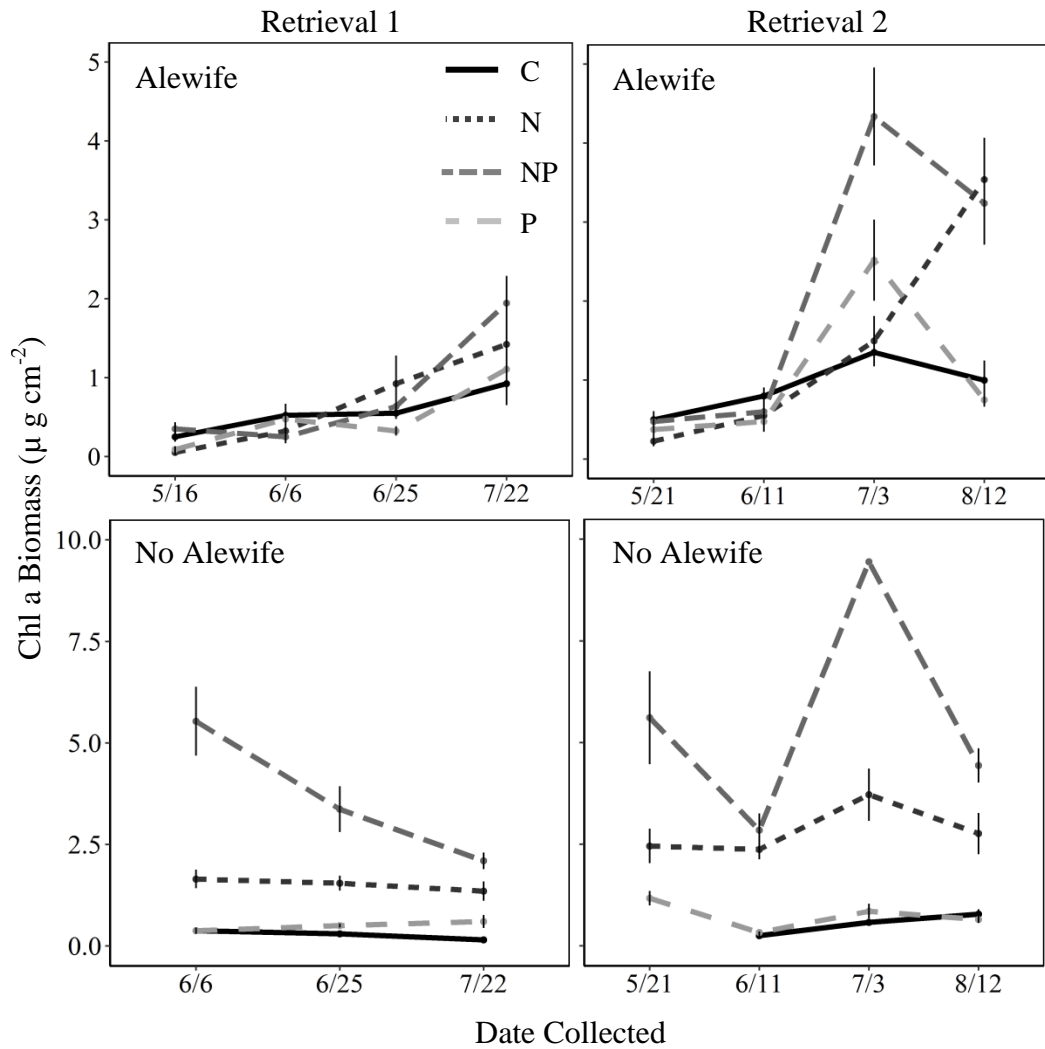


Figure 3.5. Chlorophyll a biomass for four nutrient treatments measured in the East Machias at an alewife and a non-alewife site in 2015. A set of two arrays deployed at the same time was paired by retrieval date, with Retrieval 1 collected after two weeks in the water (left panels) and Retrieval 2 after three weeks (right panels). Exact dates each array was retrieved are on x-axis. Note difference in y-axis between the two sites.

Table 3.2. Nutrient Response Ratios with values ≤ 1 at the alewife and non-alewife sites in the East Machias. Italicized rows are those where all three nutrient treatments (N, P, and NP) within one date and site resulted in ratios < 1 .

Site	Date Retrieved	Nutrient	NRR
No Alewife	8/12/2015	P	0.83
Alewife	5/16/2015	N	0.20
Alewife	5/16/2015	P	0.36
<i>Alewife</i>	<i>5/21/2015</i>	<i>N</i>	<i>0.45</i>
<i>Alewife</i>	<i>5/21/2015</i>	<i>NP</i>	<i>0.95</i>
<i>Alewife</i>	<i>5/21/2015</i>	<i>P</i>	<i>0.75</i>
<i>Alewife</i>	<i>6/6/2015</i>	<i>N</i>	<i>0.62</i>
<i>Alewife</i>	<i>6/6/2015</i>	<i>NP</i>	<i>0.48</i>
<i>Alewife</i>	<i>6/6/2015</i>	<i>P</i>	<i>0.90</i>
<i>Alewife</i>	<i>6/11/2015</i>	<i>N</i>	<i>0.69</i>
<i>Alewife</i>	<i>6/11/2015</i>	<i>NP</i>	<i>0.75</i>
<i>Alewife</i>	<i>6/11/2015</i>	<i>P</i>	<i>0.59</i>
Alewife	6/25/2015	P	0.59
Alewife	8/12/2015	P	0.75

3.4.2.2. St. Croix

In the St. Croix, there was no evidence of alleviation in nutrient limitation as control treatments had the lowest measured chlorophyll *a* biomass for all site and retrieval date combination. In both years, seasonal trends were especially pronounced for the first retrieval date, indicating that algal biomass was lower in early spring across all treatments additions. This trend, though expected, was less obvious in 2014 when fewer dates were sampled (Figures 3.6-3.8). Both NP and N additions generally led to higher chlorophyll *a* biomass for all sites and retrieval dates (Figures 3.6-3.11). In both years, GFF had the highest biomass in NP treatments except in late July. Biomass was often comparable between the control and P additions. This trend was more pronounced in

2015, and indicated that N was primarily limiting within the watershed, though further algal growth due to P additions suggested co-limitation.

Retrieval date and treatment differences were more pronounced in 2015, where all time periods were consistently sampled (Figure 3.9-3.11). Later in the season in 2015, collectors left out for two weeks had a consistent increase in N limitation between June and July, with the highest in chlorophyll *a* biomass. This was especially true in the spawning sites, which were lakes and areas with slow-flowing water.

For both years, there were statistically significant differences between site types (spawning habitat vs. areas of delayed passage), nutrient type, set date (season), and retrieval date (week 2 vs. week 3; Table 3.3). Significant interactions varied between years. Differences in chlorophyll *a* biomass between lentic and lotic sites (Table 3.3) were difficult to decipher. Lake sites potentially had less seasonal variability in chlorophyll *a* biomass associated with each nutrient addition (Figures 3.6-3.7 and 3.9-3.10). Baseline limitations indicated that in general N and P levels were higher in lakes than on the main stem of the river (Figures 3.2 and 3.3), but N:P ratio was lower in the riverine sites. Lakes generally had higher N levels in September, though sites further downstream, which were more heavily populated, had higher P concentrations during this time period. However, variability was high among all sites, and trends seemed to be related to location within the watershed rather than habitat type (Figure 3.3).

Table 3.3. Results of multi-factorial ANOVA from nutrient-diffusing substrates placed in the St. Croix River in 2014 and 2015. Seven sites were combined in two categories (Site Type) that included spawning habitat and areas with passage delays. Nutrient treatments included N, P, N+P, and a control. Statistically significant p-values (< 0.05) are in bold.

St. Croix	2014				2015			
	df	F	p-value		df	F	p-value	
Site Type	1	8.6	0.004	*	1	44.1	<0.001	**
Nutrient	3	46.8	<<0.001	***	3	195.7	<<0.001	***
Set	2	14.4	<0.001	**	3	146.8	<<0.001	***
Retrieval	1	39.9	<<0.001	***	1	167.8	<<0.001	***
Site*Nutrient	3	0.7	0.57		3	2.8	0.04	*
Site*Set	2	7.7	<0.001	**	3	1.9	0.13	
Nutrient*Set	6	2.2	0.04	*	9	7.9	<0.001	**
Site*Retrieval	1	0.2	0.66		1	4.1	0.04	*
Nutrient*Retrieval	3	6.0	0.001	*	3	8.4	<0.001	**
Set*Retrieval	2	1.6	0.21		3	1.3	0.26	
Site*Nutrient*Set	6	0.8	0.57		9	2.4	0.01	*
Site*Nutrient*Retrieval	3	1.4	0.24		3	0.6	0.65	
Site*Set*Retrieval	1	12.8	<0.001	**	3	6.7	0.002	*
Nutrient*Set*Retrieval	6	1.3	0.25		9	1.2	0.28	
Site*Nutrient*Set*Retrieval	3	1.2	0.30		9	0.4	0.94	
Residuals	190				701			

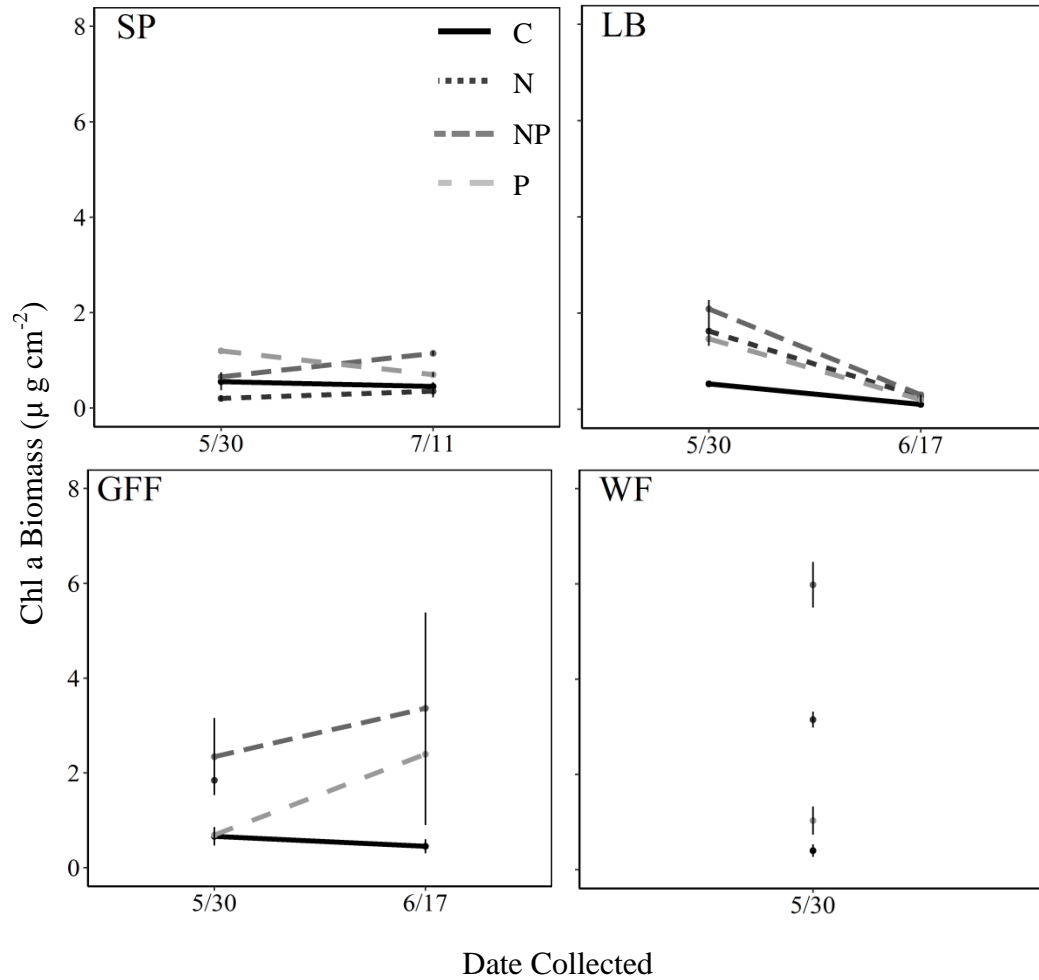


Figure 3.6. Chlorophyll a biomass related to four nutrient treatments retrieved after two weeks in the St. Croix River at spawning habitat sites in 2014. Exact dates each array was retrieved are on x-axis.

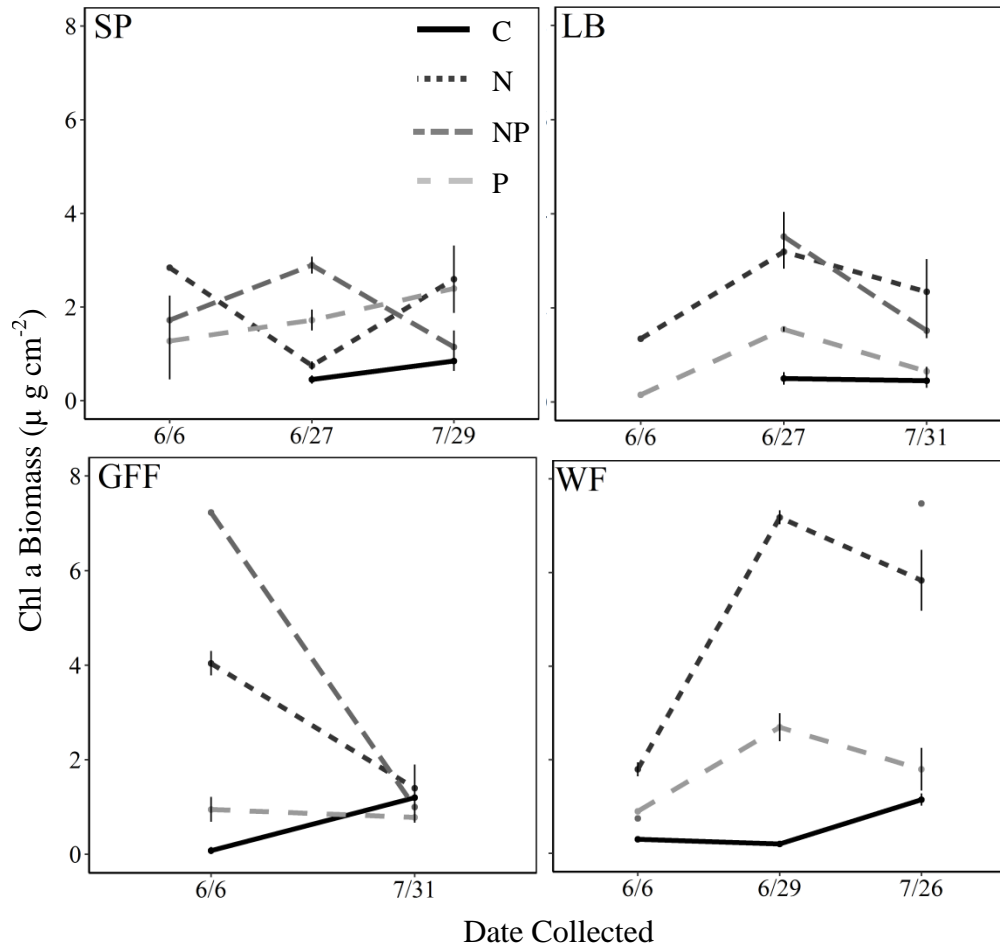


Figure 3.7. Chlorophyll a biomass related to four nutrient treatments retrieved after three weeks in the St. Croix River at spawning habitat sites in 2014. After retrieval, new arrays were placed at the sites. Exact dates each array was retrieved are on x-axis.

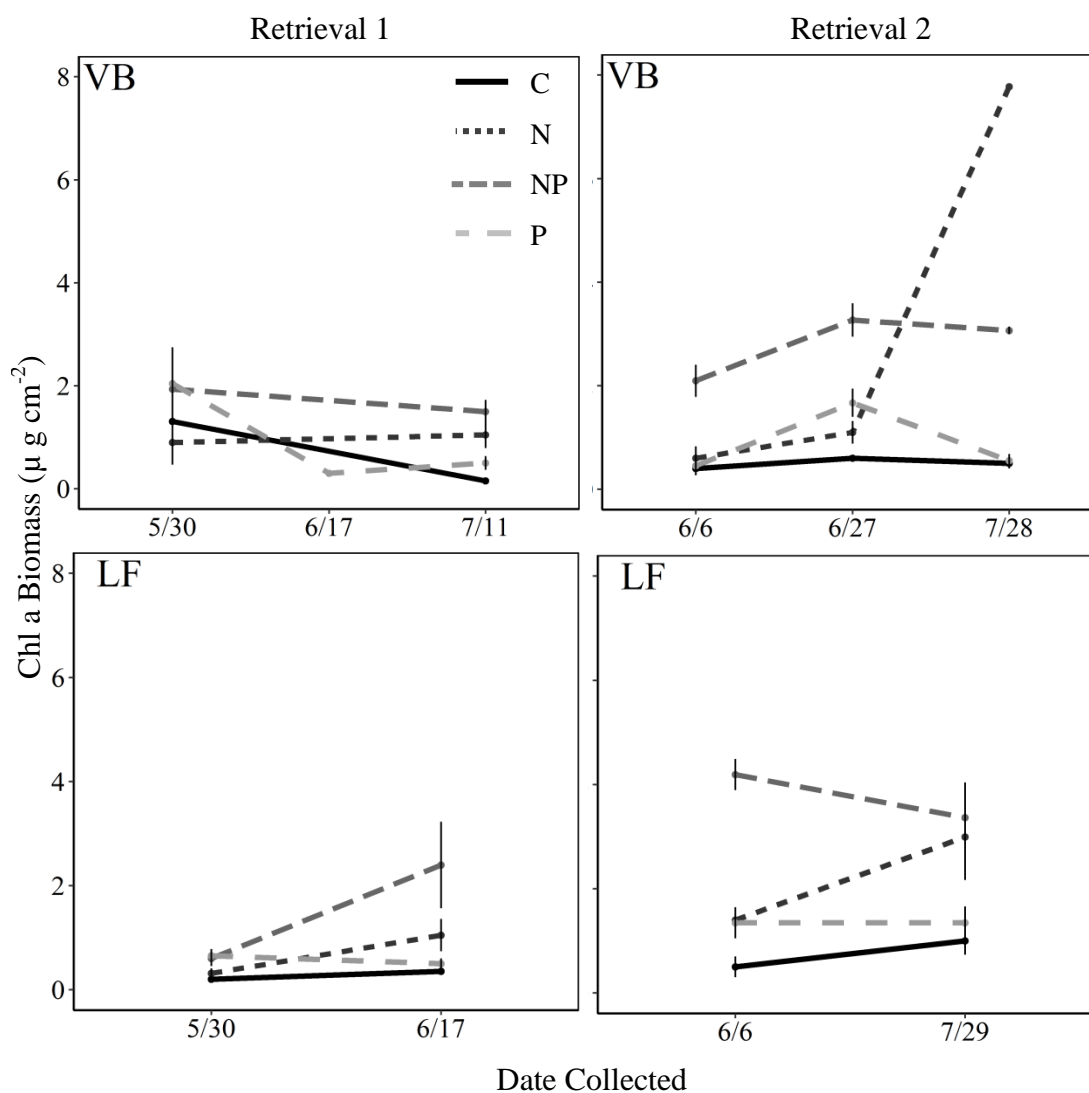


Figure 3.8. Chlorophyll a biomass related to four nutrient treatments measured in the St. Croix River at sites with potential passage delays in 2014. A set of two arrays deployed at the same time was paired by retrieval date, with Retrieval 1 collected after two weeks in the water (left panels) and Retrieval 2 after three weeks (right panels). Exact dates each array was retrieved are on x-axis.

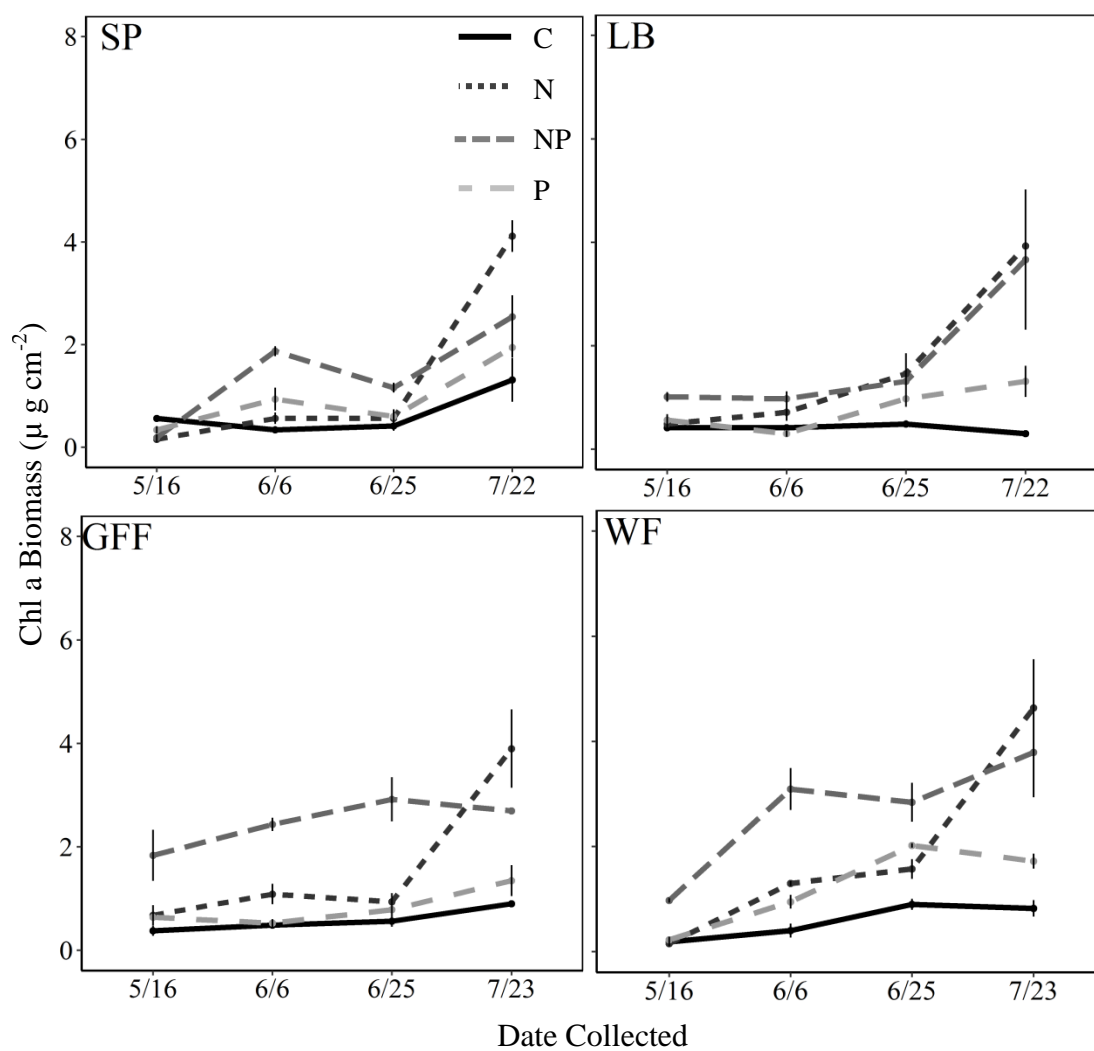


Figure 3.9. Chlorophyll a biomass related to four nutrient treatments retrieved after two weeks in the St. Croix River at spawning habitat sites in 2015. Exact dates each array was retrieved are on x-axis.

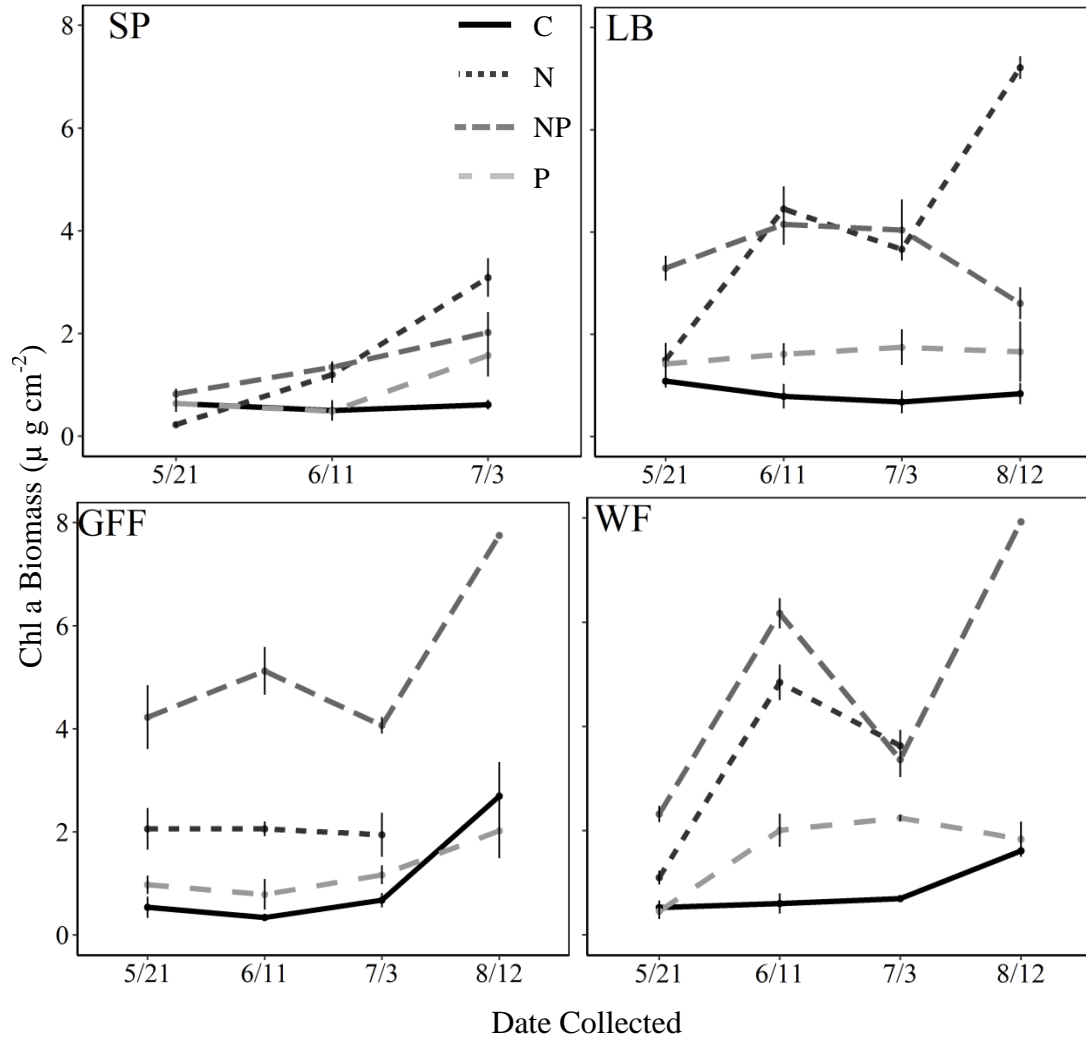


Figure 3.10. Chlorophyll a biomass related to four nutrient treatments retrieved after three weeks in the St. Croix River at spawning habitat sites in 2015. Exact dates each array was retrieved are on x-axis. After retrieval, new arrays were placed at the sites.

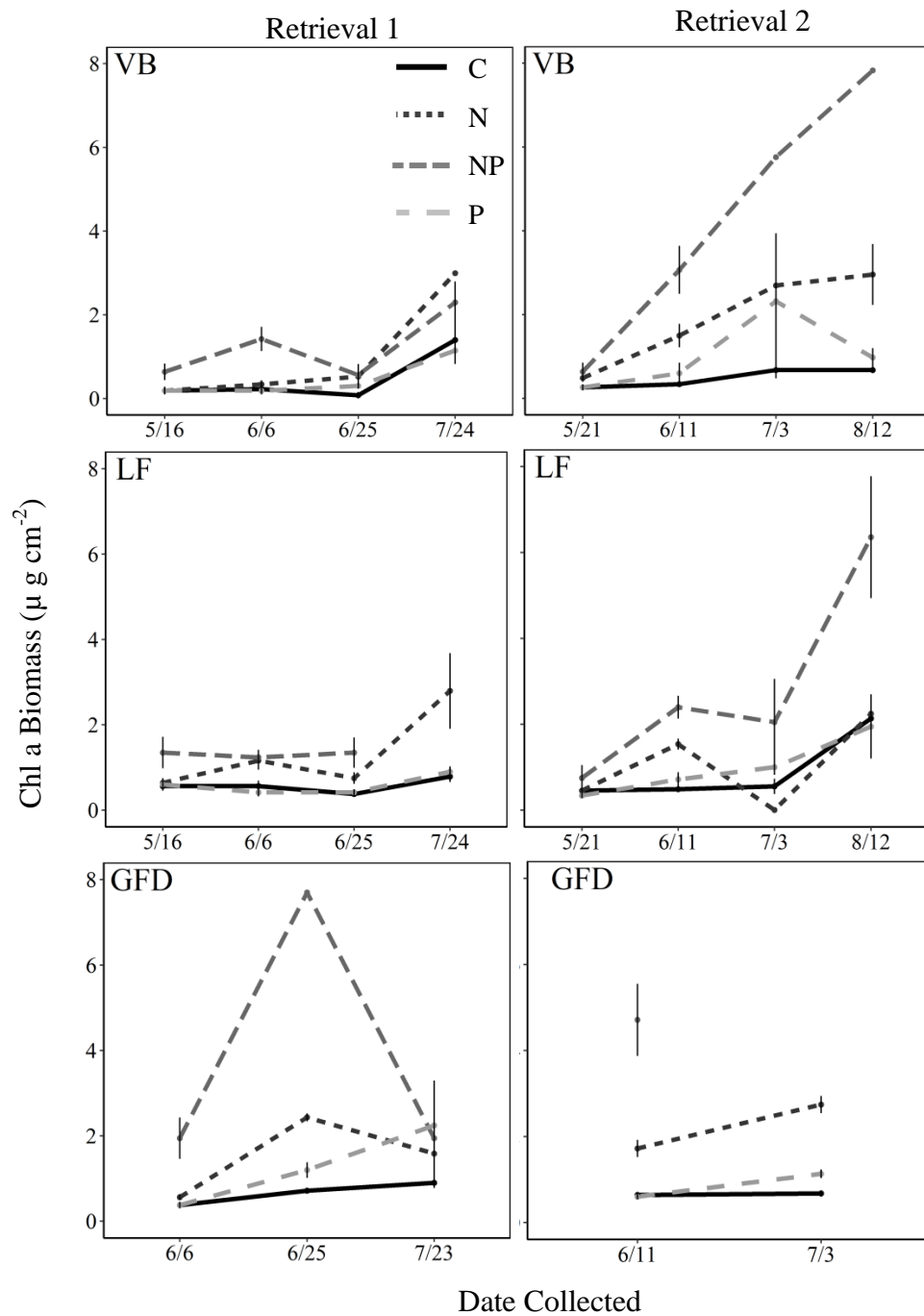


Figure 3.11. Chlorophyll a biomass related to four nutrient treatments measured in the St. Croix River at sites with potential passage delays in 2015. A set of two arrays deployed at the same time was paired by retrieval date, with Retrieval 1 collected after two weeks in the water (left panels) and Retrieval 2 after three weeks (right panels). Exact dates each array was retrieved are on x-axis.

3.5. Discussion

3.5.1. General Patterns of Nutrient Limitation

The same general pattern in baseline nutrient limitation occurred within a watershed regardless of habitat type. While NP addition led to the highest chlorophyll *a* biomass of the four treatments, for most site and time combinations the NDS results indicated independent co-limitation. Here, additions of either N or P increased algal biomass in relation to the control treatments, but NP additions increased growth even further (Harpole et al. 2011). However, N additions led to increased chlorophyll *a* biomass levels more often than P additions. This suggests that, in general, sites in both watersheds are primarily limited by N availability and secondarily by P. This was surprising as ambient total dissolved phosphorus and orthophosphate levels at sites were very low, meaning N:P values were high and phosphorus should be limiting. The sites furthest upstream had the highest N:P, but differences were not large between sites and standard errors were wide.

Both watersheds had similar spatial and temporal trends in nutrient limitation, and previous studies employing NDS arrays indicate similar levels of variability (Sanderson et al. 2009a; Marcarelli et al. 2014). Ambient N and P limitation may vary annually or within a year at a given site, affecting the relative influence of nutrient additions (Sanderson et al. 2009a). Site-specific limitations have been attributed to an assortment of factors, including anthropogenic land use, sediment nutrient retention, and rates of denitrification (Downing & McCauley 1992; Welch & Cooke 1995; Carpenter et al. 1998). Algal growth is also determined by light availability and temperature, which can vary annually (Sanderson et al. 2009a). In the St. Croix River, seasonal trends indicated

a general increase in primary productivity from May to June, then constant levels or a decrease into late July, followed by an increase in growth for the last retrieval date in August. This trend is especially pronounced when grouping NDS results by retrieval date. These trends could have to do with the release rate of nutrients from the diffusers which are affected by higher temperatures (Rugenski et al. 2008), but are more likely the result of increased natural productivity in the river and increased flow rates in the fall.

3.5.2. Lentic vs. Lotic Sites

Although there were no differences between the habitat types, there were general trends in algal growth that were more distinct at lake sites than at sites on the main-stem river (interactions table). For lake sites, chlorophyll *a* biomass accumulation was similar between the control treatment and the P addition. At these sites the NP and N additions resulted in consistently similar algal growth, which was greater than the control and P treatments. This indicated sequential limitation, first assuaged through N additions and then further alleviated when both N and P were provided. This separation was generally seen for all sampled time periods at the lentic sites, indicating less variability in nutrient availability than at lotic sites, where higher flow rates would lead to faster turnover and downstream movement of nutrient subsidies.

Ambient nutrient limitation within the watershed also reflected location and season. In May, upstream sites generally had higher N and P levels than downstream sites, though the magnitude differed between years. By September the sites furthest downstream, which received higher anthropogenic influences from surrounding towns, had the highest N and P levels. The N:P ratio within a site remained fairly consistent regardless of date, indicating relatively stable nutrient input and cycling.

3.5.3. Influence of Alewives

The two sites sampled in the East Machias, one with alewife present and one without, indicated marked differences in annual trends. However, this may have been partly due to an abbreviated sampling season in 2014 as compared to 2015. In 2014, deployment timing for NDS arrays was not lined up as well with the alewife run as it was in 2015. However, sampling in 2014 was still concentrated toward the end of May and beginning of June, which likely bracketed the peak of the alewife run. For this year, nutrient additions did not lead to statistically significant differences between the two sites, though NP co-limitation seemed higher at the non-alewife site across three of the four time periods.

In 2015, time periods in May and June that coincided with the peak of the alewife run in Maine indicated low algal growth with nutrient additions and higher growth in the control treatment. For these time periods, at least one nutrient treatment had lower algal growth than the control. These results are in line with the alleviation of nutrient limitation, as has been seen related to salmon MDN subsidies (Ruegg et al. 2011). The same time periods had high NP nutrient limitation at the non-alewife site, indicating that limited algal growth at the alewife site was not simply a seasonal trend. By July, NP limitation was seen at both sites. This indicates that if nutrient alleviation is due to alewife input, it occurs over a relatively short time period.

The low ambient nutrient levels measured at the alewife site compared to the non-alewife site could also be due to differences in productivity between the two streams. It is possible that biological demand at the alewife site was high, and any N or P that became available was quickly sequestered (Kohler et al. 2012). Previous studies

involving Pacific salmon runs have seen an increase in stream water nutrient concentrations (Welch et al. 1998; Mitchell & Lamberti 2005). In addition, invertebrate grazing could suppress algal growth on the filters, leading to a lower measured biomass.

The alleviation of nutrient limitation has been documented in other studies exploring the effect of large fish migrations on freshwater communities. Marcarelli et al. (2014) found N limitation associated with biofilm accrual decreased with Steelhead and Chinook salmon carcass additions but not with fish meal carcass analogs in central Idaho streams. The presence of migratory salmon in streams in southeast Alaska led to the alleviation of nutrient limitation in autotrophic biofilm communities (Ruegg et al. 2011). In New Brunswick and Nova Scotia, algal abundance increased in streams with alewife, Atlantic salmon, and rainbow smelt (Samways et al. 2015). However, nutrient inputs do not always lead to increases in autotrophic community biomass (Moore & Schindler 2004). In six side channels of the Elwha River, WA, salmon carcass additions did not lead to reductions in N and P limitation in algal growth (Morley et al. 2016). In this study, seasonal variation in nutrient dynamics had a greater influence than carcass additions (Morley et al. 2016). Species-specific variation in nutrient limitations can determine the relative effect that MDN inputs have on a particular freshwater community (Ballantyne IV et al. 2008). In addition, species may adapt within a particular community to take advantage of nutrient “niches” in order to co-exist with site-specific nutrient limitations (Gorban et al. 2011; Harpole et al. 2011).

Nutrient additions associated with spawning long nose suckers indicated that eggs and excretion were the primary source of N and P, rather than carcasses (Childress & McIntyre 2015). Excretion was likely the most influential MDN input at the alewife site

in the current study, as the holding pen for a commercial fishery was located directly upstream of the sample area. This, in addition to migratory delays associated with a small dam at the outlet of the lake likely led to high levels of excretion inputs over a short period of time. Excretion inputs are immediately bioavailable for uptake by primary producers (Morley et al. 2016), and so this pathway may be important in oligotrophic streams when a large alewife run is present.

Our study indicated that MDN input due to alewife presence potentially alleviated the nutrient limitation of the algal community. However, this was not seen for both years of the study, highlighting temporal variability in the dynamics of nutrient import. Annual differences in flow rates, site-specific baseline limitations, anthropogenic inputs, and spawner abundances can affect the retention of nutrient additions. Despite high alewife density, algal growth on the control treatment was low, suggesting that in northern Maine these nutrient subsidies may play a smaller role than temperature in regulating stream productivity. However, lake habitats with low turnover rates are more likely to retain nutrient subsidies, and so the influence of alewife input could be higher at spawning sites. The results from this study can be used as a baseline to monitor alewife MDN input in the St. Croix River as the population recovers to help address concerns about nutrient subsidies.

CHAPTER 4

DOES WHAT GO UP ALSO COME DOWN? USING A RECRUITMENT MODEL TO BALANCE ALEWIFE NUTRIENT IMPORT AND EXPORT

4.1. Chapter Abstract

Migrating adult alewives are a source of marine-derived nutrients on the east coast of North America, importing nitrogen and phosphorus into freshwater habitats. Juvenile migrants subsequently transport freshwater-derived nutrients into the ocean. We developed a deterministic model to explore the theoretical nutrient dynamics of alewife migrations at differing spawner abundances. Net nutrient balance was calculated relative to these abundances along the spawner-recruit curve. The ecological consequences of these subsidies in a particular watershed depend on the magnitude of adult escapement relative to the habitat's carrying capacity for juveniles. At low escapement levels and assuming complete habitat access, the number of recruits produced per spawner was high and juvenile nutrient export dominated. At high escapement levels, fewer recruits were produced per spawner because recruitment is density dependent. As a result, adult nutrient import dominated. At varying levels of freshwater productivity and fisheries mortality on upstream spawners, this trend remained the same while the magnitude of the endpoints changed. Productivity level was the major determinant of export, while fisheries mortality had the strongest effect on adult import. The dynamics of this nutrient tradeoff are important for managers to consider as a recovering population will likely

shift from net export to net import as escapement increases. This transition will be sensitive to harvest rates and to fish passage efficiency at dams and other barriers.

4.2. Introduction

In freshwater systems nitrogen and phosphorus concentrations are major determinants of primary production rates (Vanni 2002; Allan 1995; Durand et al. 2011), and net ecosystem production can increase or decrease based on the relative availability of these nutrients. Anadromous species that migrate from the ocean into freshwater to spawn can affect resident ecosystems by supplying pulsed inputs of energy and marine-derived nutrients (MDN) that enter the food web through direct consumption of carcasses and gametes or indirectly through excretion (Bauer & Hoyer 2014; Childress et al. 2014). This can be particularly important in temperate regions where marine habitats are often more productive than freshwater habitats and anadromous fish exhibit rapid growth in the ocean (Gross et al. 1988). While these inputs are important to the innate functioning of a system, the dynamics of import and export have not been fully explored.

Anadromous fish have complex interactions with their environment, and the ecological effects of these species on freshwater communities can be difficult to study because of the transient nature of their influence. In freshwater systems, nutrient limitations and responses to shifts in biologically available nitrogen and phosphorus (N and P throughout) are dynamic, changing spatially and temporally. Within a site, different plant and algal taxa have distinct nutrient requirements, and often the N:P ratio of the environment influences the relative dominance of different algal groups (Klausmeier et al. 2004; Allan 1995). Competition for allochthonous resources can

therefore affect food web structure, influencing nutrient control through both bottom-up and top-down pathways (Huxel et al. 2002; Wood et al. 2016).

The influence of marine-derived nutrient input on freshwater systems has been explored in semelparous species such as Pacific Salmon (*Oncorhynchus* spp.) that leave carcasses in streams to decay (for reviews, see Cederholm et al. 1999; Naiman et al. 2002; Schindler et al. 2003). In the Columbia River watershed, Pacific Salmon contribute roughly 3,000 metric tons of nitrogen and 360 metric tons of phosphorus per year (Moore & Schindler 2004). Carcasses and gametes are incorporated slowly throughout the season as they are broken down and nutrients become bioavailable. Such additions increase primary production (Richey et al. 1975; Cederholm et al. 1999), biofilm growth (Wipfli et al. 1998), macroinvertebrate density (Piorkowski 1995; Minakawa et al. 2002; Wipfli et al. 1998) and fish growth (Bilby et al. 1996). Studies on other semelparous species such as Sea Lamprey (*Petromyzon marinus*) have demonstrated that the nutrient input released by carcasses is incorporated by stream macroinvertebrate and algal communities at a local scale (Guyette et al. 2014; Weaver et al. 2016a).

All of the anadromous fish species that were historically present along the northeast coast of North America are severely depressed from historic numbers (Saunders et al. 2006). Of these species, alewives (*Alosa pseudoharengus*) are the most abundant and have the highest potential for population restoration. Alewives exhibit a north-south gradient in life history traits, with high rates of iteroparity occurring throughout New England's watersheds (Bozeman & Van Den Avyle 1989). Alewives have a high reproductive potential, and a small number of returning adults can produce a large

number of offspring (Gibson & Myers 2003). Density-dependent processes limit the number of recruits that a given habitat can produce such that the number of recruits will plateau regardless of additional spawners (Gibson & Myers 2003). Thus density-dependent production of juvenile alewives, as illustrated by a spawner-recruit (SR) curve, can be a major determinant of net nutrient flow. A population with low spawner density will deliver fewer nutrients but have a higher per capita rate of juvenile production that would drive greater export, resulting in a negative net nutrient flow (Moore & Schindler 2004; West et al. 2010). As spawner biomass increases, upstream nutrient transport is expected to increase in proportion to spawner biomass. As the habitat available for juvenile alewives is more fully utilized, nutrient export is expected to continue to increase. However, the rate of export per capita would be expected to decrease as juvenile abundance approaches carrying capacity. Thus, as spawner abundance increases, a shift to a net positive flow might be expected (Nislow et al. 2004). West et al. (2010) demonstrated this trend when estimating P dynamics during recovery of an alewife population to a small pond (9.4 ha) in Connecticut. They modeled a measured low juvenile survival rate (6.39 juveniles/spawner) and found export to be negligible. However, when they modelled a higher hypothetical rate (63.9 juveniles/spawner) they found that P export dominated until escapement reached roughly 6,500 adults, after which P import became large enough to outweigh juvenile export.

For alewife populations, excretion may be the most influential input (West et al. 2010) because inorganic forms of nutrients are available for immediate uptake by primary producers. Smaller fish have higher mass-specific nutrient excretion rates, meaning alewives could contribute a higher nutrient load to a site per unit biomass through

excretion than Atlantic Salmon (Twining et al. 2017). Alosines also likely produce more N through excretion and more P through gametes and carcasses (Twining et al. 2017). Adult nutrient import to freshwater systems is coincident with increased freshwater aquatic ecosystem metabolism early in the year (Levi et al. 2013; Samways & Cunjak 2015). Even if the autumnal juvenile exodus results in a net zero nutrient gain or loss for the system, this pulse of nutrients would boost primary productivity in the spring when other sources of input are limited.

Previous studies have modelled the net nutrient balance of alewife populations and have estimated recruitment for specific lakes and streams, but the inputs used were site-specific (Durbin et al. 1979; Walters et al. 2009; West et al. 2010), which hinders the direct comparison of the results. Variability in spawner escapement, mortality rates, and input pathways led to a wide range in annual estimates. Walters et al. (2009) used a high spawner density ($4\text{--}8 \text{ spawners}\cdot\text{m}^{-2}$), low mortality (0.1%), and used excretion and carcasses as the primary source of N and P as the study site was a small stream. Mortality was higher for studies conducted in lake habitats as nutrient sources were primarily from carcass and gamete inputs. Both Durbin et al. (1979) and West et al. (2010) used a lower spawning density ($0.9 \text{ spawners}\cdot\text{m}^{-2}$ and $0.3 \text{ spawners}\cdot\text{m}^{-2}$, respectively) and a higher mortality rate (37.5% and 56%, respectively). These different scenarios resulted in a range of N input from $63.6 \text{ mg}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ to $2700 \text{ mg}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ and P input from $7.4 \text{ mg}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ to $430 \text{ mg}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$. Even when comparing the two lake studies, input calculations varied as they used the same estimate of P concentration for carcasses, but different estimates for excretion and gametes. Both Durbin et al. (1979) and West et

al. (2010) calculated juvenile export, but concluded it was negligible when compared to adult delivery given the escapement level at the time of study.

These previous efforts highlight the wide variability seen in alewife populations related to estimates of spawner density and mortality rates. While they focused on nutrient dynamics related to an established spawning run, many questions remained with respect to how deviations in population input affect restoration and growth. This study was developed to explore how variation in alewife population levels could theoretically affect nitrogen and phosphorus dynamics related to adult import and juvenile export. To answer this, we developed a deterministic population dynamics model that was linked to estimates of nutrient delivery by adults and export by juveniles. We then used this model to explore how nutrient dynamics would be expected to: 1) differ as a function of spawner abundance; 2) to change through the process of population growth; 3) to vary among watersheds with different carrying capacities; and 4) to vary with different levels of in-river fishing mortality.

4.3. Methods

4.3.1. Model Overview

The model developed for this study included two main components: *i*) population dynamics, and *ii*) nutrient import and export. Several examples of age-structure population models have been developed specifically for river herring (Gibson & Myers 2003; ASMFC 2012), but these do not estimate juvenile abundance directly and so could not be used to calculate export. For the population component, fish were moved through the life cycle using a stepwise annual progression. Stocks in the ocean entered freshwater to spawn and produce juveniles. A proportion of these survived to “graduate” into

juveniles which then became part of the ocean population, completing the cycle (Figure 4.1). This deterministic model did not include any measure of environmental stochasticity, and the population was assumed to be unimpacted by connectivity issues to explore fundamental patterns in nutrient dynamics.

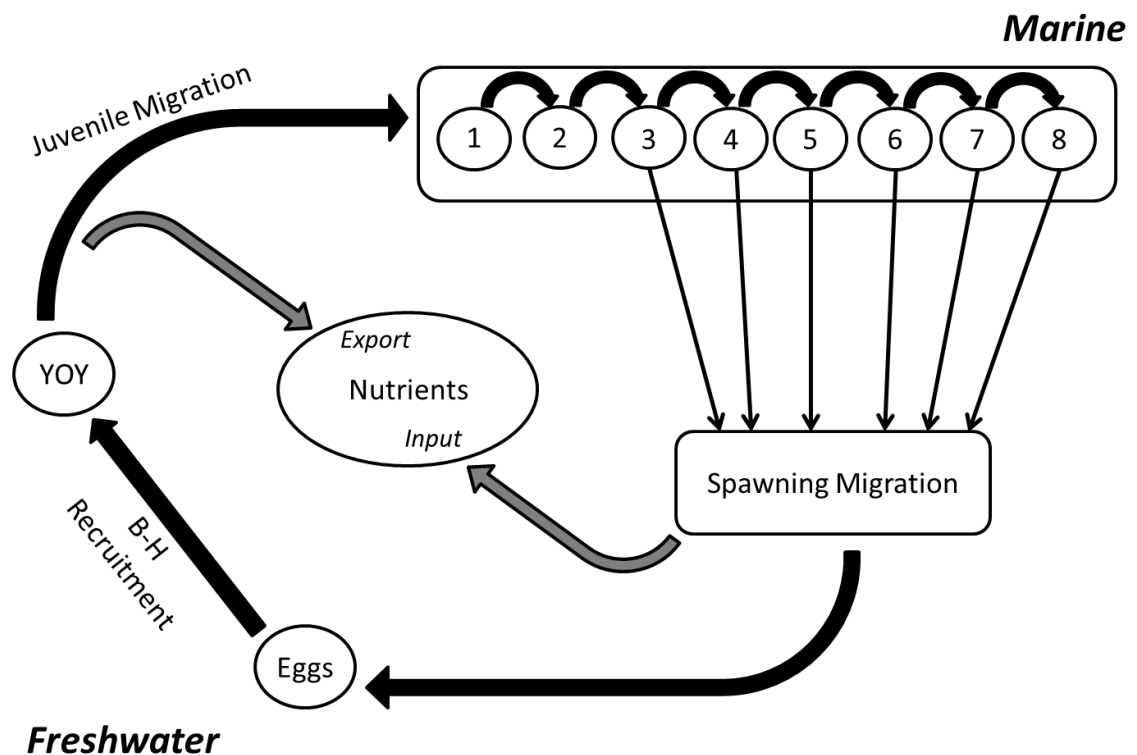


Figure 4.1. Basic structure of deterministic alewife population model. For each annual timestep, ocean population Ages 2-7 mature and enter the spawning run. These fish move into spawning habitat where they lay eggs that hatch, with survivors entering the YOY age class. Nutrient dynamics are calculated in the model through adult import (carcasses, gametes, excretion), and YOY nutrient export.

4.3.2. Forward-Projecting Population Model

The forward-projecting population model consisted of a series of equations for each life history stage. Egg production for a given year t , $N_{eggs,t}$, is calculated using the number of females that survived to spawn multiplied by the fecundity relationship as below:

$$N_{eggs,t} = \sum_{a=3}^8 [S_t (e^{-M_{spawn} \cdot 0.25}) \cdot 0.5] * F_a,$$

in which S_t is the total number of fish in the spawning population in year t (described below), M_{spawn} is the probability of mortality associated with the spawning run prorated for 3 months (or 0.25), ϕ is the probability of spawning after fish mature, 0.5 is the assumed female:male ratio, and Fa is the fecundity relationship (Table 4.1). For this model, mortality associated with the spawning run was assumed to occur before spawning such that only females that survived contributed to egg production.

Table 4.1. Population inputs used in alewife model, including those taken from the literature and those estimated from the St. Croix (SC) Milltown Trap Data (1981-2016).

Parameter	Value	Description	Data Source
<i>Forward-Projecting Population Model</i>			
M_T	0.85	Instantaneous natural mortality rate	ASMFC 2012; Gibson 2004
M_{spawn}	2.391	Instantaneous mortality rate Ages 3-8	Kissil 1974; Durbin 1979
M_{ocean}	0.648	Instantaneous mortality rate Ages YOY-8	Iteratively calculated
ϕ	0.95	Probability of Spawning Ages 3-8	Bailey and Zydlewski 2013
F_a	y=bx-c	Fecundity relationship	SC Milltown Trap
\tilde{R}_{asy}	51.4	Asymptotic recruitment level (t/km ²)	Gibson 2004
$\tilde{\alpha}$	2.96	Log maximum lifetime reproductive rate	Gibson 2004
m_3	0.35	Maturity between Ages 2-3	Gibson and Myers 2003a
m_4	0.51	Maturity between Ages 3-4	Gibson and Myers 2003a
m_5	0.96	Maturity between Ages 4-5	Gibson and Myers 2003a
m_6-m_8	1.0	Maturity from Age 6 to Age 8	Gibson and Myers 2003a
<i>Parameter Value Derivation</i>			
α	0.0015	Lifetime reproductive rate	Gibson 2004
	0.0017	10 th Percentile	
	0.0022	90 th Percentile	
R_{asy}	3283	Asymptotic recruitment level (YOY/acre)	Gibson (pers. comm.)
	1917	10 th Percentile	
	5626	90 th Percentile	
b	871.72	Fecundity slope	SC Milltown Trap
c	50916	Fecundity Intercept	SC Milltown Trap
W_3	0.144	Mass Age 3 (kg)	SC Milltown Trap
W_4	0.186	Mass Age 4 (kg)	SC Milltown Trap
W_5	0.209	Mass Age 5 (kg)	SC Milltown Trap
W_6	0.244	Mass Age 6 (kg)	SC Milltown Trap
W_7	0.277	Mass Age 7 (kg)	SC Milltown Trap
W_8	0.353	Mass Age 8 (kg)	SC Milltown Trap

The number of juveniles produced in a year class was modelled as a density dependent process, which was characterized using a spawner-recruit (SR) relationship. The choice of SR curve can affect the dynamics of the recruitment rate as the spawning population increases, which can in turn affect net nutrient balance through time (Elliott 1985; Needle 2001; Subbey et al. 2014). While there are many different types of SR curves used in fish population modelling (Hilborn & Walters 1992) and the Ricker curve has been used to explore the alewife SR relationship (Tommasi et al. 2015), the Beverton-Holt (BH) curve was used for this model because Gibson (2004) found it provided a better fit to the data for eight alewife populations in the northern part of their population range than did the Ricker, and that the data available for these populations were not sufficient to fit a three parameter model. The BH curve was used to model a density-dependent relationship in the population model by tying egg production to juvenile production (J_t) as follows:

$$J_t = \frac{\alpha N_{eggs,t}}{1 + \frac{\alpha N_{eggs,t}}{R_{asy}}}$$

Here, juvenile abundance was calculated for year t based on the total number of eggs for year t ($N_{eggs,t}$), the asymptotic recruitment level (R_{asy}), and the maximum number of juveniles given the average fecundity per unit mass at the origin of the SR relationship (α).

The population of immature fish in the ocean was divided into age classes between Age-0 and Age-8 fish, each with an associated instantaneous mortality rate for fish in the ocean, M_{ocean} , and probability of maturing at that age, m_a (Table 4.1). The

ocean population was linked to juvenile production in freshwater by setting the number of Age-0 fish in the ocean population in year t , $O_{0,t}$, equal to the number of juveniles produced in that year:

$$O_{0,t} = J_t.$$

Abundance of immature fish in other age classes was calculated by projecting the abundance forward using the mortality rates and maturity probabilities:

$$O_{a+1,t+1} = O_{a,t} e^{-M_{ocean}} (1 - m_{a+1}).$$

Immature fish between Age-2 and Age-7 also had a probability of maturing, which allowed them to enter the spawning run the next year (Ages 3-8), with survival occurring between spawning year classes. For age a and year t , first-time spawners ($S_{a+1,t+1,0}$) and repeat spawners ($S_{a+1,t+1,p+1}$) that spawned p times previously were calculated as follows:

$$S_{a+1,t+1,0} = O_{a,t} e^{-M_{ocean}} (m_{a+1})$$

$$S_{a+1,t+1,p+1} = \varphi S_{a,t,p} e^{-[M_{ocean} \cdot 0.75 + M_{spawn} \cdot 0.25]} + (1 - \varphi) S_{a,t,p} e^{-[M_{ocean}]}$$

Each year class had an associated probability of spawning (φ), which was separate from the probability of maturing and allowed those individuals that did not successfully spawn to return to the ocean.

Mortality rates were used in several population equations, and total natural mortality for mature spawners was split into ocean mortality (M_{ocean}) and spawning mortality (M_{spawn}) to estimate carcass nutrient inputs. The instantaneous natural mortality rate for adults was reported as 1 by Gibson and Myers (2003a) and an average rate of 0.7

was reported by the ASMFC (2012), and so an instantaneous rate of 0.85 was used in this study. A range of interval spawning mortality was reported in both Kissil (1974) and Durbin (1979). The average of those reported values (45%) was used to calculate an instantaneous spawning mortality rate. The ocean mortality rate was then calculated as the difference between total mortality and spawning mortality rates (Table 4.1). Ocean mortality was iteratively adjusted based on age-class proportions and probabilities of spawning such that the product of M_{ocean} and M_{spawn} was equal to the total mortality rate. M_{ocean} was applied as an annual rate to both immature fish and the small percentage of individuals that did not successfully enter the river to spawn ($1-\phi$). Only the ocean mortality rate was used to project their abundance forward, whereas a higher mortality rate associated with spawning, M_{spawn} , was included for fish that spawned successfully. M_{ocean} was prorated to 9 months and M_{spawn} to 3 months to reflect the timing of the alewife spawning run.

The total number of fish in the spawning population in year t (S_t) was calculated as:

$$S_t = \sum_{a,p} S_{a,t,p} \phi.$$

The number of spawners was used to calculate egg production, thereby closing the loop for calculating population dynamics associated with each portion of the alewife life history.

4.3.3. Parameter Value Derivation

The equations in the forward-projecting population model required the derivation of multiple parameters. We based the alewife population for this “Model River” on data from the St. Croix watershed, which forms the northeast border between Maine and New Brunswick. Morphometric information collected from the St. Croix River (1981-2016) was used as inputs for mass and fecundity (Table 4.1; St. Croix Milltown Trap 1981-2016). For mass-at-age, an average mass was calculated for each age class combining males and females. Maturity rates were averaged from Gibson and Myers (2003a, Table 4.1). Spawner-recruit parameter derivation was taken from the alewife model developed by Gibson (2004) based on multiple alewife populations in northeastern North America. Parameters of the SR curve were adjusted based on the habitat amount, which for this study was set arbitrarily at $4.047 \times 10^6 \text{ m}^2$ or 1,000 acres. So while the underlying population information was taken from the St. Croix River, the model results presented here are for a theoretical “Model River”.

Four parameters were used in the calculation of the egg deposition from the number of spawners. The probability of spawning was kept constant for all ages at 95%, the sex ratio was assumed to be 50%, and spawning mortality was calculated for 3 months as described above. Fecundity slope and intercept were calculated using a linear regression with average mass-at-age and corresponding average gonad mass-at-age recorded from the St. Croix River (St. Croix Milltown Trap 1981-2016). For each female with a recorded ovary mass, the total egg mass was calculated by subtracting a spawned gonad mass from an unspawned gonad mass with the assumption that the former represented the mass of just the organ itself. The spawned gonad weight was an average

mass from 14 downstream migrants from the St. Croix River. A total egg count for each fish was then calculated by multiplying the total egg mass by $7,890 \text{ eggs} \cdot \text{g}^{-1}$ (Kissil 1974). This led to an average of ~130,000 eggs per female (range: 5,050 - 305,659 eggs). The total number of eggs per fish then was regressed against mass to get a slope and intercept that was used to estimate average egg production for each age class. This was done to account for differences in fecundity with the age of the fish when calculating the total number of eggs produced in a given year. A linear regression function provided the best fit to the data ($R^2 = 0.66$; $y = 871.72x - 50916$) when compared with an exponential ($R^2 = 0.4711$), a logarithmic ($R^2 = 0.63$), and a power function ($R^2 = 0.51$), though the difference was small.

Juvenile production involved an estimate of density-dependent survival using a Beverton-Holt SR relationship. Two parameters were derived for this equation in addition to egg deposition: R_{asy} and α , neither of which are available for the St. Croix River alewife population. These two parameters were both calculated from the results of a meta-analysis of the dynamics of alewives based on eight populations in the northern part of their distribution ranging from Rhode Island, USA to Nova Scotia, Canada (Gibson 2004). Following the approaches of Myers et al. (1999) and Myers et al (2001), Gibson (2004) standardized the data prior to analysis to produce probability distributions for the maximum lifetime reproductive rate ($\tilde{\alpha}$), and the asymptotic recruitment levels in terms of the spawning population size (\tilde{R}_{asy}). For his analysis, Gibson defined the age-of recruitment as Age-3. For our analysis, the relationship was rescaled from Age-3 recruits and SSB to juveniles and egg production in order to calculate nutrient parameters. R_{asy}

was the asymptotic recruitment level in terms of number of juveniles, and was calculated as follows:

$$R_{asy} = \frac{\frac{\tilde{R}_{asy}}{SPR_{F=0}}}{(e^{-M_{ocean}*3})}.$$

M_{ocean} is multiplied by 3 because the age of recruitment was defined as 3 years in Gibson's meta-analysis (2004). \tilde{R}_{asy} was divided by the spawning biomass per recruit in the absence of fishing mortality ($SPR_{F=0}$). This value represented the rate at which Age-3 recruits produce spawners throughout their lives (Gibson 2004) and can be calculated for a specific population as follows:

$$SPR_{F=0} = \sum_{a=3}^8 SS_a W_a,$$

in which SS_a = spawning stock for a given age class and W_a is the average mass for each age class. Each year class contribution reflected *i*) probability of maturity, *ii*) cumulative adult mortality and *iii*) juvenile mortality such that:

$$SS_3 = m_3$$

$$SS_4 = SS_3 e^{-M_{adult}} + (1 - m_3) e^{-M_{juv}} m_4$$

$$\vdots$$

$$SS_8 = SS_7 e^{-M_{adult}} + (1 - m_3)(1 - m_4)(1 - m_5)(1 - m_6)(1 - m_7) e^{-5M_{juv}} m_8,$$

in which M_{adult} = instantaneous mortality rate of mature fish, M_{juv} = instantaneous mortality rate of immature fish, and m_a = probability that immature fish alive at age a will

mature at that age (Gibson 2004; Table 4.1). For this paper, an average SPR was used from Gibson's meta-analysis ($SPR_{F=0}$: 0.357 kg/recruit; 2004).

The alpha value (α) is the slope of the origin for the SR curve, and was calculated similarly. Gibson (2004) provided a probability distribution for the maximum lifetime reproductive rate ($\tilde{\alpha}$), expressed in units of spawners/spawner, which was first divided by SPR in the absence of fishing mortality to calculate the number of Age-3 recruits per unit spawner biomass and then by $M_{ocean} \cdot 3$ to convert the units of recruitment to number of juvenile fish:

$$\alpha = \frac{\frac{\tilde{\alpha}}{SPR_{F=0}}}{(e^{-M_{ocean} \cdot 3})}.$$

A second standardization was required to change from units of spawner biomass to the number of eggs. SSB_t was calculated for each year of the model based on the number of fish in the spawning population as follows:

$$SSB_t = \sum_{a=3}^8 \sum_{p=1}^5 S_{a,t,p} W_a,$$

in which for each year t , $S_{a,t,p}$ is the number of fish of age a that have spawned p times and W_a is the mass at age a (Gibson, AJ and Myers 2003). The model was run with a habitat size of $4.047 \times 10^6 \text{ m}^2$ for 300 years to allow the population to stabilize, and outputs then were used to iteratively estimate the α value that described the slope at the origin of the SR curve that related egg and juvenile production.

4.3.4. Nutrient Model

The second component of the model calculated nutrient import and export. We assumed that adults were not feeding while in freshwater so that nutrient import was solely from the marine environment. Total N or P inputs (I_t) were calculated for year t based on total carcass inputs (C_t), total gametes produced by both males and females (G_t), and total excretion rates (E_t) for year t as follows:

$$I_t = C_t + G_t + E_t.$$

4.3.4.1. Carcasses

Total carcass input for each year t (C_t) was calculated using separate N and P values for somatic and gonad tissues, which differ in elemental composition (Durbin et al. 1979), with the assumption that alewives die before spawning. For both tissue types, total wet mass from carcass inputs was calculated for year t using separate mass-at-age for males and females:

$$C_t = C_{Somatic,f,t} + C_{Somatic,m,t} + C_{Ovaries,t} + C_{Testes,t},$$

in which $C_{Somatic,f,t}$ = female somatic input, $C_{Somatic,m}$ = male somatic input, $C_{Ovaries}$ = ovary input, and C_{Testes} = testes input. Male and female mass-at-age, ovary mass-at-age, and testes mass-at-age were calculated using data collected from the St. Croix River (St. Croix Milltown Trap 1981-2016; Table 4.2). For this dataset, 563 fish were aged using scales and corresponding gonad weights were recorded (306 females and 257 males). For each individual fish gonad mass was subtracted from total mass to get a somatic mass. These were averaged by age class and sex to calculate somatic input, and total carcass input was calculated as follows:

$$C_{Somatic,f,t} = [\sum_{a=3}^8 (S_{a,t} (1 - e^{-M_{spawn} \cdot 0.25}) \cdot 0.5) \cdot W_{Somatic,f,a}] \cdot DW_{Somatic} \cdot n_{Somatic},$$

$$C_{Somatic,m,t} = [\sum_{a=3}^8 (S_{a,t} (1 - e^{-M_{spawn} \cdot 0.25}) \cdot 0.5) \cdot W_{Somatic,m,a}] \cdot DW_{Somatic} \cdot n_{Somatic},$$

$$C_{Ovaries,t} = [\sum_{a=3}^8 (S_{a,t} (1 - e^{-M_{spawn} \cdot 0.25}) \cdot 0.5) \cdot W_{Ovaries,a}] \cdot DW_{Ovaries} \cdot n_{Ovaries},$$

$$C_{Testes,t} = [\sum_{a=3}^8 (S_{a,t} (1 - e^{-M_{spawn} \cdot 0.25}) \cdot 0.5) \cdot W_{Testes,a}] \cdot DW_{Testes} \cdot n_{Testes},$$

in which $S_{a,t}$ = number of spawners at age a for year t , M_{spawn} is the instantaneous mortality rate due to spawning calculated for 3 months (0.25), $W_{Somatic,f,a}$ = average somatic mass of females age a , $W_{Somatic,m,a}$ = average somatic mass of males age a , $DW_{Somatic}$ = the wet mass to dry mass conversion for somatic tissue, $n_{Somatic}$ = percent dry mass content of nitrogen or phosphorus for somatic tissue, $W_{Ovaries,a}$ = average ovary mass for age a , $DW_{Ovaries}$ = wet mass to dry mass conversion for ovaries, $n_{Ovaries}$ = percent dry mass content of nitrogen or phosphorus for ovaries, $W_{Testes,a}$ = average testes mass for age a , DW_{Testes} = wet mass to dry mass conversion for testes, and n_{Testes} = percent dry mass content of nitrogen or phosphorus for testes (Durbin et al. 1979).

Table 4.2. Nutrient inputs used in alewife model. Data sources indicated below. Mass is in g unless otherwise indicated. Values in parentheses are the number of fish sampled from each age class. DW/WW is the dry mass to wet mass conversion. Columns labelled 3-8 indicate age-specific values, otherwise value used for all age classes.

Carcass	3	4	5	6	7	8
Female carcass mass*	129 (2)	171 (204)	189 (195)	247 (38)	277 (5)	311 (1)
Male carcass mass*	131 (10)	161 (212)	177 (171)	199 (32)	212 (3)	
Carcass DW/WW [‡]	0.288					
N content (% dry mass) [‡]	0.0866					
P content (% dry mass) [‡]	0.0147					
Gametes	3	4	5	6	7	8
Pre-spawn ovary mass*	15 (1)	18 (142)	21 (128)	29 (26)	31 (4)	43 (1)
Change in ovary mass*	11 (1)	14 (142)	17 (128)	25 (26)	27 (4)	39(1)
Pre-spawn testes mass*	6 (3)	6.8 (139)	9.3 (90)	10 (17)	11.8 (2)	
Change in testes mass*	4.5 (3)	5.2 (139)	7.7 (90)	8.5 (17)	10.2 (4)	
Post-spawn ovary mass*		4 (13)				
Post-spawn testes mass*		1.6 (33)				
Ovary DW/WW [‡]		0.295				
Ovary N content (% dry mass) [‡]		0.115				
Ovary P content (% dry mass) [‡]		0.0112				
Testes DW/WW [‡]		0.249				
Testes N content (% dry mass) [‡]		0.137				
Testes P content (% dry mass) [‡]		0.0354				
Excretion						
N rate (µg/g wet mass/hour) [⌈]		24.71				
P rate (µg/g wet mass/hour) [⌈]		2.17				
YOY Export						
N content (gN/g wet mass) [‡]		0.02735				
P content (gP/g wet mass) [^]		0.0058				
YOY mass ~		3.5				

*SC Milltown Trap 1981-2016 ‡Durbin et al. 1979 ⌈ Post and Walters 2009 ~ Havey 1973 ^ West et al. 2010

4.3.4.2. Gametes

Total gamete contribution for year t (G_t) was calculated separately from carcass gamete contribution to account for the difference between spent and unspent gonad mass. Gamete contribution included sperm input ($G_{Sperm,a,t}$) and egg input ($G_{Eggs,a,t}$) for age class a in year t as follows:

$$G_t = G_{Sperm,a,t} + G_{Eggs,a,t}.$$

Total female gonad mass was calculated as the age-specific ovary mass of inbound females minus the average ovary mass for outbound females so that only the spawned egg mass was included (Table 4.2). For male gamete contribution, total wet mass of sperm input for age class a ($W_{Spent,a}$) was calculated by subtracting spawned testes mass from unspawned testes mass (St. Croix Milltown Trap 1981-2016). Unspawned (inbound) testes mass was determined by age class, but spawned (outbound) testes mass was an average that combined age classes because only 33 individuals were sampled (Table 4.2).

The total contribution from sperm and eggs were calculated separately using the following equations:

$$G_{Sperm,a,t} = \sum_{a=3}^8 [(S_{a,t}(e^{-M_{spawn} \cdot 0.25})p_{a,t} \cdot 0.5) \cdot W_{Spent,a}] \cdot DW_{Testes} \cdot n_{Testes},$$

$$G_{Eggs,a,t} = \sum_{a=3}^8 N_{Eggs,a,t} \cdot W_{Egg} \cdot DW_{Eggs} \cdot n_{Eggs}.$$

Here, the total wet mass of sperm input is calculated using the number of surviving male spawners in year t and age a times the weight of spent testes for each age class. Total egg contribution involved $N_{Eggs,a,t}$ = the number of eggs from age class a for year t and W_{Egg} = average mass of 1 egg (0.1267 mg; Kissil 1974). Both sperm and egg contributions were then multiplied by a separate wet weight to dry weight conversion (DW) and the nitrogen or phosphorus percent dry mass content of each respective tissue (n) (Durbin et al. 1979).

4.3.4.3. Excretion

Total excretion inputs (E_t) were estimated for year t based on the number of fish that successfully entered the spawning habitat as well as an estimate of residence time as follows:

$$E_t = RT \cdot (E_n \cdot 24 h) \cdot SSB_t,$$

in which RT is residence time of spawning adults, E_n is the excretion rate of 24.71 $\mu\text{g N}$ or 2.17 $\mu\text{g P} \cdot \text{g wet fish mass}^{-1} \cdot \text{hour}^{-1}$ (Post & Walters 2009) multiplied by 24 hours to get a daily input, and SSB_t is the spawning stock biomass in year t . A residence time of 14 days in the river was used for each individual regardless of water temperature (Kissil 1974; West et al. 2010). While this may be a conservative estimate, this nutrient input is consistent with previous alewife studies (Post & Walters 2009; West et al. 2010; Twining et al. 2017). Alewife residence time in rivers can be ≥ 25 days (Frank et al. 2010); however, a study in the Ipswich River in Massachusetts reported an average residence time of 10 days (Frank et al. 2010).

4.3.4.4. Juvenile Export

The final portion of the nutrient balance calculations was total juvenile export from the watershed in year t , and was calculated as follows:

$$\mathbf{Export}_t = J_t \cdot W_{juvenile} \cdot n_{juvenile}.$$

Juvenile abundance in year t (J_t) was calculated as described above, and then multiplied by the average juvenile mass ($W_{juvenile}$; (1973) and the nitrogen or phosphorus content of emigrating juveniles ($n_{juvenile}$, Table 4.2). Total P export was based on a concentration of 0.0058 g P·g wet mass⁻¹ as measured in West et al. (2010). In the absence of a juvenile-specific N concentration, we estimated a value based on the measured adult content (0.02735 g N·g wet mass⁻¹; Durbin et al. 1979).

4.3.5. Sensitivity Analysis

Once values for the parameters of the model were selected, simulations were run and local sensitivity of model outputs to model parameters was evaluated. We assessed sensitivity of *i*) total ocean population, *ii*) spawning population, *iii*) Age-3 recruitment, *iv*) spawning stock biomass, *v*) import of nutrients and *vi*) export of nutrients (both N and P) to a suite of parameters. We varied mortality rates, maturity rates, stock-recruitment constants, fecundity coefficients, and demographic parameters such as mass and fork length. Analyses were performed by shifting each parameter input 1%, 10%, 15%, and 25% and evaluating model output (Bailey & Zydlewski 2013; Childress et al. 2014). When inputs had age-specific values, all of the values were increased by simultaneously for simplicity (Table 4.1). For example, ocean mortality was increased for Ages 1-7 as

opposed to increasing by each age class separately. Because probability of maturity after Age-5 was 100%, sensitivities in changes of m only influenced Ages 2-4.

The sensitivities of all major outputs to base model inputs were estimated (Table 4.2). A sensitivity index was calculated for each input change by output combination. Sensitivities were calculated as follows:

$$S = \frac{(O_i - O_n)/O_n}{(I_i - I_n)/I_n},$$

in which O_i is the output value after the input was increased, O_n is the base output value, I_i is the altered input value, and I_n is the original input value. Inputs were considered “highly sensitive” to change if $|S| > 1.00$.

4.3.6. Population Variability and Nutrient Exchange

Scenarios were run to explore among-population variability using Stella 10.0.6 (High Performance Systems, Inc., Hanover, New Hampshire). To explore changes in spawner abundance and nutrient dynamics due to variability in life history traits and habitat carrying capacity, the model was run using the 10th, 50th, and 90th percentiles of the log lifetime reproductive rate (a) and the asymptotic recruitment level (R_{asy}) measured in Gibson (2004; Table 4.1). These scenarios represented the range of realistic low, medium, and high levels of freshwater productivity for alewife populations sampled in New Brunswick, Maine, and New Hampshire (Gibson 2004). Thus each percentile represents the fraction of alewife populations that are assumed to be lower than that value (i.e. for the 10th percentile value, 10% of alewife populations are expected to have lower values while 90% would have higher values; Figure 4.2; Gibson and Myers 2003).

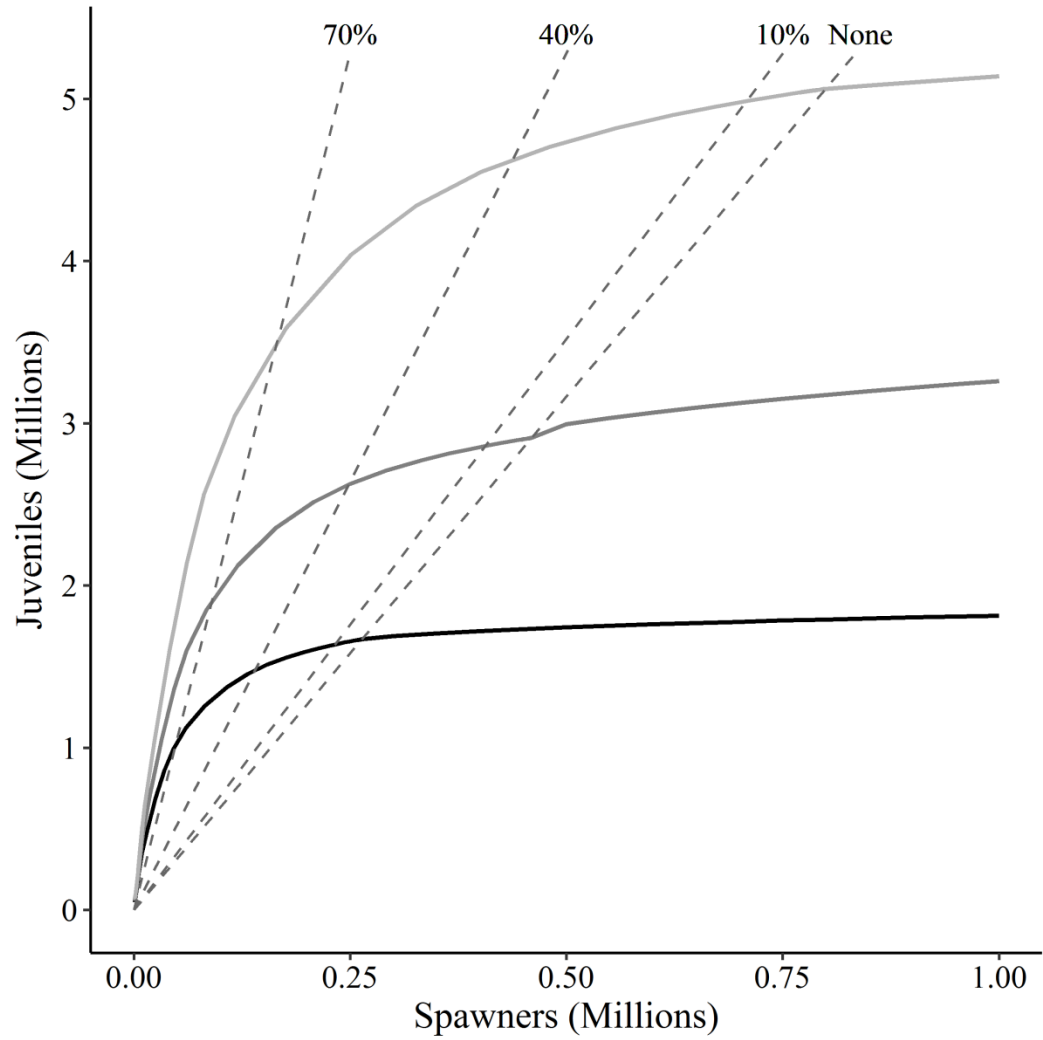


Figure 4.2. Spawner-juvenile relationship for three productivity scenarios. Scenarios involved variation in α and R_{asy} (black = 10th percentile, dark grey = 50th, light grey = 90th). Dashed lines indicate replacement lines associated with four fisheries mortality scenarios (no mortality, 10% spawner mortality, 40%, and 70%).

The combined effect of freshwater productivity and an in-river intercept fishery on nutrient dynamics was explored by comparing spawner abundance as well as net annual exchange (adult import – juvenile export, hereafter referred to as Δ) for N and P. Fishing mortality was assumed to remove a percentage of the spawning population each year after individuals matured but before they contributed reproductively to the juvenile abundance. The model was run using low (10% of the spawning run removed annually), medium (40%), and high (70%) fishing mortality ($M_{Fishery}$). Total spawner abundance after fishing mortality (SF_t) was calculated by multiplying the spawner abundance for fish of age a in year t that spawned p times previously by the survival rate as follows:

$$SF_t = \sum_{a,p} S_{a,t,p} \cdot (1 - M_{Fishery}) \cdot \varphi.$$

Each of the models with these differing levels of imposed fishing mortality was assessed at the low, medium and high productivity scenarios described above. Results for each scenario were compared graphically.

4.3.7. Model Initialization and Output Evaluation

The model was initialized with the starting spawning run size set at 1,000 adults that were distributed among age classes using the proportions-at-age from a stable population determined by simulation. The model was run for 250 years to ensure the SR relationship reached its plateau. However, the spawning population stabilized around 55 years into the model run, so only the first 100 years of data are presented in the results. Adult nutrient import, juvenile export, and Δ values were calculated annually for both N and P. Import was estimated separately for carcass inputs, excretion, and gamete inputs.

The dynamics between import, export, and net nutrient balance were evaluated in the context of spawning run size, as well as temporally for the first 30 years of the model. The shifts between these nutrient components were also evaluated between scenarios and relative to the population's location on the SR curve.

4.4. Results

4.4.1. Sensitivity Analyses

Several trends were seen in output sensitivities when inputs were increased by 1%, 10%, 15%, and 25%. An increase in escapement did not affect any outputs at any level of increase (Table 4.3). All model outputs regardless of percentage of increase were sensitive to R_{asy} (asymptotic recruitment) and habitat size, both of which are related to the estimate of carrying capacity of the spawning habitat. The calculated sensitivity value (S) for these two inputs was almost directly proportional to the percent increase, was the same value for all outputs, and was the widest range (1-25; Table 4.3). For α which is also related to carrying capacity, all outputs were sensitive to an increase of 10% or more, though S only ranged between 1.7-3.5. All outputs were highly sensitive to a 25% increase of input values except escapement and juvenile mass. These outputs were also sensitive to a 15% increase in all inputs except probability of maturity, which did not result in $S > 1$ for ocean and juvenile abundance, and well as nutrient export. However, other adult metrics were sensitive to probability of maturity. Juvenile mass only affected nutrient export, but at all levels of input increase, as would be expected. Juvenile metrics, including abundance and N and P export, were highly sensitive to a 10-25% change in ocean mortality, but not a 1% change. Interestingly, juvenile metrics were not sensitive to juvenile mortality until it was increased by at least 15%, but adult metrics

were all sensitive at a 10% increase and above. All adult metrics, including the ocean population, spawning run, SSB, and N and P import rates, were sensitive to ocean mortality with an expected decrease in output value as mortality increased. Increasing the mass of each age class by 1% led to a higher spawning stock biomass, and at 10% and above demonstrated sensitivity for all outputs. Inputs related to egg estimation did not result in sensitivity values greater than one when increased by 1%. All outputs were sensitive to a 10-25% increase in both the fecundity slope and female to male ratio, and a 15-25% increase in the fecundity intercept.

Table 4.3. Sensitivity index calculated after each input (listed in first column) was individually increased by 1%, 10%, 15%, and 25%. When inputs had different values for age classes, all of the values were increased by simultaneously. Outputs (listed in top row) were recorded for each increase and sensitivity was calculated using $S = \frac{(O_i - O_n)/O_n}{(I_i - I_n)/I_n}$ where O and I are output and input and i and n are altered and original values, respectively. Absolute values > 1.00 (in bold) are considered sensitive. SSB is spawning stock biomass, F:M is the female to male ratio, a is the slope of the origin of the SR curve, and R_{asy} is the asymptotic recruitment level.

	Change	Ocean Pop	Spawner Pop	Juvenile Pop	SSB	N Adult	N YOY	P Adult	P YOY
Escapement	1%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	10%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	15%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	25%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ocean Mortality	1%	-1.19	-2.46	-0.38	-2.52	-2.52	-0.38	-2.52	-0.38
	10%	-7.56	-19.90	-3.71	-20.47	-20.48	-3.71	-20.48	-3.71
	15%	-10.20	-26.02	-5.18	-26.73	-26.73	-5.18	-26.73	-5.18
	25%	-16.99	-39.91	-9.39	-40.86	-40.86	-9.39	-40.86	-9.39

Table 4.3 Continued

Probability of Maturity*	1%	-0.04	0.63	0.07	0.53	0.53	0.07	0.53	0.07
	10%	-0.44	6.30	0.66	5.17	5.15	0.66	5.15	0.66
	15%	-0.61	8.33	0.85	6.80	6.77	0.85	6.78	0.85
	25%	-1.05	13.44	1.31	10.88	10.83	1.31	10.84	1.31
Spawning	1%	-0.10	-0.10	-0.10	-0.10	0.26	-0.10	0.37	-0.10
Mortality	10%	-1.18	-1.18	-1.18	-1.18	2.63	-1.18	3.84	-1.18
	15%	-1.62	-1.62	-1.62	-1.62	3.46	-1.62	5.07	-1.62
	25%	-2.78	-2.78	-2.78	-2.78	5.33	-2.78	7.91	-2.78
Probability of Spawning	1%	0.23	0.83	0.27	0.86	0.89	0.27	0.88	0.27
	10%	1.12	4.39	1.37	4.52	4.68	1.37	4.65	1.37
	15%	1.12	4.39	1.37	4.52	4.68	1.37	4.65	1.37
	25%	1.12	4.39	1.37	4.52	4.68	1.37	4.65	1.37
α	1%	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.17
	10%	1.72	1.72	1.72	1.72	1.72	1.72	1.72	1.72
	15%	2.25	2.25	2.25	2.25	2.25	2.25	2.25	2.25
	25%	3.45	3.45	3.45	3.45	3.45	3.45	3.45	3.45
R_{asy}	1%	1.01	1.01	1.01	1.01	1.01	1.01	1.01	1.01
	10%	11.09	11.09	11.09	11.09	11.09	11.09	11.09	11.09
	15%	14.99	14.99	14.99	14.98	14.99	14.99	14.99	14.99
	25%	25.01	25.01	25.01	25.01	25.01	25.01	25.01	25.01
Habitat size	1%	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	10%	11.10	11.10	11.10	11.10	11.10	11.10	11.10	11.10
	15%	15.00	15.00	15.00	15.00	15.00	15.00	15.00	15.00
	25%	25.00	25.00	25.00	25.00	25.00	25.00	25.00	25.00
Fecundity Slope	1%	0.25	0.25	0.25	0.25	0.30	0.25	0.29	0.25
	10%	2.43	2.43	2.43	2.43	2.95	2.43	2.82	2.43
	15%	3.13	3.13	3.13	3.13	3.83	3.13	3.66	3.13
	25%	4.65	4.65	4.65	4.65	5.84	4.65	5.54	4.65
Fecundity	1%	-0.08	-0.08	-0.08	-0.08	-0.10	-0.08	-0.09	-0.08
Intercept	10%	-0.96	-0.96	-0.96	-0.96	-1.12	-0.96	-1.08	-0.96
	15%	-1.32	-1.32	-1.32	-1.32	-1.54	-1.32	-1.48	-1.32
	25%	-2.32	-2.32	-2.32	-2.32	-2.67	-2.32	-2.59	-2.32
F:M	1%	0.17	0.17	0.17	0.17	0.20	0.17	0.19	0.17
	10%	1.73	1.73	1.73	1.73	2.07	1.73	1.99	1.73
	15%	2.25	2.25	2.25	2.25	2.73	2.25	2.61	2.25
	25%	3.45	3.45	3.45	3.45	4.25	3.45	4.05	3.45

Table 4.3 Continued

Adult Mass	1%	0.25	0.25	0.25	1.25	0.73	0.25	0.55	0.25
	10%	2.43	2.43	2.43	13.80	7.81	2.43	5.79	2.43
	15%	3.13	3.13	3.13	18.60	10.45	3.13	7.71	3.13
	25%	4.65	4.65	4.65	30.81	17.04	4.65	12.40	4.65
Juvenile Mass	1%	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
	10%	0.00	0.00	0.00	0.00	0.00	11.10	0.00	11.10
	15%	0.00	0.00	0.00	0.00	0.00	15.00	0.00	15.00
	25%	0.00	0.00	0.00	0.00	0.00	25.00	0.00	25.00
Juvenile Mortality	1%	-0.08	-0.08	0.35	-0.08	-0.08	0.35	-0.08	0.35
	10%	-5.49	-5.49	-0.85	-5.49	-5.49	-0.85	-5.49	-0.85
	15%	-7.36	-7.36	-1.16	-7.36	-7.36	-1.16	-7.36	-1.16
	25%	-12.01	-12.01	-1.97	-12.01	-12.01	-1.97	-12.01	-1.97

*Only Ages 2-4

4.4.2. Nutrient Dynamics Over Range of Productivity and Mortality

Scenarios

In all scenarios, the spawning population and juvenile abundances produced by each year of spawners increased until recruitment reached its equilibrium. The value at which equilibrium is attained was dependent on the scenario, with a range of roughly 500,000 spawners and 3.4 million juveniles between populations with low and high freshwater productivity (Figure 4.2). The median scenario demonstrated a stabilized population of 459,000 spawners and 2.9 million juveniles. Replacement lines shifted toward lower juvenile production for a given spawner abundance as adult mortality rates increased.

Results were qualitatively similar for all three productivity scenarios in that at a low spawning population net export of both N and P occurred, but as spawner abundance increased dynamics switched to net import (Figure 4.3). The spawner abundance at

which this switch occurred was lower for N than for P in all three productivity scenarios. Adult import dominated ΔN except for the first 2-6 years after recruits produced by the model (year 4) entered the spawning population (Figures 4.3 and 4.4). This net N export may not occur in a scenario with the same habitat size if the initial spawning population is already near the equilibrium and is unimpacted by additional adult mortality. The magnitude of net N export for all three productivity scenarios was low relative to the stabilized maximum adult import. The maximum net export of N for low and medium freshwater productivity scenarios was less than 1 kg and 5.5 kg, respectively.

In the high productivity scenario, a maximum difference of 16 kg N was seen with 23,000 spawners present and 1 million juveniles produced. Adult N import increased linearly with the spawning population, so ΔN quickly became larger than the amount of N that juveniles were removing from the system. Nutrient import dominated as the number of juveniles approached their carrying capacity, but export plateaued at low spawner abundance (Figure 4.3). The magnitude of adult import and juvenile export, as well as the number of years net export occurred, increased with freshwater productivity (Figure 4.4). Despite large differences in spawner and juvenile abundance among productivity scenarios, the shift from net export to net import for all three scenarios occurred within a similar time frame (6 to 10 years).

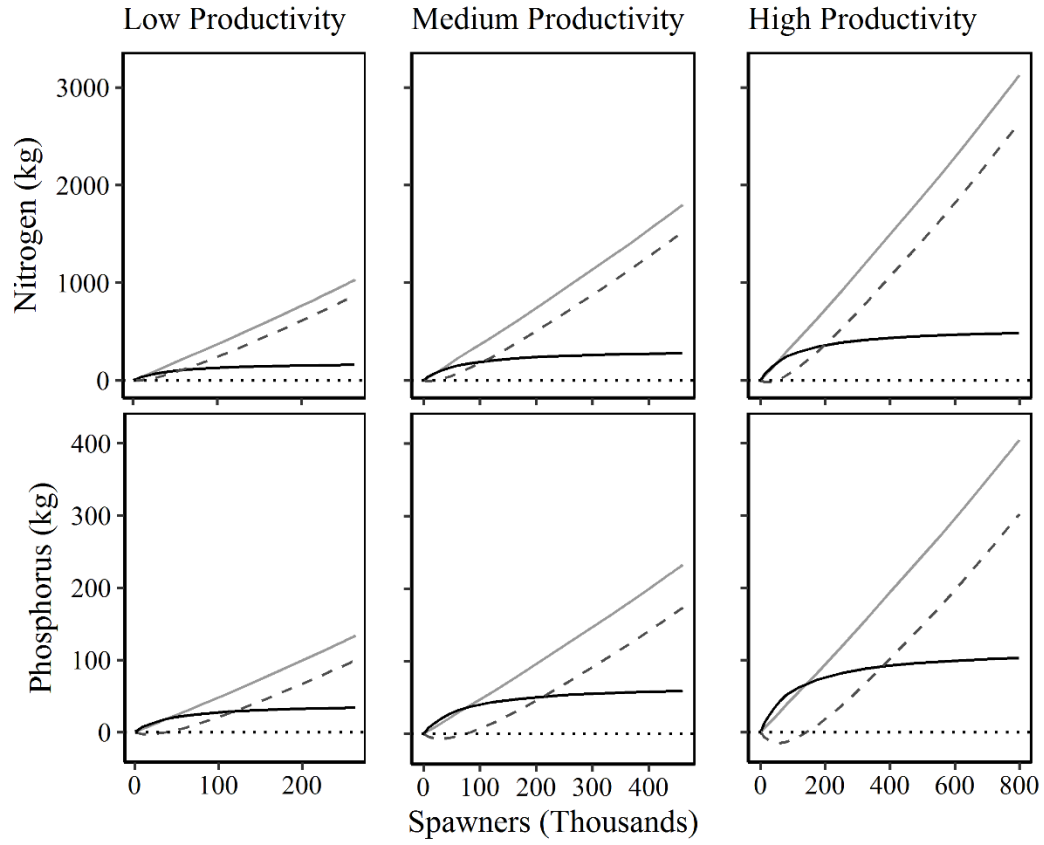


Figure 4.3. N and P dynamics in relation to spawner abundance for three freshwater productivity scenarios assuming unconstrained access to spawning habitat. Grey solid line = import, black solid line = export, grey dashed line = net nutrient flow (import – export). The dotted line delineates the transition between net export (below) and net import (above). Productivity scenarios included the 10th (low), 50th (medium), and 90th (high) percentiles of the parameters α (lifetime reproductive rate) and R_{asy} (asymptotic recruitment level).

Net phosphorus (P) dynamics were similar to the trend seen in N except that export occurred for a longer time period and at higher spawner abundance. Initially, juvenile P export dominated when spawner density was low (Figure 4.3) and the per-capita production of juveniles was the highest. However, ΔP increased over the course of 11-13 years. This corresponded to a maximum export for the low, medium, and high scenarios of 2.8 kg, 6.5 kg, and 14.7 kg, respectively. The spawner abundances associated with these maximums also increased with increasing freshwater productivity (low=15,600 spawners; medium = 32,000 spawners; high = 60,900 spawners). After this, per-capita export declined, though it still outweighed import for two more years in all three scenarios. P dynamics then switched from net export to net import at 35,000, 61,000, and 116,000 spawners and 859,000, 1.6 million, and 3 million juveniles. At this point, the SR curve was starting to plateau as density-dependent effects began to dominate the relationship, meaning fewer juveniles were being produced per capita as a result of larger numbers of spawners entering the system (Figures 4.2 and 4.3). Juvenile export quickly followed this trend, plateauing at 34, 59, and 103 kg even as adult import continued to increase from one year to the next, reaching a maximum value of 133, 232, and 404 kg and a net difference of 99, 173, and 302 kg.

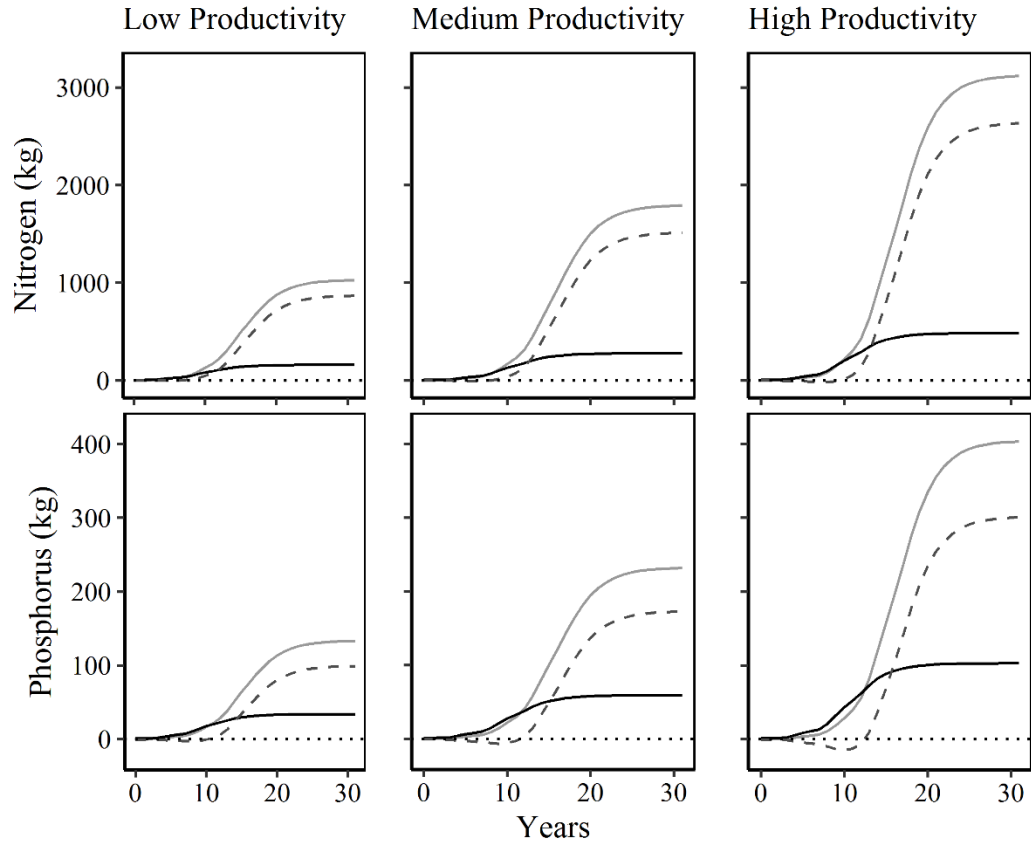


Figure 4.4. N and P nutrient dynamics for the first 30 years of the model run for three freshwater productivity scenarios assuming unconstrained access to spawning habitat.

Grey solid line = import, black solid line = export, grey dashed line = difference (import – export), dotted line is shift between net export and net import. Productivity scenarios included the 10th (low), 50th (medium), and 90th (high) percentiles of the parameters α (maximum lifetime reproductive rate) and R_{asy} (asymptotic recruitment level).

Within each productivity scenario the same pattern was seen in the N and P dynamics, but the magnitude of import and export differed. As freshwater productivity increased, the number of juveniles produced per spawner also increased and led to net export at low spawner abundance. This was less pronounced in N than in P because of the relative nutrient content of adults and juveniles. At a stabilized population, P values were smaller by an order of magnitude than the values for N because the N:P ratio in alewives is high. The amount of N in adult tissue was 6 times higher than P for a carcass, 10 times higher for ovaries, 4 times higher for testes, and 13 times higher for excretion. This dynamic was highlighted in the sharp increase in N:P value coincident with increasingly high population growth (Figure 4.5). At a low spawner number net export was seen for both N and P, and the ratio was both small and positive. N switched to net import before P for all three scenarios, resulting in a negative N:P. This P export was only seen for a small range of spawner abundances within all three scenarios, and nutrient dynamics quickly switched to net import as juvenile production began to plateau. The highest N:P value for net import was seen in the medium productivity scenario, and the lowest in the high productivity scenario. As the population stabilized, a consistent ratio of 8.75:1 was seen for N:P in all three scenarios.

Spawner abundance decreased as mortality rate increased, but the most striking difference seen among scenarios was in the magnitude of ΔN and ΔP (Figure 4.6). Freshwater productivity determined the level of juvenile export that occurred, and this was especially pronounced in ΔP . For all three mortality rates, increasing juvenile productivity resulted in a higher occurrence of net export (Figure 4.6). The shift from net export to net import occurred at approximately the same number of spawners regardless

of mortality rate, but was much higher when the productivity level was at the 90th percentile than the 10th percentile. Both mortality rate and productivity level determined the magnitude of adult import, and so the maximum ΔN and ΔP decreased drastically as mortality increased and productivity decreased.

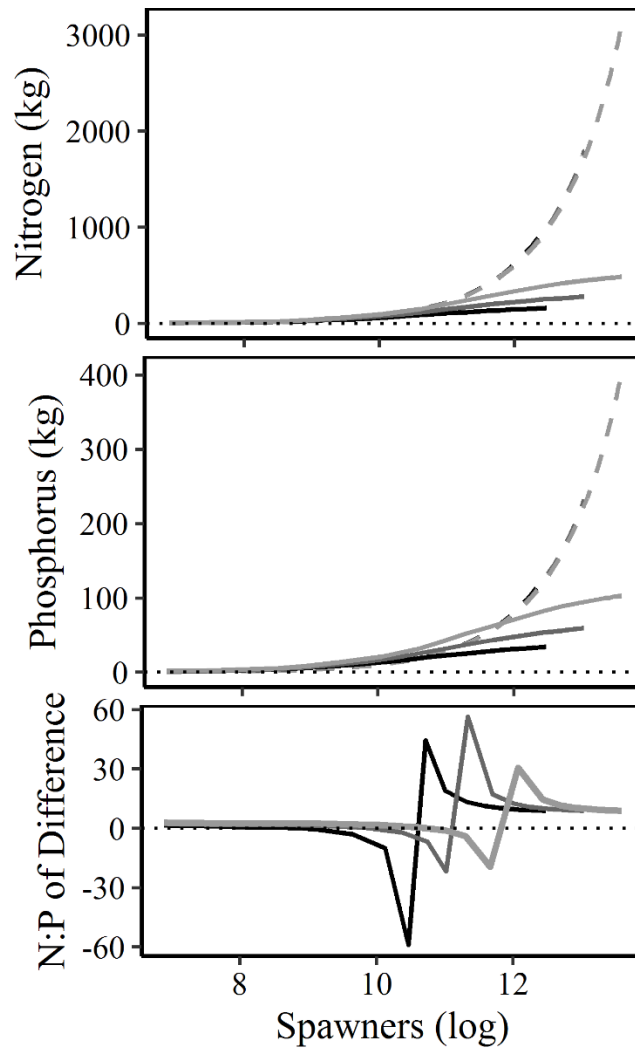


Figure 4.5. N, P, and N:P for the difference (import – export) related to the log of spawner abundance. Nutrient import is shown as dotted lines, and export is solid lines in the top two panels. For all panels, the 10th percentile scenario = black, 50th = dark grey, 90th = light grey. The N:P ratio is negative when N import and P export are occurring, but switches to positive as P import dominates.

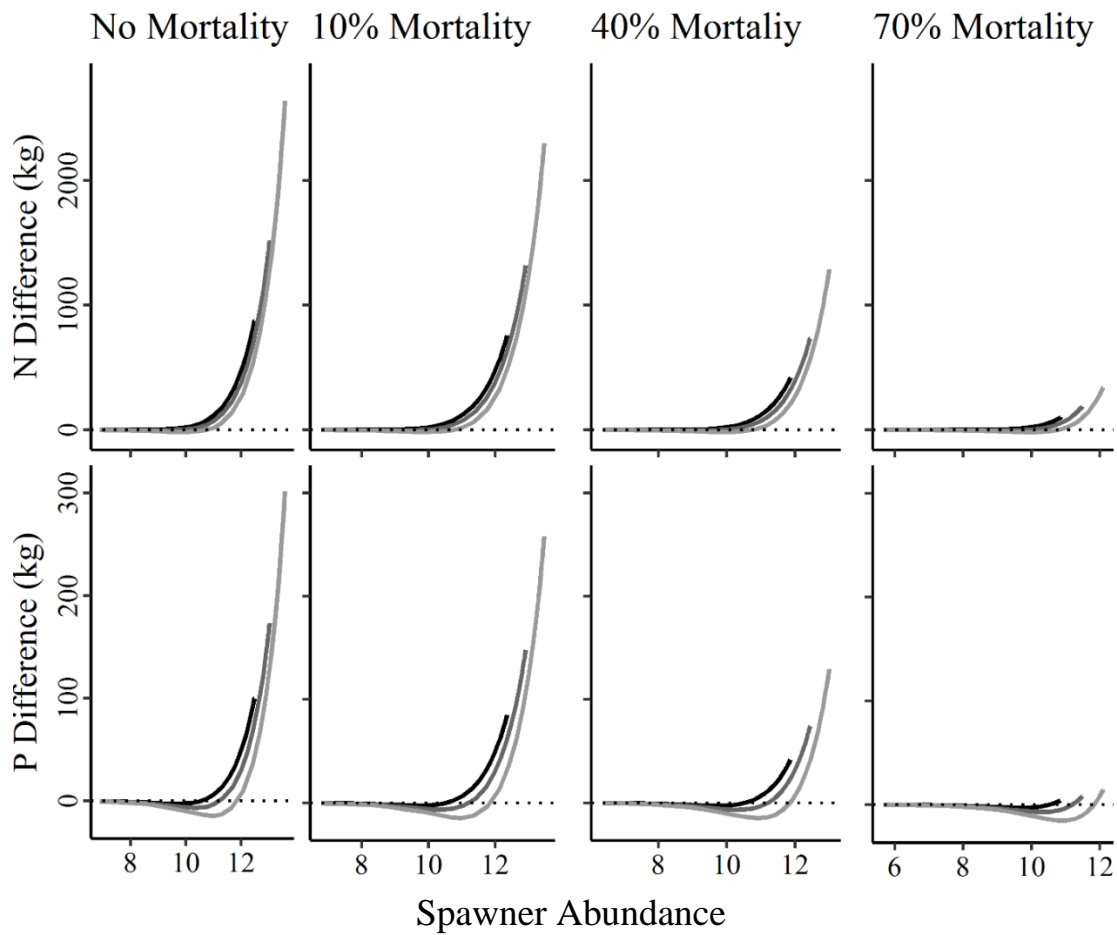


Figure 4.6. N and P difference (import – export) for four levels of spawner mortality as might be experience through harvest (None, 10%, 40%, and 70%) and three productivity levels (black = 10th percentile, dark grey = 50th, light grey = 90th). Dotted line indicates a nutrient balance of 0, meaning import and export are equal. Negative values indicate net export, and positive net import.

4.5. Discussion

4.5.1. Spawner Abundance and Nutrient Import and Export

Within a specific lake or watershed, the ecological role alewives play in net nutrient balance will depend on many factors. These include, but are not limited to, the status of the population relative to its potential within the watershed and the spawner mortality rate. We found that at a low spawning density, where the effect of density-dependence on recruitment was negligible, ΔP was negative as high juvenile production and subsequent nutrient export outweighed adult delivery. The magnitude of export was dependent on productivity level, as this determined the number of juveniles produced per spawner. For ΔN , this initial export phase was smaller in relation to maximum import because each adult contained higher N than P. The model demonstrated that density-dependent production of juveniles related to the SR curve became more pronounced as the spawning population grew, so an established alewife population with no fishery or other impediments to habitat access would persist with high adult returns and relatively low per-capita juvenile production.

When comparing productivity scenarios, the measured range of values for the spawner-recruit relationship resulted in a change in the magnitude of spawner abundance, adult nutrient import, and juvenile export. However, the same pattern in nutrient dynamics was seen regardless of scenario. Net export occurred at low spawner abundance, but the dynamics switched to net import as the number of adults increased. The spawner abundance at this transition point was determined by the values being used in the spawner-recruit curve. For a , standard deviation of the distribution for this parameter was relatively small (Gibson and Myers 2003a) so the difference between the 10th and 90th percentiles was also small. However, variability in the asymptotic

recruitment level (R_{asy}) per unit area among alewife populations was much greater and resulted in large differences in nutrient dynamics as this determined maximum juvenile production.

Spawner mortality can shift the population from higher to lower recruitment levels contingent on density-dependent effects. Many alewife populations are harvested as fish ascend a river to spawn, and most streams have some additional impediment to passage (i.e. dams, sediment buildup, water quality issues, etc.) that affects spawner survival and the ability to reach spawning habitat (Hall et al. 2011). Passage success or mortality (both upstream and downstream) can also influence population demographics (Maynard et al. 2017). As was demonstrated (and is intuitive), a population with an in-stream fishery will have fewer spawners than an unfished population. If a population persists at the steeper part of the SR curve, more recruits will be produced per capita due to reduced density dependent effects, resulting in persistent net nutrient export.

However, the magnitude of maximum spawner abundance changes when considering the synergistic effects of spawner mortality and freshwater productivity. Spawner mortality limited adult import, but productivity levels determined juvenile export. Within a productivity scenario, maximum net export levels were similar regardless of spawner mortality. More juveniles were produced when spawner survival was high, but this was balanced by higher adult import making maximum net export values similar regardless of mortality scenario. Maximum net import was affected more by changes in spawner mortality than by productivity.

The results from this analysis may help explain some of the variation in nutrient dynamics seen in other alewife studies. As was shown by this modelling work, it is important to consider the location of the population on the SR curve when estimating ΔP . Previous studies that have estimated net nutrient balance have indicated that juvenile export is negligible in smaller lakes with established alewife runs (Durbin et al. 1979; West et al. 2010). This result falls in line with the results from the modelling work presented in this paper as these populations fall along the plateau of the SR curve. However, a larger lake with a spawning population that is maintained at a low level relative to the habitat's capacity could see juvenile P export (West et al. 2010). Alewife populations could fluctuate along the SR curve as run size changes over time. For a founding population, an initially small spawning abundance will result in a high recruitment rate and net P export, though the magnitude of ΔP is also sensitive to juvenile mass and ocean mortality rates. However, as the number of spawners increases steadily with time, the asymptotic recruitment level for that habitat will be approached and the population will plateau with import as the dominant nutrient dynamic (Figure 4.3). Given the high variability in carrying capacity found by Gibson (2004), habitat quality is also a key determinant of the magnitude of adult import. When testing model sensitivities, we found all output variables were sensitive to R_{asy} and habitat size because these two parameters determined the asymptotic recruitment level, thus an increase in either resulted in greater fish production. However, nutrient delivery does not guarantee assimilation into the freshwater habitat. Hocking and Reimchen (2009) found lower rates of nutrient incorporation as watershed size increased.

The opposite trend will occur when a declining population has consistently high mortality, especially when the number of spawners that enter the habitat is small relative to its productivity level. In this scenario, P export will dominate as spawner abundance continues to decrease. In addition to adult mortality rates, changes in density-dependent juvenile survival can influence nutrient export, and vice versa. In a large habitat with reduced resource competition, larger juveniles are produced that will export a higher level of N and P (Moore & Schindler 2004). On the other hand, if the alewife spawning population is persistently small, a negative feedback loop could develop with net P export reducing the productivity of a watershed, increasing density-dependence for juveniles (Scheuerell et al. 2005). This pattern has been seen for both Chinook Salmon (*O. tshawytscha*) and Atlantic Salmon (*S. salar*) where, as spawner abundance decreased, smolts exported proportionally higher levels of P from the watershed (Nislow et al. 2004; Scheuerell et al. 2005).

We did not include environmental stochasticity in our model. Effects of environmental variability would be expected to have only a minor effect on the relationships between spawner abundance and nutrient import, primarily via its effect on the age structure of the population. Its effect on nutrient export could be greater depending on recruitment variability. For example, Tommasi et al. (2015) reported that environmental variability explained more of the variance between adult and juvenile alewife abundance than density dependence for four alewife populations in the northeast U.S. Additionally, it is important to remember that the model is not intended as a dynamic forecasting model but rather a heuristic simulation that represents the “average” scenario based on the inputs that are used (Ford 1999). If environmental stochasticity

were included, it is possible that it would take more or less time for the population to reach its equilibrium abundance. However, as the model is run for several hundred years, instances of poor recruitment would be expected to be balanced by years of excellent recruitment. A large number of simulations, each with random variability drawn from the same distribution, would give in the same “average” result. The general trends will therefore remain similar regardless of variation in the endpoints.

4.5.2. The Role of Alewives in Freshwater Productivity

The results of this model indicate that when freshwater productivity is high and spawner mortality is low, alewives have the potential to deliver substantial nutrient loads to freshwater systems. Whether these nutrients are incorporated into a system will depend on baseline nutrient limitations, the method of delivery, and the existing freshwater community. Whether a system is N or P limited, or co-limited, can determine the influence of a nutrient subsidy. Previous studies have shown that nutrient input from anadromous species often boosts the productivity of a stream or lake, but these effects seem to be most pronounced when the habitat is oligotrophic (Cederholm et al. 1999; Chaloner et al. 2002; Bellmore et al. 2014; Samways & Cunjak 2015). A high N:P value during the recovery of a population, as was seen in this study, could mean that much of the N brought into a system is not retained and immediately used by organisms.

Geographic variability in life history traits may also affect N:P. Alewives exhibit a north-south cline in life history traits, with northern populations displaying greater iteroparity (Pardue 1983). For northern populations nutrient delivery is likely dominated by excretion, but for southern populations carcasses are likely the dominant mode of delivery. The latter populations receive a higher biomass of nutrient delivery, and for

alewives N:P for carcasses is roughly twice that of excretion (Durbin et al. 1979). However, alewife carcasses can take more than 240 hours to decay (Garman 1992), and so this method of nutrient delivery is not immediately bioavailable. Excretion inputs are immediately available for uptake by primary producers, so N and P delivered to oligotrophic watersheds in the northern part of the alewife range can be quickly sequestered and used for the short spring growing period.

Nutrient incorporation can also depend on the method of delivery and how the existing freshwater community is able to access this subsidy. Alewives may have both bottom-up and top-down effects on freshwater communities because they represent both a short and long term subsidy throughout the season. Nutrients immediately available through excretion could boost biofilm, periphyton, and phytoplankton productivity, though studies have indicated that these effects are short-lived on the scale of weeks to months (Post & Walters 2009; García et al. 2017). Decomposition of eggs and carcasses can play the same role and provide a protracted source of nutrients throughout the season for primary production. Marine-derived nutrients can also be incorporated at the top of a food web (S. F. Collins et al. 2016). All anadromous fish species represent nutrient-rich subsidies for a variety of predators, including aquatic fish (Jaecks & Quinn 2014; Willson & Halupka 1995) and foraging mammals and birds (Dalton et al. 2009; DeBruyne et al. 2012). Scavenging macroinvertebrates feed on carcasses during their freshwater juveniles phase, then transport marine-derived nutrient into the terrestrial environment after emergence (Polis et al. 1997; Vanni 2002; Hocking & Reimchen 2009). Both bottom-up and top-down pathways likely determine nutrient incorporation, but the relative influence of each will depend on the species that are present and whether

freshwater invertebrates are released by predation pressure when subsidies are present (S. F. Collins et al. 2016; Sato et al. 2016).

4.5.3. Management Implications

While managers are often concerned about alewife nutrient import causing water quality issues, the relative magnitude of MDN inputs are likely well below the extent of anthropogenic influences that already control baseline nutrient levels within New England lakes (Twining et al. 2013). Also, increasing temperatures could lead to elevated metabolic demands at the community level (Woodward et al. 2010), producing a partial outlet for excess nutrients. Several alewife studies have reported low levels of nutrient delivery because of reduced spawning populations and a trend of shifting to a smaller adult size (Norris 2012; Twining et al. 2017). Currently, watershed contributions to a Connecticut lake, mostly due to lakeshore development, account for three times as much P and 19 times as much N as are brought in by alewives (Twining et al. 2013). For an oligotrophic watershed such as the St. Croix River in Maine, from which the demographic information for this model was gathered, alewife-derived nutrient import may play a more substantial role, especially if the population is large in relation to its carrying capacity. In the St. Croix, the current alewife spawning population is only about 0.5% of its estimated capacity (Flagg et al. 2007), so nutrient import could markedly increase if recovery occurred.

As was seen in the results, while alewives have the potential for rapid population growth, site-specific variability can have a large influence on the net nutrient dynamics. This variability can be determined by sources or spawner mortality, as well as differences in habitat quality within a watershed. In-river fisheries mortality can have the same

influence as a dam on net nutrient balance by limiting the number of fish that are allowed to move upstream (Hall et al. 2011), and reduced adult downstream passage could affect the age structure and therefore the fecundity of a population (Jessop 1993). In addition to direct mortality, migratory delays can affect population growth and nutrient dynamics. If dams, waterfalls, or even open stretches of river delay upstream fish passage, then fewer adults successfully enter the spawning habitat (Meixler et al. 2009; Hall et al. 2011; Pess et al. 2014). This causes the population to shift toward a lower equilibrium in which juvenile production and export decreases, but to a lesser extent than the decrease in spawner biomass and nutrient import. Many large rivers in New England have multiple dams, and this population reduction can become additive (Brown et al. 2013). This means downstream spawning habitat may demonstrate adult import, but upstream habitat may exhibit greater juvenile export because fewer adults are able to access it.

The outputs values estimated by a model are only as good as the inputs used, so there are still limitations associated with alewife population modelling because of data deficiencies related to specific portions of their life history, such as ocean mortality rates. Ocean mortality was one of the more sensitive inputs in the model, but is also the most difficult parameter to estimate due to stochasticity in the marine environment (ASMFC 2012). Mortality is often estimated based on the age structure of spawner returns and the number of repeat spawners within a river because reliable ocean mortality assessments remain elusive. Until more informed estimates are obtained fisheries managers have to make do with the best available information. Deterministic models such as the one developed here address general trends in a population and can help inform management decisions by testing sensitivities within life histories, but because variation in the

spawning run is averaged these models are not predictive. This model can be tailored to fit any watershed and alewife population, and could be a useful tool where management decisions are made to control either excessive or meager nutrient inputs.

CHAPTER 5

THE INFLUENCE OF VARIABLE PASSAGE ON ALEWIFE POPULATION RECOVERY AND NUTRIENT DYNAMICS USING THE ST. CROIX RIVER AS A CASE STUDY

5.1. Chapter Abstract

Anadromous alewives are a source of marine-derived nutrients, with adults importing nitrogen and phosphorus into freshwater habitats during their spawning run. High juvenile productivity per spawner leads to export at low spawner abundance. Persistently poor passage efficiencies at dams or annual fishing mortality could maintain anadromous alewives at low spawner abundance. A population and nutrient model was developed to explore the effect of variable upstream and downstream passage efficiencies due to one or multiple dams on spawner abundance, net nitrogen balance, and net phosphorus balance on a system-wide and site-specific scale. Our results demonstrated that when one or more dams were part of a system, the reduction in upstream passage determined adult abundances, which also controlled future recruitment potential. Downstream survival rates determined the number of fish that recruited into a population, as well as nutrient export rates. In addition, when at least one dam was present and adult downstream passage rates were poor, the age structure of the alewife population shifted to favor younger fish. A smaller average adult size could lead to an overall reduction in nutrient import. The effect of poor passage at sequential dams depended on their location in relation to spawning habitat within the watershed. The St. Croix River, used as a case study, has the majority of spawning habitat upstream. When passage in the lower river

was varied, the general trend indicated that ΔP was relatively insignificant until both upstream and downstream passage was high. When passage was varied in the upper river, import dominated at a wider range of upstream passage rates, but this only occurred when downstream passage was high. This led to a combined effect of higher carrying capacity producing more surviving juveniles per capita spawner, but a narrower range of passage rates that resulted in substantial P import. Scenarios were also run including a 50% in-river fishery in the lower and upper part of the river to explore the influence on population recovery. When the fishery was located further upstream a larger number of spawners could enter the river, and so the system-wide total was higher regardless of site-specific distribution. Our results highlight the need to consider both dam and fisheries locations in relation to spawning habitat when estimating population recovery and nutrient dynamics.

5.2. Introduction

Dam construction has led to declines in migratory fish populations through a suite of direct and indirect effects. While upstream migration can also be hindered by natural topography and stream flow (Meixler et al. 2009), anthropogenic barriers contribute to extensive habitat loss (Pess et al. 2014) as well as alterations in natural stream hydrology that lead to changes in water velocity, reduced occurrence of flooding events, increased water temperatures and a reduction in the downstream transport of nutrients and sediments (Gregory et al. 2014). The presence of dams on a stream can also indirectly effects that lead to population declines, reduced species diversity (Gregory et al. 2014), reduced fitness and increased energetic costs (Castro-Santos & Haro 2003; Jonsson et al.

2010), life history fragmentation (Noonan et al. 2012; Hall et al. 2010), and the loss of freshwater productivity (Hall et al. 2012).

Passage structures (hereafter generically referred to as “fishways”) differ in efficiency. This can be based on their type, length, slope, and elevation (Noonan et al. 2012; Cooke & Hinch 2013), but the effect of each of these factors on migrants also depends on the biology of the species. Differences in swimming ability, jumping height, and level of attraction to a fishway entrance can affect individual movement and ultimately population recovery (Meixler et al. 2009; Bunt et al. 2012; Noonan et al. 2012). Each fishway has a maximum functional capacity that limits the daily number of individuals that can pass, and this may be far below the number of fish that approach the dam. Seasonal variation in flow rates can also influence an individual’s attraction to and movement through a fishway (Meixler et al. 2009). While passage efficiency through one dam may be high, many individuals have to pass through multiple dams to reach upstream spawning habitat. This has a compounding effect that reduces watershed-level passage efficiencies (Brown et al. 2013). Even when passage structures are present at each dam, delays in migration occur for individuals attempting to move upstream and reproduce (Hall et al. 2010; Pess et al. 2014).

Downstream passage efficiency must be high for population growth to occur. For iteroparous species, both upstream and downstream mortality of adults can reduce the productivity of a population by reducing average age and therefore overall population fecundity (Leggett et al. 2004; Oldani et al. 2007). Successful adult passage becomes irrelevant to recruitment if juveniles do not survive downstream migration to recruit into a population (Cooke & Hinch 2013). Juveniles migrating downstream are transitioning

from freshwater to salt water adaptations, and downstream passage delays can significantly reduce juvenile survival as individuals lose the ability to osmoregulate in freshwater (Castro-Santos & Haro 2003).

Population recovery can be greatly affected by the location of these migratory bottlenecks, the magnitude of which may differ throughout the course of the run (Castro-Santos & Haro 2003), because more energy is required to successfully access spawning habitat (Jonsson et al. 2010; Brown et al. 2013). Bottlenecks can include both dams and the presence of a fishery. For species that migrate further up a system, the location of spawning habitat in relation to a bottleneck can effect recovery rate (Jonsson et al. 2010; Lake et al. 2012). If the majority of habitat is located upstream of a bottleneck and fish are impeded, delayed, or incur high energetic costs, recruitment could be reduced. The magnitude of this loss will depend on the species in question, as some tend to use lower regions of rivers while others migrate further upstream to spawn. For example, alewife (*A. pseudoharengus*) harvests have experienced a shift in location over the past 70 years from inland spawning areas to focusing at the head of tide in many systems (Hall et al. 2012). This is an important distinction that could change recruitment rates because harvest shifted from fish that have already contributed reproductively to targeting fish before they have a chance to even enter their spawning habitat (Hall et al. 2012).

5.2.1. Alewives as Nutrient Subsidies in Freshwater Habitats

Anadromous alewives are native to the east coast of North America and range from South Carolina to Newfoundland (Durbin et al. 1979). In the northern part of their range they are iteroparous, and adults prefer to spawn in slow moving water such as lakes or flowages where juveniles rear for 2-7 months (Richkus 1975; Bozeman & Van Den

Avyle 1989; Flagg 2007). Alewife were historically numerous throughout New England, but populations have been in decline for decades, partially due to water quality issues and the construction of dams (Hall et al. 2012). However, in Maine population growth has followed dam removals in the Penobscot and Sebasticook Rivers which had 1.2 million and 3.5 million returning adults in 2016, respectively (Trap count statistics, Maine DMR). These recoveries are likely related to alewives' remarkably high reproductive potential, with each returning adult producing roughly 19 age-3 recruits (Gibson & Myers 2003). For alewife, inefficient passage at dams will reduce a population's recovery rate, however a small number of successful spawners can still produce enough recruits to allow the population to persist and grow. Despite this, there will likely still be an effect on age structure and overall population fecundity. This means that even if passage is poor, a recovering alewife population may rebound quickly given the fact that some adults are able to access upstream spawning habitat.

Throughout the course of their spawning migration, alewives provide a pulse of marine-derived nutrients (MDN) to river systems in the spring during immigration, spawning, and emigration. This subsidy potentially boosts productivity in temperate regions where marine habitats are more productive than freshwater habitats (Gross et al. 1988; Bilby et al. 1996). Anadromous fish exhibit rapid growth in the ocean and many adults die during the course of migration, leaving carcasses in streams to decay (Bilby et al. 1996; Wipfli et al. 1998). They also release nutrients through excretion and gametes. In large rivers and lakes where light availability is high, nitrogen (N) and phosphorous (P) concentrations are the major determinants of primary production rates (Sanderson et al. 2009b; Vanni 2002), but the effect of marine-derived nutrients at a given site will

partly depend on whether or not that site is already limited in N, P, or co-limited by both (Paerl et al. 2016).

Alewives prefer to spawn in slow-moving water, so the retention of nutrients at a site may be high because of low flushing rates (Cederholm et al. 1999; Flagg 2007). In lentic systems, the size of the habitat relative to the size of the run can also determine whether or not a large effect is seen (Cederholm et al. 1999). Recovery of a large alewife spawning run could potentially put strain on lake systems that are already eutrophic due to agricultural runoff and sewage deposition (West et al. 2010). In oligotrophic systems, however, alewife recovery may help boost freshwater productivity. An increase in the availability of limiting nutrients could cause a net increase in primary productivity, leading to a bottom-up effect by increasing biomass of macroinvertebrates, which could in turn support a larger number of both freshwater and terrestrial predators (Wipfli et al. 1998; Naiman et al. 2002; Cederholm et al. 1999; Minakawa et al. 2002).

The timing of this nutrient pulse may determine its effect on the freshwater food web. Sato et al (2016) found that a pulsed subsidy early in the spring increased the growth rate of trout populations in a stream, but a pulse later in the season did not demonstrate the same effect. The authors suggested this effect was because an early pulse provided a food subsidy that prevented trout from focusing solely on benthic invertebrates, allowing system productivity to be high. When the subsidy came later in the season, trout had already predated heavily on the invertebrate community, thereby reducing overall community productivity and forcing higher rates of competition among individual fish. This study illustrated the subtle ways that subsidies can affect nutrient dynamics and productivity within a system.

Alewives can have very large spawning runs, and previous studies have suggested that despite differences in life history characteristics they could play an ecological role similar to that of Pacific salmon (Walters et al. 2009; Garman & Macko 1998; Durbin et al. 1979; West et al. 2010). Nutrient modelling has suggested that, in the absence of dams, juvenile P export dominated at low spawner abundance when juvenile production was high (Barber et al. in press). As population recovery progresses, anadromous juveniles annually removed more from the watershed than was added by spawning adults, making them a nutrient sink (Cederholm et al. 1999). However, marine-derived nutrients are still available for freshwater growth in the spring when adult alewives are present in the watershed. The relative magnitude of export to import and the population size at which this switch occurs was dependent on the size of the spawning habitat available, assuming homogeneous habitat quality (Barber et al. in review).

The ability to estimate the effect of variable upstream and downstream passage rates on both population and nutrient dynamics could lead to more informed management decisions. This spring pulse is part of the nutrient budget of intact coastal systems, so when anadromous migrations are blocked or delayed by dams the resultant loss of nutrients could influence the resident species assemblage (Twining et al. 2017). In addition, the location of a commercial fishery within a watershed can affect the recovery of the alewife population. If a fishery exists at a passage bottleneck, the compounding effect of mortality and reduced upstream movement can have a greater influence on population recovery. The objective of this chapter was to explore alewife population and nutrient dynamics related to 1) variability in efficiency of both upstream adult passage and downstream juvenile passage and 2) fisheries mortality. These population and

nutrient dynamics were considered at two scales: a small (lake-specific) and a large (river-wide) watershed.

5.3. Methods

5.3.1. Alewife Population and Nutrient Model

A deterministic alewife model that was developed by Barber et al. (in review) using Stella 10.0.6 as a graphic user interface (Higher Performance Systems, Inc., Hanover, New Hampshire) to explore the effect of varying freshwater productivity and fisheries mortality on population growth and net nutrient dynamics. For the population portion of the model, cohorts of alewives were moved through the life cycle using stepwise annual progression with age classes for the ocean population ranging from ages 1-8, and spawners ranging from ages 3-8 as explained in Barber et al. (in press; Chapter 4). Spawner biomass was used to calculate fecundity, and a Beverton-Holt spawner-recruit curve led to juvenile estimates. Adult nutrient import was determined using spawner biomass and weight-specific estimates of carcass and excretion inputs, as well as gamete production based on fecundity. Nutrient export was calculated using an average juvenile weight and survival estimates. Net nutrient balance (here after referred to as Δ) was calculated as adult import – juvenile export.

This simplified model structure was associated with several assumptions. First, no effect of passage impediments was taken into account for either population or nutrient estimates. Poor upstream passage for spawners and downstream passage for both adults and juveniles could affect overall population abundance, net nutrient balance, and age structure of repeat-spawners. Many systems have multiple dams, and their effect on

population structure is compounding both on a spatial and temporal scale. Second, this model only took into account one potential spawning area, whereas many watersheds may have several distinct habitat units or a complex network of lakes and ponds. Depending on the spatial layout of a river, the location and size of a spawning habitat relative to passage delays can affect population recovery and net nutrient balance. To develop more realistic estimate of alewife population and nutrient dynamics, a river must be considered in its entirety.

5.3.2. Construction of a System-Wide Model

To explore system-wide dynamics, a model was developed that incorporated multiple spawning habitat units to investigate both watershed-scale and site-scale outputs for scenarios where passage rates differed at individual dams. This was done by developing a set of dispersal rules for alewife migrating upstream through a system, as well as integrating the effects of upstream and downstream passage at the entrance to spawning habitats. A river system was divided into habitat units, each with their own spawning abundance, nutrient balance, and juvenile production. All surviving juveniles from each habitat unit were combined into a single ocean cohort to determine future spawner abundance.

Dispersal was first estimated to determine spawner abundance within each separate habitat unit. In the absence of dam passage effects, fish distributed throughout production units ($u+1$, $u+2$, etc.) according to the relative proportion of spawning habitat available in each. This allowed us to determine the distribution of fish that entered the system, despite not having information associated with motivation. Each age class in the spawning run was distributed through each successive habitat unit in the watershed. This

allowed size at age to be used for both fecundity and nutrient estimates. The total number of spawners in year t (S_t) was calculated as:

$$S_t = \sum_{a,p} S_{a,t,p} \varphi,$$

in which $S_{a,t,p}$ was the number of spawners of age a in year t that had spawned p times previously, and φ was the probability of spawning.

Within the model framework, successive habitat units were separated by a dam or other passage barrier. In many instances, though, the presence of a dam creates flowages that act as spawning habitat for alewife. Upstream passage efficiencies were applied at each dam (P_i) to determine how many fish successfully passed, and there was an additive effect for spawners passing multiple dams. Of the fish that successfully passed a dam in year t , a proportion stayed to spawn in each habitat unit u ($S_{t,u}$) based on the relative amount of spawning habitat available (h_u) such that:

$$S_{t,u} = S_t \cdot P_i \cdot h_u.$$

The rest moved upstream to approach the next dam (m_{u+1}) as follows:

$$m_{u+1} = S_t \cdot P_i \cdot (1 - h_u).$$

Fish that moved upstream to approach the next habitat unit were subjected to a passage probability associated with the next associated dam (P_{i+1}) as follows:

$$S_{t,u+1} = m_{u+1} \cdot P_{i+1}.$$

Those fish that did not successfully pass a dam were returned downstream to become part of the spawning population of the previous habitat unit. These two portions were summed together to get total spawner abundance (S_T) to use in nutrient calculations for each habitat unit u in year t as follows:

$$S_{T,u} = S_{t,u} + (m_{u+1} \cdot (1 - P_{i+1})).$$

Fish that successfully passed the second dam on the system were similarly divided into fish that stayed to spawn in the production unit and fish that continued to move upstream. Dispersal and passage calculations were repeated for each habitat unit in a system. For the dam farthest upstream, spawners were not divided into groups. Instead, all fish that successfully passed either died or spawned and moved to the next year class.

Juvenile production was estimated for each habitat unit. Recruitment curve coefficients were adjusted based on the surface acreage of available spawning habitat within a unit, with the assumption that habitat quality in each lake was homogeneous (Table 5.1; Dill et al. 2010). Downstream passage acted on juveniles separately for each habitat unit, and was treated as a source of mortality in the population portion of the model. As fish moving downstream from the uppermost habitat units have to pass through multiple dams, passage efficiencies were cumulative as follows:

$$DS = P_t^N$$

in which DS = cumulative downstream passage, P_t = probability of passing a particular dam in year t , N = number of dams that are passed. Adult downstream passage, used to look at the effect of passage on age structure, was calculated using the same formula,

though this source of mortality was only calculated for individuals who survived spawning.

5.3.2.1. Nutrient Parameters

Total N and P inputs (I_t) were calculated for each habitat unit ($u+i$) based on carcass inputs (C_t), gametes produced by both males and females (G_t), and excretion rates (E_t) as follows (see Barber et al. in review for complete description):

$$I_{t,u+i} = C_{t,u+i} + G_{t,u+i} + E_{t,u+i}.$$

We assumed no feeding by adults during migration, meaning nutrient import was solely from the marine environment. It was also assumed that fish spawned before contributing to mortality estimates. Mortality inputs for N and P were estimated by calculating separate values for carcasses (excluding gonads), for ovaries, and for testes because of differences in elemental composition between somatic and gonadal tissue (Durbin et al. 1979). Carcass input was calculated using total wet weight for each habitat unit and separate weight-at-age for males and females assuming a 1:1 sex ratio. The total for each habitat unit was then multiplied by the N and P content for unspawned adult carcasses as calculated in Durbin et al. (1979). Gamete inputs (eggs and sperm) were calculated differently from carcass input to account for the difference between spent and unspent gonad mass as described in Barber et al. (in review).

Excretion inputs were estimated based on both the number of fish that successfully passed into each habitat unit as well as an estimate of how long fish stayed in each unit. Average alewife residence time has been reported at 10 days, though some individuals may spend up to a month in the river (Frank et al. 2011). To stay consistent

with previous studies, a 14-day residence time was used despite potentially being an underestimate for larger rivers (West et al. 2010; Kissil 1974; Post & Walters 2009; Twining et al. 2017). This timing was constant regardless of water temperature. Resident time was divided amongst the four habitat units based on the relative size of each because spawners migrating upstream would spend differing amounts of time within each area. Travel distance between spawning habitats was estimated and used to calculate proportional residence time for each habitat unit. If, for example, four habitat units were being considered, total excretion (E_t) in year t for each habitat unit u would be calculated as follows:

$$E_{t,u} = [(RT \cdot SSB_u) + (d_u \cdot SSB_{u+1}) + (d_u \cdot SSB_{u+2}) + (d_u \cdot SSB_{u+3})] \cdot (E_n \cdot 24 \text{ h})$$

$$E_{t,u+1} = [((RT - d_u) \cdot SSB_{u+1}) + (d_{u+1} \cdot SSB_{u+2}) + (d_{u+1} \cdot SSB_{u+3})] \cdot (E_n \cdot 24 \text{ h})$$

$$E_{t,u+2} = [((RT - d_u - d_{u+1}) \cdot SSB_{u+2}) + (d_{u+2} \cdot SSB_{u+3})] \cdot (E_n \cdot 24 \text{ h})$$

$$E_{t,u+3} = [(RT - d_u - d_{u+1} - d_{u+2}) \cdot SSB_{u+3}] \cdot (E_n \cdot 24 \text{ h})$$

in which RT is total residence time, SSB_u is the standing stock biomass for each habitat unit starting above the head of tide (u) and moving upstream ($u+i$), d_{u+i} is the time taken to migrate through each production unit (Table 5.1), E_n is the excretion rate of $24.71 \mu\text{g N}$ or $2.17 \mu\text{g P} \cdot \text{g wet fish mass}^{-1} \cdot \text{hour}^{-1}$ multiplied by 24 h to get a daily input. Age-structured SSB was calculated for each year t based on the number of spawners in each habitat unit as follows:

$$SSB_{u+i} = \sum_{a=3}^8 \sum_{p=1}^5 S_{a,t,p,u+i} W_a,$$

in which $S_{a,t,p,u+i}$ is the number of fish of age a that have spawned p times from habitat unit $u+i$ and W_a is the weight at age a (Gibson and Myers 2003b; St. Croix Milltown Trap 1981-2016).

5.3.2.2. Juvenile Export

Juvenile abundance in year t (YOY_t) for each production unit ($u+i$) was used to calculate nutrient export as follows:

$$\mathbf{Export}_{t,u+i} = YOY_{t,u+i} \cdot W_{juvenile} \cdot n_{juvenile} \cdot DS_{u+i}$$

in which $W_{juvenile}$ was the average mass (Havey 1973), $n_{juvenile}$ was the N or P content of emigrating juveniles, and DS_{u+i} was the downstream passage efficiency for fish leaving a habitat unit. Total P export was estimated using a concentration of 0.0058 g P*g wet mass⁻¹ taken from West et al. (2010). As a juvenile-specific N concentration could not be found in the literature, we estimated a value based on the measured adult content (0.02735 g N*g wet mass⁻¹; Durbin et al. 1979).

5.3.3. Parameterization for the St. Croix River

The modelling framework as described produces a hierarchy of outputs that can be used to explore population and nutrient dynamics on both a habitat-specific and system-wide scale. Many questions can be addressed, such as age structure associated with downstream passage and nutrient balance associated with population recovery. To fully explore the subtleties of alewife influence, this system-wide model was parameterized using data from the St. Croix River, which forms the border between northeastern Maine, USA and southern New Brunswick, Canada (Figure 5.1).

Lake-specific and system-wide dynamics were explored using the alewife model based on data from the St. Croix River population. The St. Croix alewife population presents a novel opportunity to predict the course of a recovering population. Alewives were historically abundant in this river, but logging practices, ecological misconceptions, and political polarity in the past century and a half nearly led to their extirpation (Willis 2009; Chapter 1 this document). Alewife production in the St. Croix, assuming complete habitat access, has been estimated at between 12-24 million fish based on a potential of 118-235 adult returns per acre of spawning habitat (Flagg 2007).

Given the history of fishway closures and limited passage data in the St. Croix River, the most important questions moving forward with alewife recovery center on how well the fishways function at each dam. Upstream passage efficiencies at all four dams on the main stem vary due to differences in the length and type of each fishway. Two of the fishways on the river are denils, which may be more difficult for small fish such as alewives to navigate (Haro & Castro-Santos 2012). The denil at Woodland Dam is 745 feet long (227 m), making it one of the longest such fishways in the eastern United States (Decker 1967). Fishways with persistently poor passage can delay passage resulting in individuals that do not have the energy to move as far upstream before spawning (Castro-Santos & Haro 2003). These migratory delays could cause the majority of fish to spawn in the lower part of the river, concentrating nutrient input into a smaller area. The effect that marine-derived nutrients will have on freshwater food webs depends on the magnitude of input (West et al. 2010), and variable results could be seen if this input is concentrated in one section of the river or is spread throughout the whole watershed.

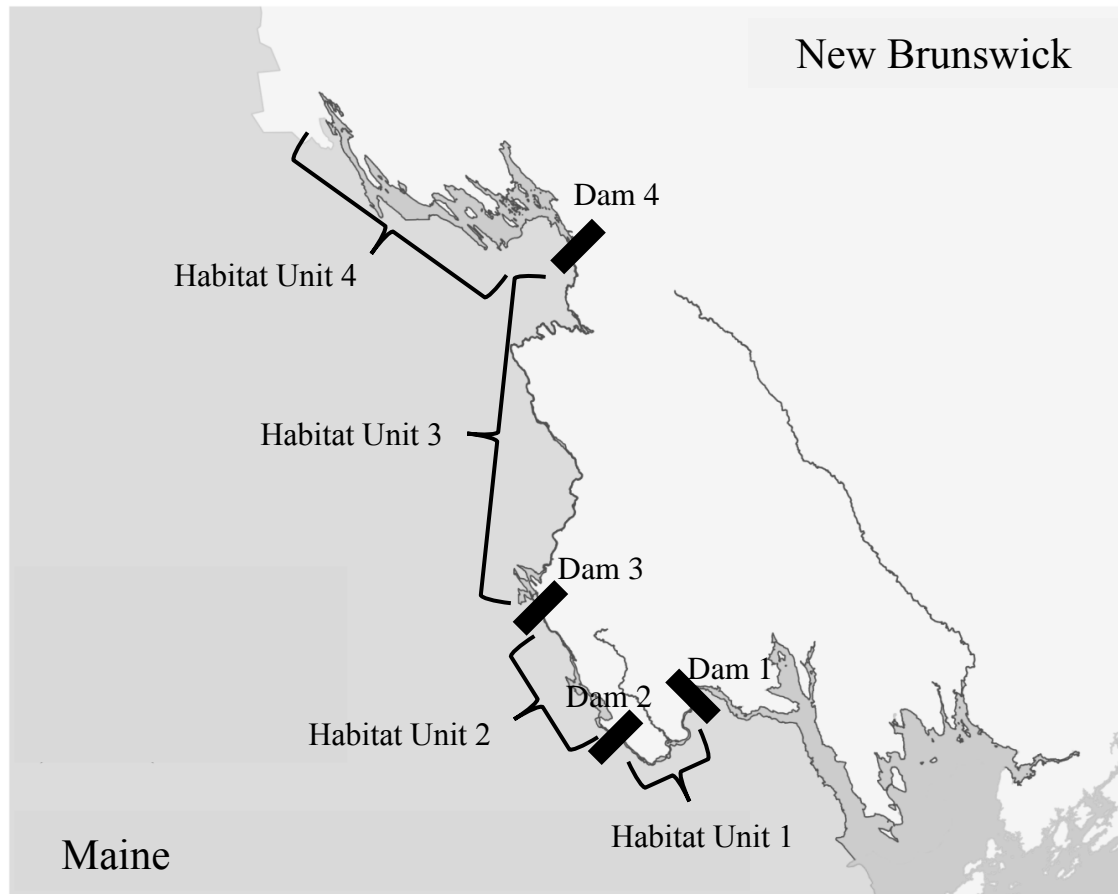


Figure 5.1. Habitat units and dams along the St. Croix River.

5.3.3.1. River-Specific Data

Morphometric and demographic inputs for the alewife model were taken from data collected in the St. Croix watershed from 1981-2016 at the fish count facility located at the head of tide (St. Croix Milltown Trap). This included information on the total number of fish passing the fishway and entering the river, as well as sex, weight, length, age, and information on repeat spawning for individuals sampled for 17 years from 1981-2016. These measurements were used to parameterize the model with the assumption that the sampled fish correctly represented the entire population. When model inputs

could not be estimated directly from the St. Croix data, information was gathered from assessments and published studies conducted in watersheds with iteroparous runs, including ocean mortality (River Herring Benchmark Stock Assessment, 2012; Gibson 2004), spawning mortality (Havey 1961; Kissil 1974) and the probability of spawning for each age class (Gibson & Myers 2003). For the scenarios tested, the spawning population was started at 100,000 fish (roughly the current run count) and the model was run for 300 years to ensure stabilized distributions were reached. Initial abundance was proportionally allocated across ocean and spawning run age classes based on a stabilized population distributions. After this initial distribution was defined, population parameters for year t were calculated as outlined in Barber et al. (in review).

5.3.3.2. Passage Efficiency and Dispersal

Baseline upstream passage efficiency was estimated based on escapement information from 1984-1988 recorded at the first three dams (St. Croix Milltown Trap). While these calculations were useful, the majority of the results presented in this chapter focused on dynamics associated with changes in passage rather than baseline values because data were limited. Escapement values were used to calculate an average proportion of fish within each habitat unit (Table 5.1). This proportion was then used to calculate baseline passage probability (P_B) for each dam (Table 5.2).

Table 5.1. Recorded escapement levels from 1984-1988 and associated proportions entering Habitat Units 2 and 3.

Year	Escapement Dam 1	Escapement Dam 2	Proportion entering Unit 2	Escapement Dam 3	Proportion entering Unit 3
1984	152,900	78,000	0.51	65,000	0.425
1985	368,900	93,000	0.252	87,000	0.236
1986	1,984,720	1,300,000	0.655	625,000	0.315
1987	2,624,700	930,000	0.354	800,000	0.305
1988	2,590,750	1,004,200	0.388		
Average			0.432		0.32

Table 5.2. Calculated baseline upstream passage probability for dams 1-4 based on the average proportion entering habitat units as well as best estimates for dams with no historic data available.

Dam	Average Proportion Entering Unit	Equation	Baseline Passage Probability (P_{B1-4})
Dam 1	(1)		changed to 0.6
Dam 2	0.432	$P_{B2} = 0.4/P_{B1} = 0.4/1.0$	0.4
Dam 3	0.32	$P_{B3} = 0.3/(P_{B1}*P_{B2}) = 0.3/(1.0*0.4)$	0.75
Dam 4	0.2	$P_{B4} = 0.2/(P_{B1}*P_{B2}*P_{B3}) = 0.2/(1.0*0.4*0.75)$	0.67

Passage at dam 1 was initially set at 1.0 to calculate escapement probabilities, but this is not a realistic rate. However, we have no information on the number of fish that approach this dam and therefore cannot calculate passage efficiency based on collected data. Because of this, the passage efficiency at Milltown was estimated based on the fishway type (Noonan et al. 2012). In addition, escapement was not recorded at dam 4, and so the proportion of fish was estimated based on the slope of the relationship for the previous three dams. This proportion was used to determine passage probability (Table 5.2).

Dispersal rules, as described above, were developed for four separate habitat units that coincided with the areas between the four main-stem dams and above the dam furthest upstream (Figure 5.1). The majority of spawning habitat was located upstream, and spawners had to pass at least three dams to access it (Dill et al. 2010; Table 5.3). There were several dams with no fish passage that divided the west branch of lake systems from those connected to the main stem, and the habitat area associated with these were not included in the model. In addition, there are several lakes connected to the area furthest upstream where fish passage is currently blocked, and so these were not used in habitat size estimates.

Table 5.3. Area of habitat units in the St. Croix River with percent of total river-wide spawning habitat represented by each unit.

Habitat Unit	Acres	Percentage of Total
1	252	0.4
2	1174	1.9
3	23,212	38.1
4	36,209	59.5
Total	60,847	

5.3.4. Passage Simulations

A set of scenarios were run to explore particular questions associated with the outputs of the model. Each set of scenarios involved varying upstream and downstream passage rates between 0-100%, where 0 indicated no fish successfully passed and 100 meant all fish passed, with increments by a factor of 10. This was used to explore how changes in upstream adult passage and downstream juvenile passage affected population dynamics and net nutrient balance, calculated as adult import minus juvenile export, for each habitat unit. Spawner abundance, N and P adult import, and N and P juvenile export were recorded as outputs for each habitat unit.

5.3.4.1. One Dam

The first scenarios (A, Figure 5.2) were run with only one dam included as a constraint to population growth to test its effect on the alewife population without the compounding effect of multiple dams. Scenario A combined the acreage for all four habitat units and examined how spawner abundance, net N balance (ΔN), and net P balance (ΔP) changed when adult upstream and juvenile downstream passage rates were varied. A second simulation using this scenario was also used to explore how variable adult downstream passage rates affect the population age structure. To do this, juvenile downstream passage was held constant at 0.9, and both adult upstream and downstream rates were varied from 0 - 100% successful passage. The model was run for 300 years to ensure that the population had stabilized, and comparisons among passage rates were made using spawner abundances averaged for each age class using the last 20 years of data.

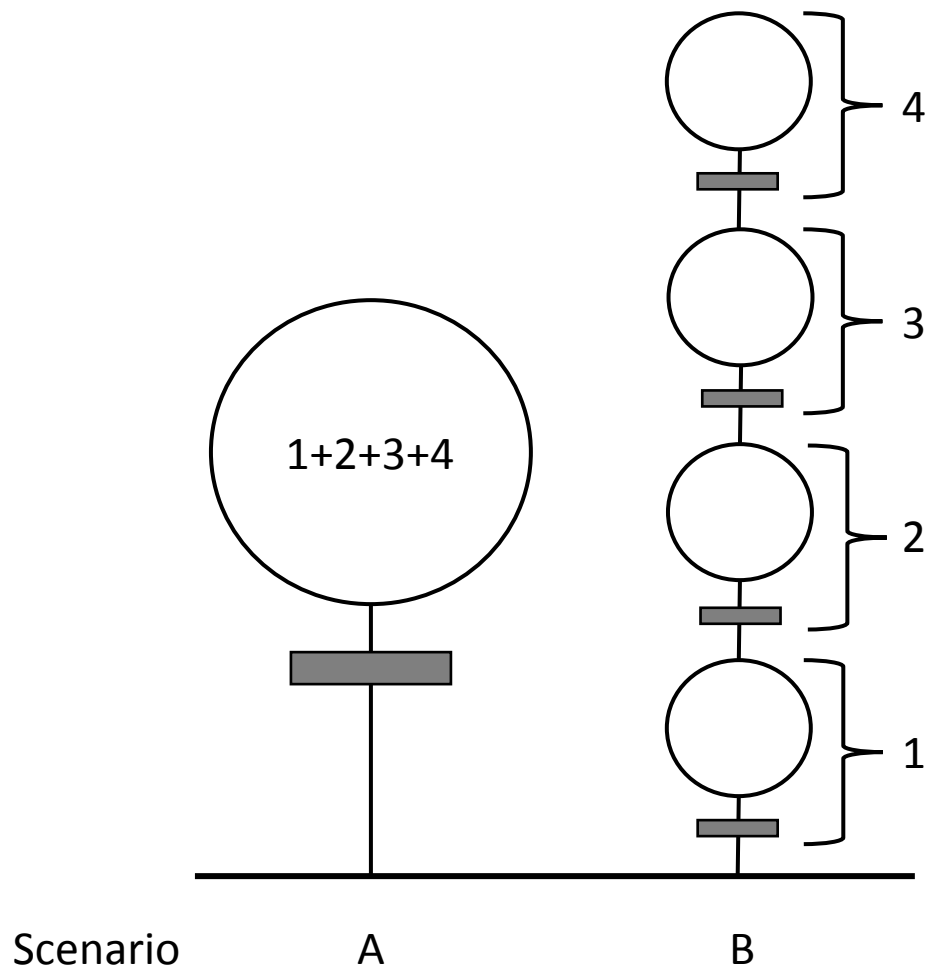


Figure 5.2. Idealized diagram of passage scenarios tested. Numbers 1-4 refer to the designation of separate production units separated by dams. In Scenario A, the habitat area for all four production units is combined and only one dam was included as an impediment to passage. For Scenario B, the river was divided into four production units each with its own habitat size and productivity. The effect of passing multiple dams was included, and fish moving upstream to production unit 4 had separate probabilities associated with passing each of the four dams.

5.3.4.2. Multiple Dams

Scenario B (Figure 5.2) explored the effect of multiple dams on spawner abundance, ΔN balance, and ΔP balance. First, the model was applied to escapement levels recorded in the St. Croix from 2008 to 2017 using baseline passage rates to estimate current nutrient dynamics. This time period was used because in 2008 the fishway at dam 2 was re-opened, marking the beginning of population recovery. Second, multiple scenarios were run where the values used for upstream and downstream passage success was increased both for all four fishways at once and for each fishway individually, with the other three kept at a baseline value based on historic escapement levels for the St. Croix River. For the former scenario, outputs were totaled for all four production units to present results for the entire river. For the latter set of scenarios, results were only shown when varying passage at dams 1 and 3. Dam 1 was located at the head of tide and represents access to the lower portion of the river (Figure 5.1). Spawner access beyond dam 3 is critical as 98% of spawning habitat appropriate for alewife in the St. Croix River is located above this barrier. Therefore, dam 3 represents access to the upper area of the river. Spawner abundance was recorded within each habitat unit, as well as adult import and juvenile export for N and P. These values were converted to a series of heat plots for visual trend comparisons.

5.3.4.3. Commercial Fishery

Four scenarios were compared to explore the compounding effects of passage efficiency and a commercial fishery: 1) no passage effect and no fishery effect, 2) passage effect but no fishery effect, 3) passage effect and 50% take fishery in the estuary, and 4) passage effect and 50% in-river fishery below dam 3. For the first scenario, a 50%

mortality rate was applied to spawners by adding it to the passage mortality at the first dam on the system. This meant that passage into habitat unit 1 (and subsequently the rest of the system) went from 60% to 30%. For the second scenario, the 50% fisheries mortality rate was added to the number of fish that passed the dam and successfully entered habitat unit 3. This was accomplished by removing 50% of the spawners that approached the third dam, and then enacting a passage effect on those fish that remained as follows:

$$S_{t,u+1} = (m_{u+1} - (m_{u+1} \cdot 0.5)) \cdot P_{i+1}.$$

The total spawner abundance and relative percentages for each habitat unit related to these two scenarios was then compared to the distribution of fish when no dams are present as well as when dams are present but no fishery is included. Dam passage rates used for these scenarios were kept constant at the baseline values calculated for the St. Croix River based on historic escapement levels as described above. The model was run for 300 years and the total spawner abundance at the end of each run was compared for each scenario.

5.4. Results

5.4.1. One Dam

For scenario A with only one dam, a maximum of 26.9 million spawners were produced when both adult upstream and juvenile downstream passage success was 100%. For a low downstream passage rate, spawner abundance remained low regardless of the level of upstream passage success (Figure 5.3). The same is true for low upstream passage and high downstream passage. With unconstrained upstream passage, spawner

abundance rises in roughly even increments for an increase in downstream passage, and vice versa. However, the relationship between the two is not linear.

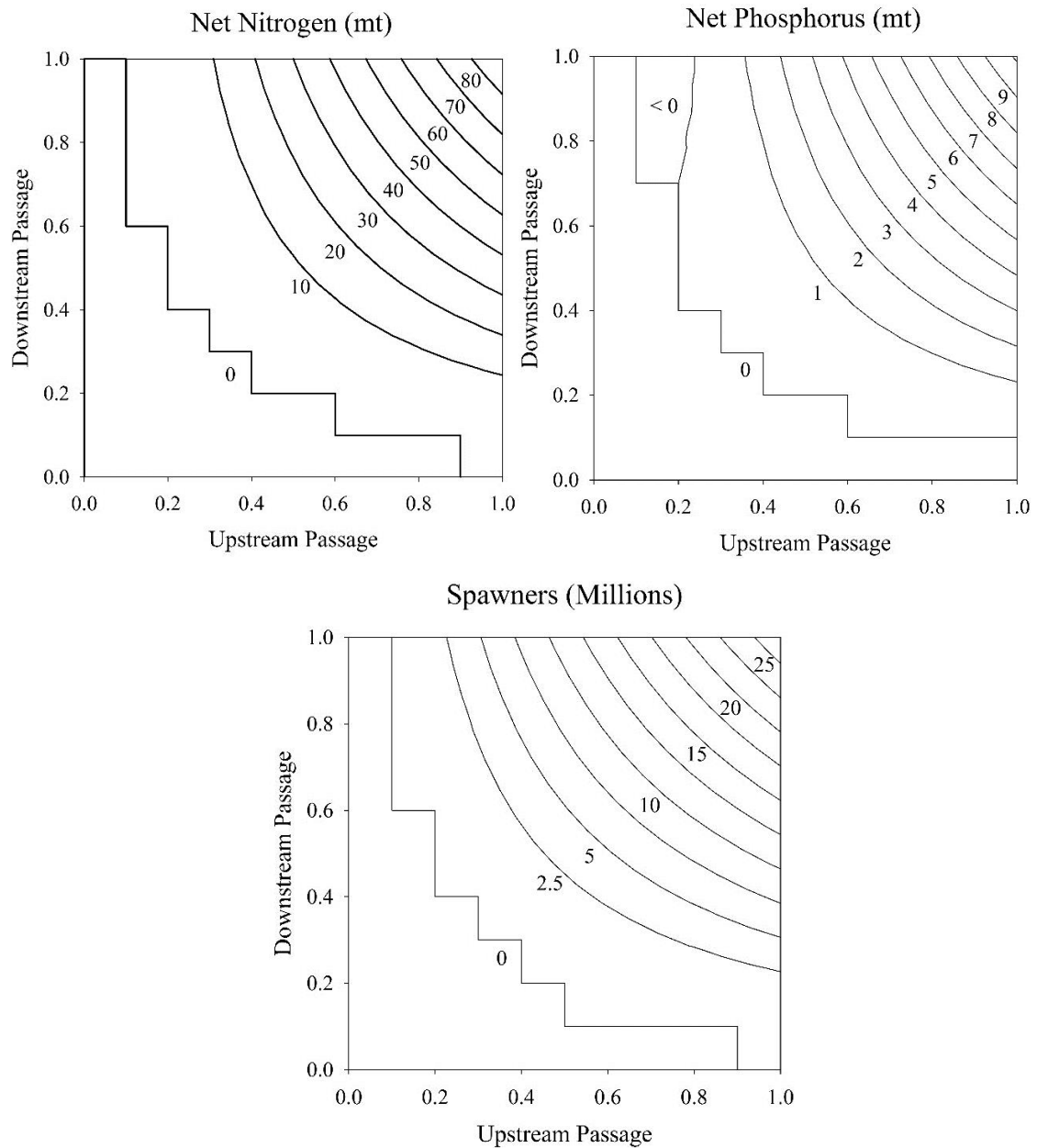


Figure 5.3. Spawner abundance, ΔN calculated as import - export (metric tons), and ΔP (mt) related to upstream adult and downstream juvenile passage rates when one dam is present. Passage is varied between 0 and 100% success.

For N, the quantity delivered by upstream passage overwhelmed juvenile export regardless of upstream and downstream passage rate (Figure 5.3). With ΔN ranging from 0 – 88,829 kg, the net import was closely proportional to spawner abundance. Juvenile export did not dominate regardless of passage rate, though ΔN was essentially zero when either upstream or downstream passage rates were low. Phosphorus had a different trend at low upstream and high downstream passage rates. Net export occurred at upstream rates between 0 - 20% and downstream rates between 60-100%, where higher downstream rates resulted in a maximum of 228 kg leaving the system. Net import occurred at upstream passage rates 30% and higher when downstream passage rates were $\geq 20\%$. Net import increased with increasing upstream and downstream passage rates, similar to the trend seen in N. The maximum value for P net balance was 10,148 kg, which was much smaller than for N.

5.4.1.1. Age Structure

Regardless of the modeled upstream passage a rate, the spawning population was dominated by fish ages 3-5, reflective of the maturity rate of the source population. However, the proportional contribution of each age class changed as passage rates varied (Figure 5.4). For all age classes, spawner abundances remained negligible when upstream adult passage was 20% or less, and at that level, only ages 3-5 were found in the population. High upstream passage rates with low downstream passage favored a population dominated by Age-3 fish with fewer repeat spawners in older age classes. A further increase in upstream passage resulted in higher abundances of all age classes, but the population structure was relatively unchanged. High downstream passage rates with low upstream passage favored a smaller population size that was more heavily skewed

toward older age classes of repeat spawners. A further increase in downstream passage resulted in a marginal change, shifting the distribution further toward older-aged fish (Figure 5.4). When upstream and downstream passage rates both reached 80%, age-4 fish were the most abundant cohort. Here the ratio of fish ages 3 and 5 was even, and age-8 fish made an appreciable contribution to the population.

5.4.2. Multiple Dams

5.4.2.1. Current Nutrient Dynamics in the St. Croix River

From 2008-2017, high population variability resulted in annual fluctuation in net nutrient dynamics. This was reflected in ΔN and ΔP for habitat unit 1, whose dynamics closely mirrored the total for the river (Figure 5.5). At the current recorded escapement levels, modeled results indicated minimal N import in habitat units 2-3 and net export in unit 4. The magnitude of this export was not enough to out-weigh import in unit 1. For P, poor upstream passage led to net export for all three of these habitat units. Export levels increased as the population grew and a larger number of spawners distributed to the productive upstream habitat.

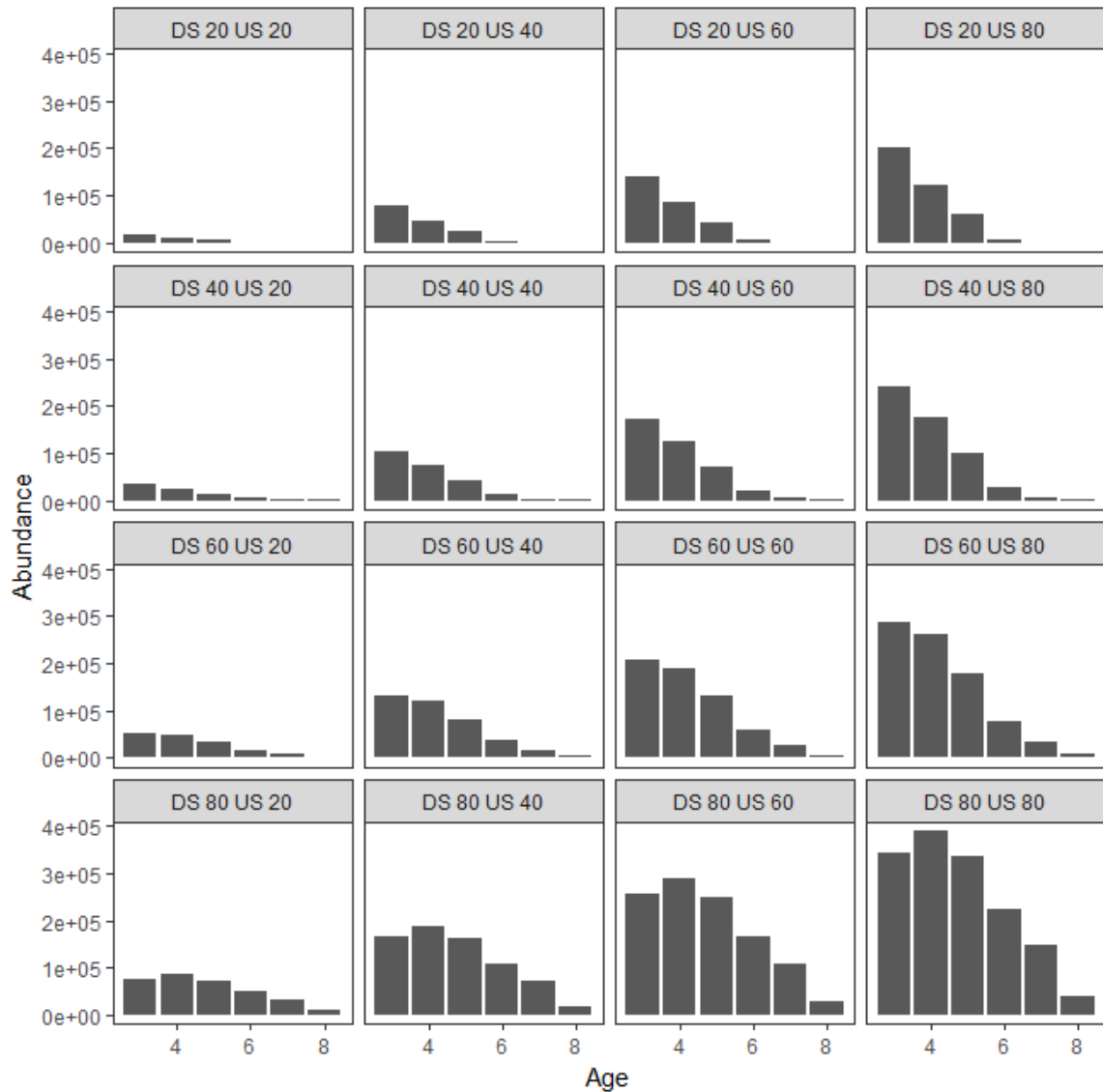


Figure 5.4. Effect of upstream (US) and downstream (DS) adult passage on age structure of alewife population. Each panel represents a passage scenario, and numbers in the grey box indicate percentage of adult spawners that successfully pass for each scenario (i.e. DS 20 US 20 = 20% of adults pass DS and 20% pass US). Bars represent the abundance of adults in each age class for every passage scenario.

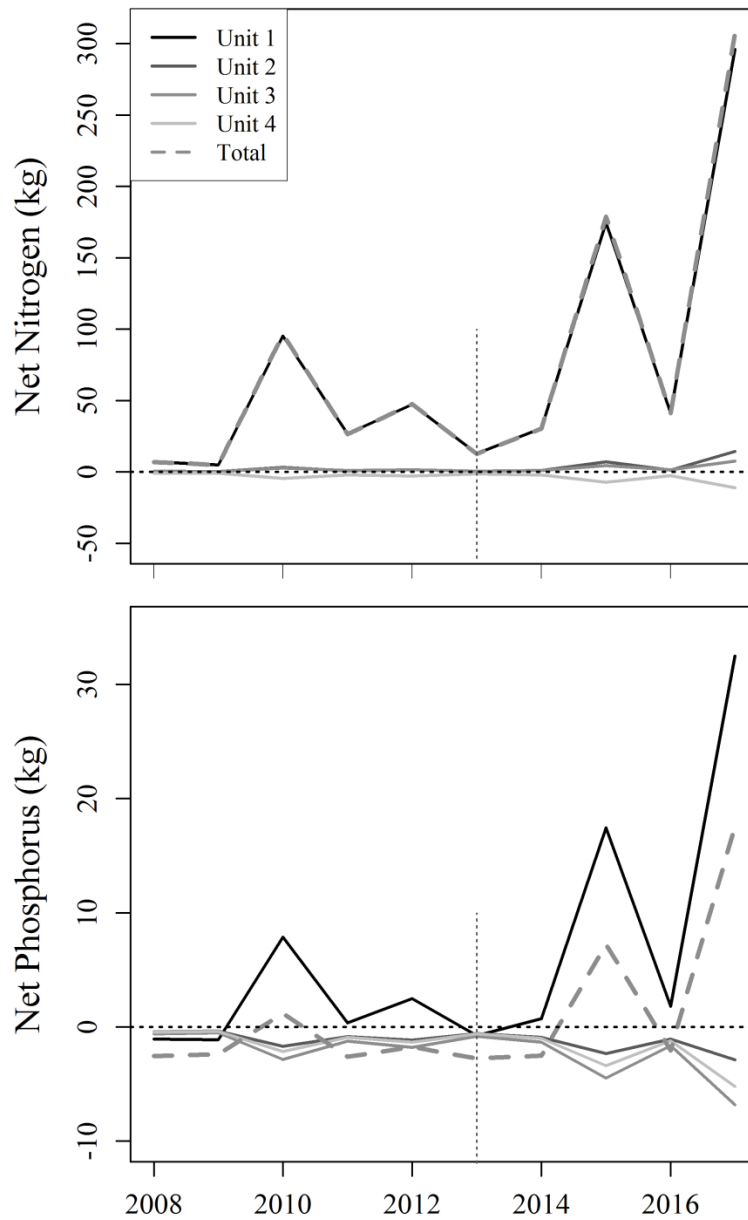


Figure 5.5. Modelled net N and P (kg) in the St. Croix River using recorded escapement at head of tide from 2008-2017 (net value = import – export). Dotted vertical line represents when fishways at dams 2-4 were reopened in 2013. Values below the horizontal dashed line represent net export, and values above net import.

5.4.2.2. System-Wide Effect of Variability in Passage Success

The addition of multiple dams to a system increased the effect that upstream passage had on the total spawner abundance in the river at a system-wide scale (Figure 5.6). Even with downstream passage held at 100%, spawner abundance was less than 500,000 until upstream passage rates reached 50%. When upstream passage was 100%, downstream passage rates of 20% or more led to a population $\geq 500,000$ fish. This serves to illustrate the importance of upstream passage given large habitat quantity higher upstream in the model system. Net nitrogen export did not dominate at any population size, though import largely reflected spawner dynamics and remained under 2 kg until upstream passage was at least 50% (Figure 5.6). For ΔP , net export occurred when upstream passage was between 10-30% and downstream passage was between 50-100% (Figure 5.6). Substantial P import began to occur at roughly the same passage rates as N, with the magnitude rising along with an increase in both upstream and downstream rates.

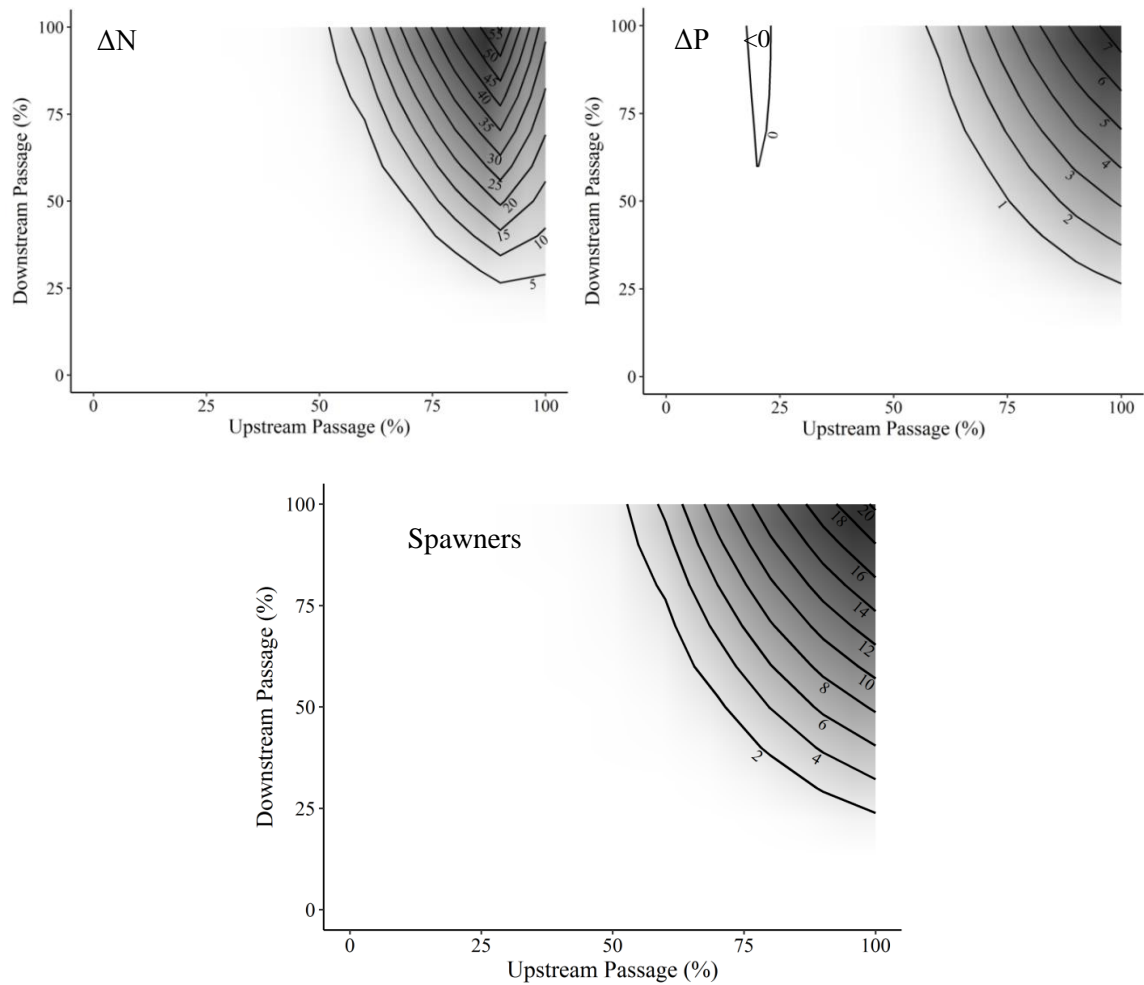


Figure 5.6. Spawner abundance (millions), ΔN (mt), and ΔP (mt) related to upstream adult and downstream juvenile passage rates when one dam is present. Passage is varied between 0 and 100% success.

Habitat unit location and size affected ΔP dynamics on a system-wide scale (Figure 5.7). Upstream passage had a more pronounced effect than downstream passage on P import, as shown by ΔP increasing to above zero at roughly 20% upstream passage. The habitat units furthest upstream displayed net P export at a relatively low level of downstream passage (50%). However, this range narrowed moving further downstream as juveniles needed to survive passage through multiple dams. Net P export was seen in

all four units when downstream passage was high, but upstream passage was relatively low. For the first habitat unit, export occurred when downstream survival was between 70-100% and upstream survival was between 10-25%. The highest P import in this unit occurred when upstream passage was between 70-80%. Upstream passage rates above 70% allowed more fish to pass the next dam and leave the first habitat unit. This resulted in those nutrients being deposited in a different unit, even though total population increased. The same pattern was also seen in habitat unit 2, though there was a larger range of export as this unit was five times larger and therefore could produce five times as many juveniles.

The effect of successful upstream passage became more evident moving up the system as the compounding effect of dams sequentially reduced spawner abundance. Net P export occurred when downstream passage rates were above 50% and upstream passage rates were between 30-70% for unit 3 and 20-60% for unit 4. In habitat units 3 and 4, ΔP export occurred at a wide range of passage rates because of both low spawner abundance and high juvenile productivity due to the large quantity of spawning habitat. Net P import only occurred when upstream passage rates were greater than roughly 75%. The system-wide passage was a multiplicative property of the number of dams passed and resulted in a greater sensitivity to changes in passage at an individual site. This led to a steeper gradient between import and export. The combination of greater habitat quantity and low spawner density produced more surviving juveniles per capita spawner, but a narrower range of passage rates that resulted in substantial P import.

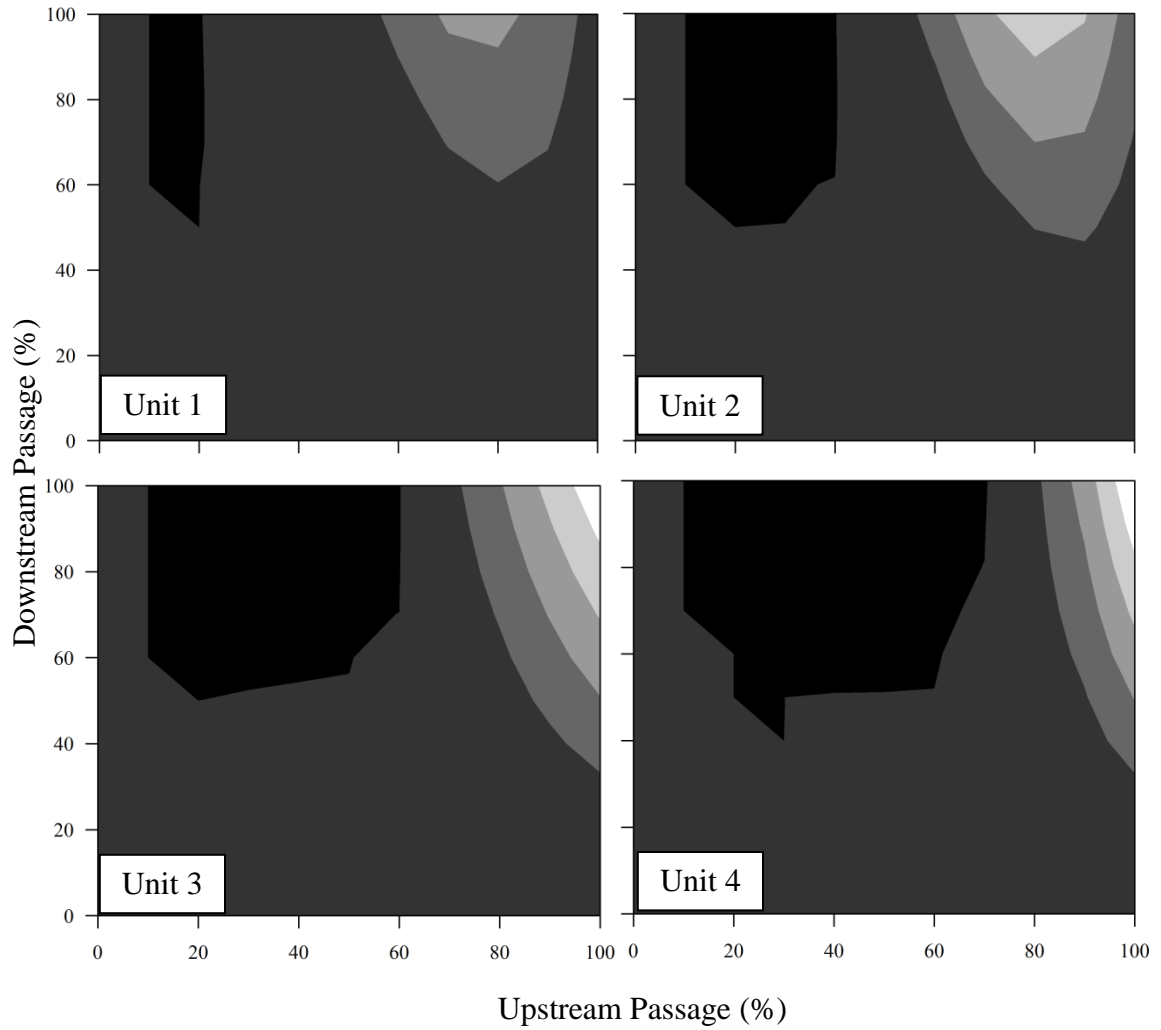


Figure 5.7. ΔP balance (in kg) for all 4 habitat units when upstream and downstream passage rates at all four dams are simultaneously increased in a stepwise fashion. Black indicates net export, dark grey indicates minimal net import, and lighter greys to white indicate increasingly larger net import.

5.4.2.3. Variable Passage Rates in the Lower River

The patterns for P dynamics within each habitat unit became more complex when passage at only one dam varied but the other three were held at a constant rate. As with the previous scenarios this was because of the interaction between juvenile production (as related to habitat size) and poor passage efficiency. The calculated baseline passage levels included relatively poor passage at the second dam, with higher passage rates at the two upstream dams. When passage rates at the first dam at the head of tide were varied, but the other three dams held at a baseline level, the effect on spawner abundance in each production unit was similar but differed with the size of the habitat unit (Figure 5.8). For all four units, the number of returning spawners was near zero if upstream or downstream passage was below ~ 40% at the first dam, even if the other passage metric was set to 100% (Figure 5.8). When both upstream and downstream passage rates were high, a small change in one of the rates led to a large change in spawner abundance, therefore resulting in nutrient import. This change in spawner abundance was almost symmetric with respect to a similar sized change in upstream or downstream passage rates.

For habitat units 1 and 2, which were the smallest, low upstream or downstream passage rates resulted in a ΔP that was either net export or negligible import (Figure 5.8). For these two units, P dynamics closely mirrored the spawner abundance. Phosphorus import into these two units did not begin to increase until upstream passage rates reached 40% and downstream rates 100%. The inverse was also true, with P import low until downstream rates exceeded 40% and upstream rates reached 100%. Once passage surpassed these rates, P import increased steadily.

The larger habitat units required higher passage rate scenarios for P import to occur (Figure 5.8). In production unit 3, maximum export levels of 67 kg occurred when downstream passage was 100% and upstream passage was around 60%. Net P balance did not become positive until upstream passage reached about 75%. At this passage level, ΔP was 0 kg between downstream passage rates of 0-50%. For habitat unit 4, which was the largest, net P export occurred when downstream passage rates were higher than 60% and upstream rates were higher than 50%. Net export only exceeded 100 kg when downstream rates were 100% and upstream rates were 60%. Export was the highest (137 kg) when upstream rates increased to 80%.

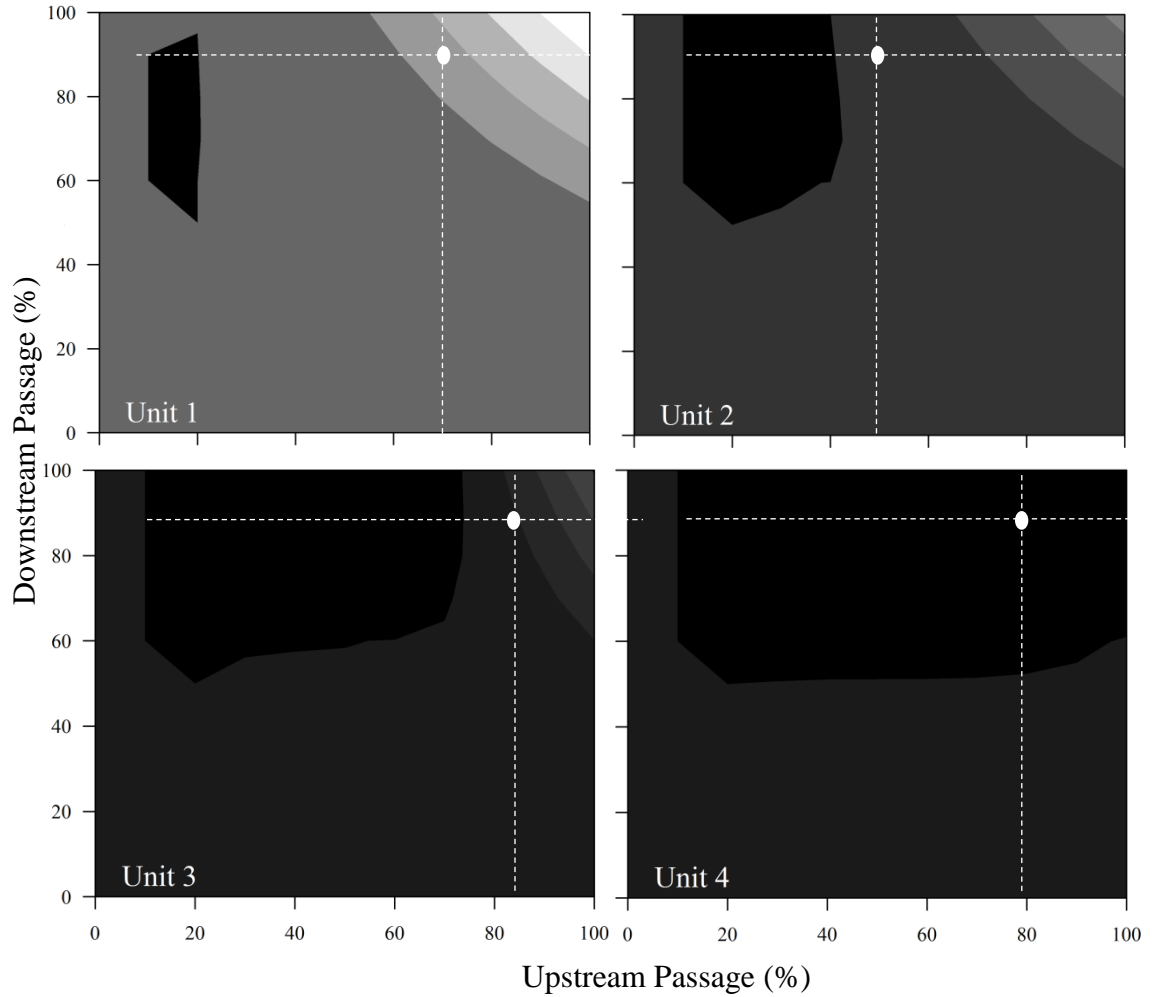


Figure 5.8. ΔP (import – export in kg) for all 4 habitat units when upstream and downstream passage rates at dam 1 are increased in a stepwise fashion and passage at all other dams is held at a baseline level. White dashed lines indicated baseline passage rates for dam immediately downstream for each habitat unit. Black indicates P export, dark grey indicates minimal net import, and lighter greys to white indicate increasingly larger net import.

5.4.2.4. Variable Passage Rates in the Upper River

When the third dam was varied in the system, the effect on spawner abundance was site-specific (Figure 5.9). Increasing upstream passage rates at dam 3 had a reduced effect on habitat units 1 and 2 compared to units 3 and 4. This was because lack of passage at dam 3 could not prevent fish from entering the first two units. However, spawner abundance in unit 1 remained small (<200 individuals) until downstream rates at dam 3 reached roughly 50%, allowing utilization of the large quantity of habitat available in units 3 and 4 to contribute to the total population. Spawner abundance in unit 2 was greater than 50,000 fish when downstream passage at dam 3 was between 70-100%, but upstream passage was less than 90%. The spawner abundance in unit 2 peaked when the upstream passage at dam 3 was 70%. At a higher upstream passage rate, the system wide population was larger, but more fish were successfully passing the third dam, thereby reducing the number remaining in habitat unit 2.

Phosphorus dynamics also were dependent on location within the watershed. When passage in the lower river was varied, the general trend indicated that ΔP was relatively insignificant until both upstream and downstream passage were high. When passage was varied in the upper river, import dominated at a wider range of upstream passage rates, but only at high downstream passage rates. No P export occurred in habitat unit 1 as its small size resulted in low juvenile production, which was more than offset by excretion from the large number of adults passing through to upstream habitat units (Figure 5.9). For habitat unit 2, ΔP was ≤ 5 kg until downstream passage rates reached almost 60%. The highest P import, 178 kg, occurred when upstream passage was roughly 70% and downstream passage was 100%.

Trends in spawner and nutrient dynamics were similar between habitat units 3 and 4. Poor passage at dam 2 led to lower spawner abundance in the larger habitat units, meaning juvenile production per capita spawner was high. As a result, the fourth habitat unit saw P export occur when both upstream and downstream passage were high, but at lower rates the net nutrient balance was near zero. Spawner abundance remained small until upstream passage rates reached roughly 30% and downstream passage 50% (Figure 5.9). From there, spawner abundance grew with increasing passage rates. For habitat unit 3, ΔP was essentially zero across all upstream rates when downstream passage was less than 60%. The same was true in unit 4 when downstream was less than 50%. Net P export only occurred for all downstream passage rates above those values, with an increase in magnitude occurring as upstream passage improved. For both habitat units, maximum export occurred when downstream rates were 100%. For habitat unit 3, a maximum of 70 kg was exported when upstream passage was 75% and for unit 4, 140 kg were exported between 90-100%. For unit 3, net P export dominated except when both passage rates were roughly 100%. Net export dominated in unit 4, though the magnitude was consistently negligible at downstream passage rates below 50%.

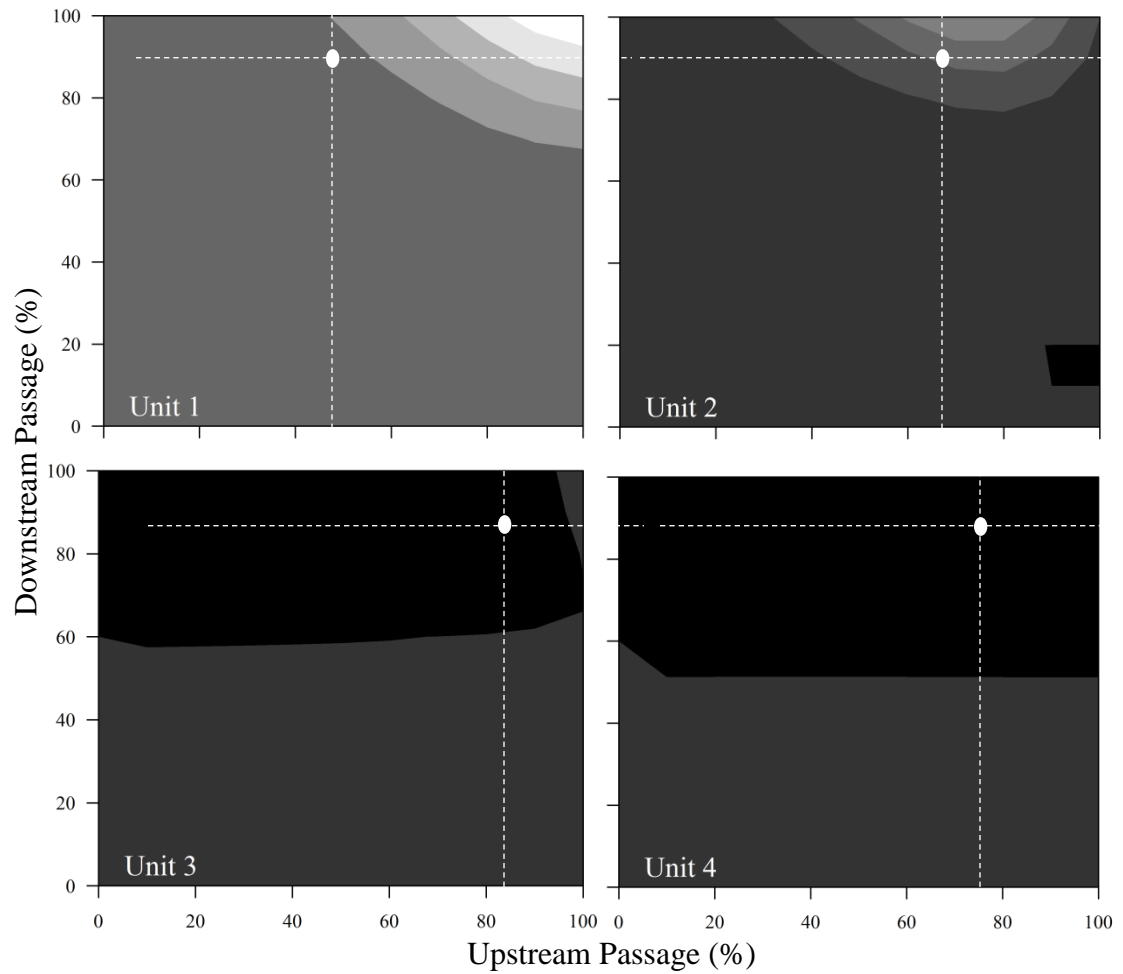


Figure 5.9. ΔP (in kg) for all 4 habitat units when upstream and downstream passage rates at dam 3 are increased in a stepwise fashion and passage at all other dams is held at a baseline level. Black indicates net P export, dark grey indicates minimal net import, and lighter greys to white indicate increasingly larger net import. White dashed lines indicated baseline passage rates for dam immediately downstream for each habitat unit.

5.4.2.5. Effect of a Commercial Fishery

Dam passage reduced the overall abundance of spawners entering the river, as well as changing the percentage of spawners found within each habitat unit (Figure 5.10). When no dams were present, spawners distributed according to the relative availability of spawning habitat, meaning the majority of adults migrated to the upper portion of the river into habitat units 3 (38%) and 4 (60%). With dams present, the total spawner abundance was reduced from 27.8 million to 2.1 million and poor passage efficiency at dam 2 resulted in a large percentage of the total population spawning in habitat unit 1 (60%). The location of the fishery affected the spawner distribution in all four habitats. The portion of the population that spawned in unit 1 was unchanged in the presence of a fishery located in the estuary and increased when it was below dam 3. For the latter scenario, the percentage of adults in units 2-4 was less than when the fishery was located in the estuary.

Spawner distribution among habitat units did not change when a 50% take fishery was enacted in the estuary, but the total number of spawners was greatly reduced. This scenario reduced the total spawner population from 2.1 million to 93,000 when compared to the baseline dam passage without a fishery. Roughly 150,000 fish could be harvested at this maximum population size. Harvest was greater than the spawning run because the location for this fishery reduced the total number of adults entering the river by half, and then poor passage efficiencies at the first two dams restricted the majority of spawners to the lower, less productive part of the river. This consistent annual restriction in spawner abundance led to a greatly reduced run size compared to the other scenarios.

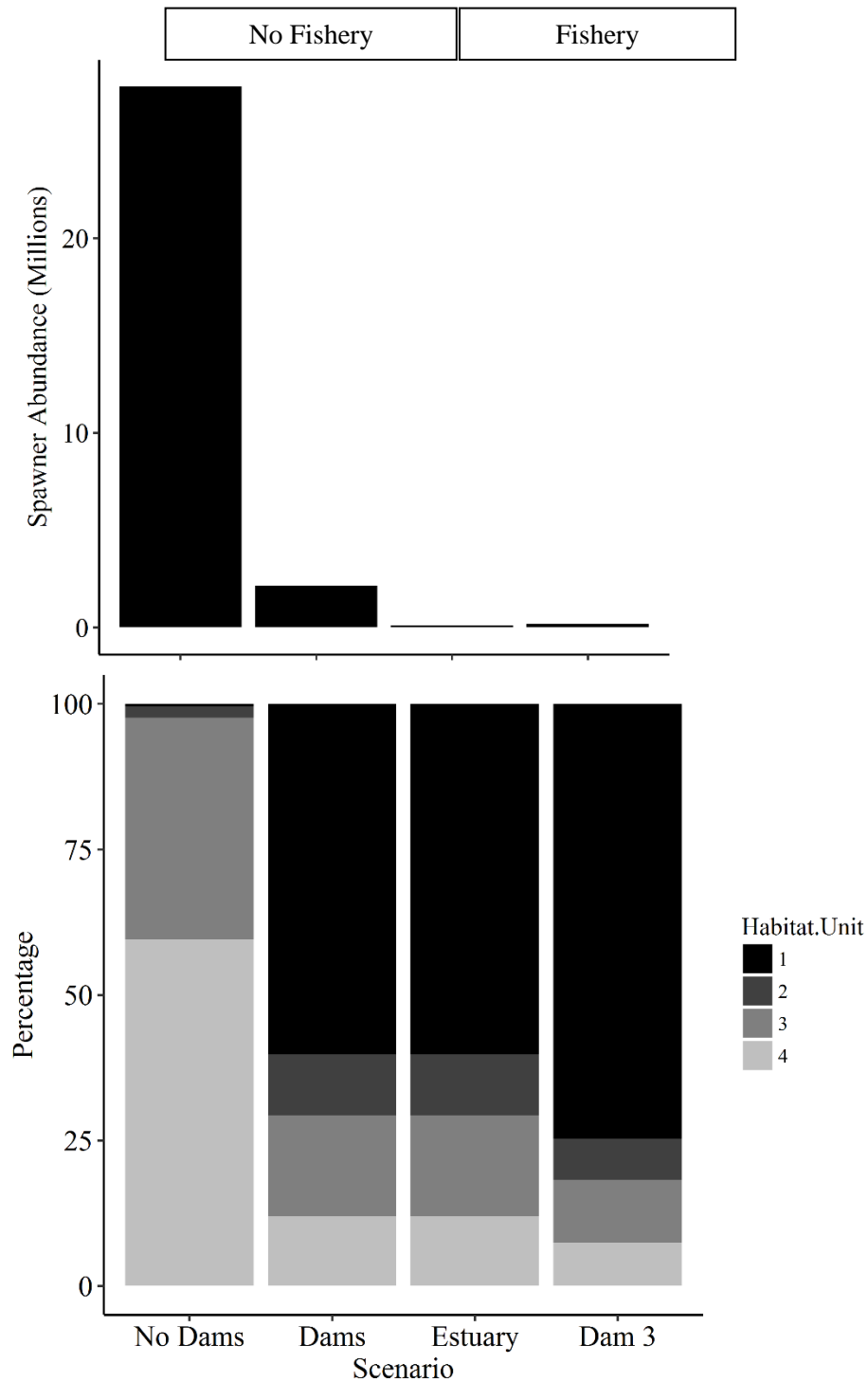


Figure 5.10. Spawner abundance and relative percentage within each habitat unit associated with four scenarios. These included: 1) no passage effects, 2) passage effects from dams only, 3) passage effects with 50% fishery in the estuary, 4) passage effects with 50% fishery immediately below dam 3.

When a 50% take fishery was enacted at dam 3, the total spawner abundance for the river was almost two times higher (175,000 spawners) than when it was located in the estuary and showed a smaller decrease from the baseline dam scenario of 2.1 million (Figure 5.10). This fishery caused a restriction of upstream habitat access, meaning the lower two habitat units were utilized by a larger proportion of the total spawners. While this would seem to restrict population productivity similarly to the previous scenario, with the fishery located further upstream a larger number of spawners could enter the river and utilize the lower habitat units. This meant the system-wide total was higher regardless of site-specific distribution of spawning. However, the number of adults harvested was much lower than when the fishery was located in the estuary, with a take of roughly 43,000 individuals.

5.5. Discussion

This alewife population model estimated high productivity in a large watershed such as the St. Croix, but also suggested that changes in connectivity can determine the status of a population in terms of spawner abundance and net N and P dynamics. The estimated spawner abundance falls in line with previous capacity estimates for the St. Croix River of around 20 million adults (Flagg 2007; Dill et al. 2010). At baseline passage levels, modeled spawner abundance reflected escapement levels in the early 1980s when the alewife population reached its recorded maximum of 2.5 million adults. For N, our results showed no significant net export regardless of juvenile production as import by adults was high for carcasses, gametes, and excretion. These estimates, however, assume homogeneous habitat quality. A higher rate of freshwater productivity would result in greater juvenile productivity per capita spawner (Chapter 2), ultimately

leading to net nutrient export at a low population abundance. However, previous alewife modelling work in Chapter 2 indicated that N export was minimal even when freshwater productivity was high.

Net P, however, shifted from export to import based on the size of the spawning population in relation to site-specific carrying capacity because juveniles had a relatively high P content in their tissue (Barber et al. in review). When the modelled population was kept consistently small, such as in the case with poor passage efficiency, a larger number of surviving recruits were produced per-capita than when the population was large. This elevated juvenile productivity meant that P export was high even when spawner abundance was low. However, adult import increased along with the spawning population, leading to an eventual shift from net export to net import. Habitat size determined at what point along the track of population recovery this shift occurred because a larger lake had higher juvenile productivity. As a habitat-specific capacity was approached, per-capita juvenile productivity plateaued while spawner abundance continued to increase and import became the dominant nutrient dynamic.

For the shift from net P export to net import to occur, the spawning population needed to increase with time as would be seen in a recovering alewife population. However, persistently low connectivity could maintain a population at net export. Our results demonstrate that when one or more dams are added to a system, the reduction in upstream passage dictates both the size of the adult population and juvenile survival. Downstream survival rates determined the number of fish that recruited into a population, as well as export rates with the assumption that those juveniles that did not successfully pass a dam stayed in the lake and those nutrients were eventually recycled in the system.

Upstream rates determined adult abundances, which also controlled future recruitment potential. When only one dam was considered, minimum downstream and upstream passage rates of about 20% was required for the run to reach 1 million fish, which was only 4% of the river's spawning potential. After this, a concurrent increase in upstream and downstream passage led to a steady population increase in a stepwise fashion. These results demonstrate the large effect of reduced connectivity, agreeing with previous work that even one barrier can lead to a vast reduction in spawner abundance (Cote et al. 2009).

5.5.1. Indirect Effects of Poor Passage

In addition to reducing the abundance of a population, passage barriers can also affect its age structure as well as enacting artificial selective pressure (Davis & Schultz 2009). Repeat spawners returning to dammed systems have a lower chance of survival simply from passing one or more dams several years in a row. Our results demonstrate that when at least one dam is present and/or when passage rates are poor, the age structure of a population shifts to favor younger fish. This change in age structure is important because fecundity increases with body size, meaning a larger female produces more eggs (Jessop 1993). Iteroparous American shad populations tend to have fewer repeat spawners when passage is poor, which has been tied to lower population egg production (Leggett et al. 2004). Previous studies have suggested that female age is a strong predictor of larval growth and survival ((Berkeley et al. 2004), and so losing this older portion of the population could affect recruitment rates.

A shift in the age structure of the population can also influence nutrient dynamics. Fecundity was calculated based on average size-at-age, meaning that fewer eggs will be

produced by a younger population (Barber et al. in review). Using an average weight, age 8 fish at 353 g produced roughly 180,000 more eggs per individual than 144 g age-3 fish (SC Milltown Report 2016). In the model, the distribution of spawners within the river is based on abundance per unit area. If we assume that the same numbers of fish are entering an area but that they are predominantly younger, then we would expect an overall reduction in nutrient import as smaller fish import less N and P by weight (Twining et al. 2017). This could mean that net P export will be dominant at a wider range of spawner abundance. In addition, ΔN may also become dominated by net export at a low adult abundance, assuming that juveniles retain the average size currently used in the model. A reduction in nutrient subsidies could result in lower freshwater productivity to support juvenile growth, though if population fecundity is also reduced by a younger age structure then this effect would be lessened.

In addition to lowered per-capita fecundity, a reduction in iteroparity could be seen as repeat spawners are removed from the spawning stock, potentially leading to lower population resilience (Davis & Schultz 2009; Jonsson et al. 2010). An iteroparous life history may be the result of strong environmental variability in the northern part of the alewife's range (Crecco & Savoy 1985). Cooler temperatures along the North Atlantic coast lead to reduced metabolic costs related to upstream movement, meaning adults have more energy to survive their downstream migration (Leggett & Carscadden 1978; Jonsson et al. 2010).

5.5.2. Multiple Dams

When multiple dams act as barriers, the compounding effect of upstream passage efficacy on the recovery of a spawning population becomes more pronounced (Brown et

al. 2013). For a fish to successfully pass multiple dams, passage efficiencies at each fishway need to be high because the combined passage rate is low (Shaw et al. 2016). When passage rates for all four dams were altered concurrently, the alewife population did not reach 1 million fish until upstream passage at all dams was greater than 50%, a much higher rate than needed for only one dam. However, downstream passage rates in this instance were similar (20%) when comparing one dam to multiple dams.

The effect that reduced spawner abundance will have on population recovery depends on the relative location of spawning habitat to the source of this decline, which is watershed specific. For the St. Croix River, the majority of spawning habitat was located upstream and spawners had to pass at least three dams to gain access. Effective cumulative passage in the lower parts of the river will therefore accelerate population recovery. In addition, the population-level effect of a 50% take fishery led to greater reduction in total abundance when it was located in the estuary as opposed to further upstream, as has been suggested in previous studies (Cote et al. 2009). Alewife harvest for the past century has been focused in coastal waters, which serves to create an additional bottleneck to that already imposed by poor fish passage (Hall et al. 2012). Records indicate that prior harvests were located inland, and likely put less strain on the productivity of a population by allowing more fish to enter the river (Hall et al. 2012), which is supported by the results of the fisheries scenarios we tested.

For this model, cumulative passability consisted of simply multiplying individual passability for successive dams, which may have led to overestimation of passage success. In reality, multiple factors such as straying, fallback, upstream motivation, and migratory delays can affect successful upstream movement, especially when multiple

dams are involved. These factors can change individual behavioral or cause negative physiological effects (Kemp & O’Hanley 2010). Straying and fallback behaviors, migratory delays, and upstream motivation can all affect passage success, especially when multiple dams are involved. Fallback, defined as when a fish moves past a dam but then “falls” back downstream, has been associated with searching for suitable spawning habitat. While alewife that exhibit straying behavior can promote recolonizing a habitat, searching can also lead to the need to pass through a dam multiple times, therefore causing migratory delays or mortality but may lead to a reduced chance of migrating further upstream as the probability of an individual surviving is reduced each time it has to pass a dam (Frank et al. 2011; Cooke & Hinch 2013; Pess et al. 2014).

Delays due to passage barriers can also affect the upstream and downstream migration of adults as well as the downstream migration of juveniles. Upstream delays can be the result of poor attraction to a fishway, causing individuals to spend more time searching for access upstream or downstream (Jonsson et al. 2010; Brown et al. 2013). Daily fishway capacities could also cause delays. Alosines are a schooling fish and prefer to enter fishways when others are present. However, overall passage efficacy is limited by capacity and can be reduced when too many fish attempt to utilize a fishway even if it has a high efficiency at lower population levels (Pess et al. 2014). Delays increase the amount of time a fish has to spend moving upstream, and may cause individuals to spawn further downstream than they would in the absence of dams (Jonsson et al. 2010). For adults moving back downstream, delays can use up already depleted energy stores. Also, downstream movement generally occurs later in the season when water temperatures are warmer, putting further stress on an adult that is having

difficulty moving past a section of a river (Schreck et al. 2001; Gregory et al. 2002; Caudill et al. 2013). For juveniles, the window of opportunity for downstream migration is small. Juveniles need to reach saltwater before they lose the ability to osmoregulate in freshwater, and downstream delays can cause stress to fish as well as a higher rate of mortality, especially given that many fishways account for upstream but not downstream passage (Oldani et al. 2007).

Passage through multiple dams is also contingent on an individual's motivation to move further upstream, and this can depend on a suite of cues such as temperature, water velocity, and natal homing (Jonsson et al. 2010; Caudill et al. 2013; Cooke & Hinch 2013). This model assumed that as one habitat unit reached spawner capacity, fish moved upstream to the next habitat (Barber et al. in review). Depending on the level of motivation for passing multiple dams, spawner abundance and therefore nutrient import may be overestimated for habitat units further upstream as it was assumed that fish distributed according to a given number per acre. There are likely limitations in interpreting the results of this modeling work associated with the inability to quantify this type of upstream motivation in spawning adults. In the St. Croix River, alewife populations were blocked from the upper habitat units for decades and fish were stocked in the second habitat unit. If alewife home to spawning habitat, it is possible that, at least initially, the majority of spawners will lack the motivation to move further upstream. This could cause the population to recover at a slower rate than occurred in the model as most of the "productive" spawning habitat is in the upper river.

5.5.3. Ecological Effects of Variable Passage Efficiency on MDN Input

On a watershed scale, the assimilation of MDN subsidies at a particular lake by the freshwater community will depend on the magnitude and timing of nutrient delivery, both of which are affected by passage efficiencies. Low passage rates, migratory delays, and changing temperatures could affect the timing of these resource subsidies and affect ecosystem linkages. When discussing nutrient subsidies and their effects on freshwater systems, it is often assumed that these are constant inputs throughout a season. Our results only explore nutrient import and export as an annual amount, but in reality these subsidies are pulsed and vary within a season (Sato et al. 2016). The timing of this pulsed subsidy can determine whether or not community growth increases within a freshwater system. If maximum subsidy input comes later in the season, then it doesn't provide either an alternative food source for predators or a pulse of resources for prey (Sato et al. 2016).

The presence of dams could also flatten out the pulse of nutrient subsidies both by affecting spawner movement directly and by affecting water flow. While construction of dams can form impoundments and increase low-flow areas in a river, creating more spawning habitat for alewife, their compounding effect makes it less likely that spawners will successfully reach upstream habitat (Cote et al. 2009). Migratory delays can prevent adults from accessing spawning grounds en masse, and even a fishway with a high passage rate can create a bottleneck for a stretch of river (Pess et al. 2014). Delays or blockages could prevent nutrient delivery at upstream sites while simultaneously inflating delivery at downstream sites. In addition to affecting upstream migration, dams also stabilize flow in a river. This can lead to higher retention of nutrients within a lake or

flowage. On the other hand, nutrient subsidies are more easily incorporated into the freshwater community in low flow conditions. Water control associated with spring floods may lead to greater retention of nutrients within site (Flecker et al. 2010; Wheeler et al. 2015).

Natural interannual variability caused by environmental stochasticity, which was not measured in the forward-projecting model, can also affect net nutrient delivery. In the St. Croix River, recorded escapement levels from 1981-2017 at the first dam indicate large annual fluctuations in population levels, primarily due to fishway closures (Figure 5.5). Estimated nutrient dynamics based on these escapement levels indicate that despite these fluctuations, ΔN for the overall system has been positive. However, when exploring nutrient dynamics within each habitat unit, the majority of the net N input is located in the first habitat unit. This is a result of both high spawner abundance within this unit due to poor passage rates at dam 2 and high excretion rates from the large number of spawners traversing through on their way upstream. In contrast, the net N import in the other three habitat units is close to zero. The ΔP in the St. Croix also reflects the variability seen in unit 1, though export is more often the dominant nutrient dynamic.

The results of this population and nutrient model indicate that spawner abundance and nutrient dynamics are affected by upstream and downstream passage efficiency, the magnitude and location of a commercial fishery, and the relative location of a site within the watershed. It highlights how poor passage through multiple dams can suppress spawner abundance in the upper portion of a watershed, leading to persistent net export. Net export occurs at sites with high juvenile productivity per-capita spawner, but low

spawner abundance. Additional sources of adult mortality, such as an in-river commercial fishery, can greatly affect population growth and spawner distribution dependent on their location in relation to productive habitat. A fishery in the estuary greatly reduced the overall population, but when located further upstream the total spawner abundance was almost six times higher. Our results put emphasis on the strong effect that the location of a particular factor within the watershed that reduces spawner abundance has on overall population recovery. Management decisions need to be based on a system-wide scale to account for population restrictions in each portion of the watershed.

CHAPTER 6

CONCLUSIONS

Modeling work indicated that alewife in the St. Croix River could be a substantial source of marine-derived nutrient subsidies. Results indicated that this alewife has the potential for large inputs of N and P, though maximum estimated values are based on “best case” scenarios and realistic inputs will be much smaller. Nutrient modeling indicated that P dynamics would be net export as population recovery begins, but switch to net import at relatively small spawner abundance as growth continues. Net N dynamics indicated minimal nutrient export at any population level, and net import occurred throughout population recovery. Modeling results also suggested that successful passage in the lower river would determine the rate of population recovery as the majority of spawning habitat is located upstream. Poor passage efficiency in the lower river could restrict population recovery, thereby maintaining P balance at net export. In addition, estimated nutrient dynamics in the St. Croix from 2013-2017 indicated net P import in the lowest section of the river and net P export at sites further upstream. Estimated differences between habitat units are primarily due to the multiplicative effect poor upstream passage rates for adult spawners.

While modeling work estimated large levels of N and P import at high spawner abundance, the retention of these nutrients within a particular site is likely determined by a suite of factors that can vary over the course of the spawning run. Environmental factors such as temperature or flushing rates could reduce the availability and detection of marine-derived nutrients. Results from water quality sampling indicated that sites along

the St. Croix are generally oligotrophic. In addition, the results from nutrient-diffusing substrates indicated that algal growth was highest when both N and P were supplemented. Taken together, these suggest that N and P input due to an alewife run could boost ecosystem productivity in the St. Croix. However, temporal differences indicated that the relative importance of marine-derived input to ecosystem productivity will likely vary over the course of the spawning run.

Stable isotope analyses in the St. Croix River showed no evidence of marine-derived nutrient incorporation. However, as the modeling work suggested, most of the river was likely experiencing net P export and minimal net N import during the course of this study. Modeling results suggested net import for both nutrient types in the lowest section of the river, but the majority of stable isotope sampling was performed upstream of this area. This downstream section often experiences high flow rates, and so retention of nutrient subsidies may be low despite estimating large potential input. In addition, alewife abundance within the watershed was small in relation to the population's theoretical maximum.

Measurements of marine-derived nutrient incorporation into freshwater communities indicated that assimilation was not merely a factor of input. At a reference site with an established spawning run, stable isotope analyses provided some indication of marine-derived nutrient incorporation. However, detection varied among macroinvertebrate and fish functional feeding groups. This suggested that marine-derived nutrient subsidies may play a different role among feeding groups within a freshwater community. In addition, a narrow time period was associated with marine-

derived nutrient detection. Future sampling in the St. Croix River may be most successful if these functional feeding groups are targeted at the peak of the spawning run.

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APPENDIX: DATA GROUPING AND STABLE ISOTOPE BIPLOTS

Table A1. Functional feeding group (FFG) for all fish species identified.

FFG	Species	Common name
detritivore	<i>Catostomus commersonii</i>	White sucker
omnivore	<i>Luxilus cornutus</i>	common shiner
	<i>Ameiurus nebulosus</i>	brown bullhead
	<i>Semotilus corporalis</i>	fallfish
	<i>Notemigonus crysoleucas</i>	golden shiner
	<i>Rhinichthys</i> spp.	dace
	<i>Rhinichthys atratulus</i>	black nosed dace
	<i>Couesius plumbeus</i>	lake chub
	<i>Chrosomus eos</i>	northern redbelly dace
	<i>Phoxinus</i> spp.	dace
Predator	<i>Micropterus dolomieu</i>	smallmouth bass
	<i>Perca flavescens</i>	yellow perch
	<i>Lepomis gibbosus</i>	pumpkinseed sunfish
	<i>Esox niger</i>	chain pickerel
	<i>Anguilla rostrata</i>	American eel
	<i>Morone americana</i>	white perch
	<i>Brosme brosme</i>	cusk
	<i>Micropterus salmoides</i>	largemouth bass

Table A.2. Functional feeding group (FFG) for all invertebrate species identified.

FFG	Taxonomic Group
collector-filterer	Hydropsychidae
	Philopotamidae
	Polycentropodidae
	Simuliidae
	Sphaeriidae
	Scirtidae
collector-gatherer	Asellidae
	Baetidae
	Caenidae
	Elmidae
	Ephemeridae
	Gammaridae
	Hydroptilidae
	Isonychiidae
	Leptohyphidae
	Leptophlebiidae
	Neoephemeridae
	Physidae
	Siphonuridae
	Uenoidae
	Molannidae
	Unknown trichoptera
detritivore	Lepidostomatidae
herbivore	Haliplidae

Table A.2 Continued

omnivore	Chironomidae
	Ceratopogonidae
	Gastropoda
	Unknown ephemeroptera
predator	Aeshnidae
	Athericidae
	Belastomatidae
	Calopterygidae
	Chaoboridae
	Chloroperliidae
	Coenagrionidae
	Cordulidae
predator continued	Corixidae
	Corydalidae
	Dytiscidae
	Gerridae
	Gomphidae
	Gyrinidae
	Lestidae
	Libellulidae
	Macromidae
	Notonectidae
	Perlidae
	Perlodidae
	Rhycophilidae
	Sialidae
	Hirudinea
	Tabanidae
	Veliidae

Table A.2 Continued

scraper-grazer	Bithyniidae
	Psephenidae
	Viviparidae
	Helicopsychidae
	Planorbidae
	Molannidae
	Oribatida
	Ephemerellidae
	Hydrobiidae
	Unknown snail
	Heptageniidae
shredder	Amphipoda
	Cambaridae
	Crambidae
	Curculionidae
	Isopoda
	Leptoceridae
	Leuctridae
	Limnephilidae
	Odontoceridae
	Tipulidae
	Capniidae
	Parapoynx
	Ptilodactylidae

Figure A.1. Correlation for four fish species between length or weight and $\delta^{15}\text{N}$.

Adjusted R^2 , slope, and p-value listed above each panel.

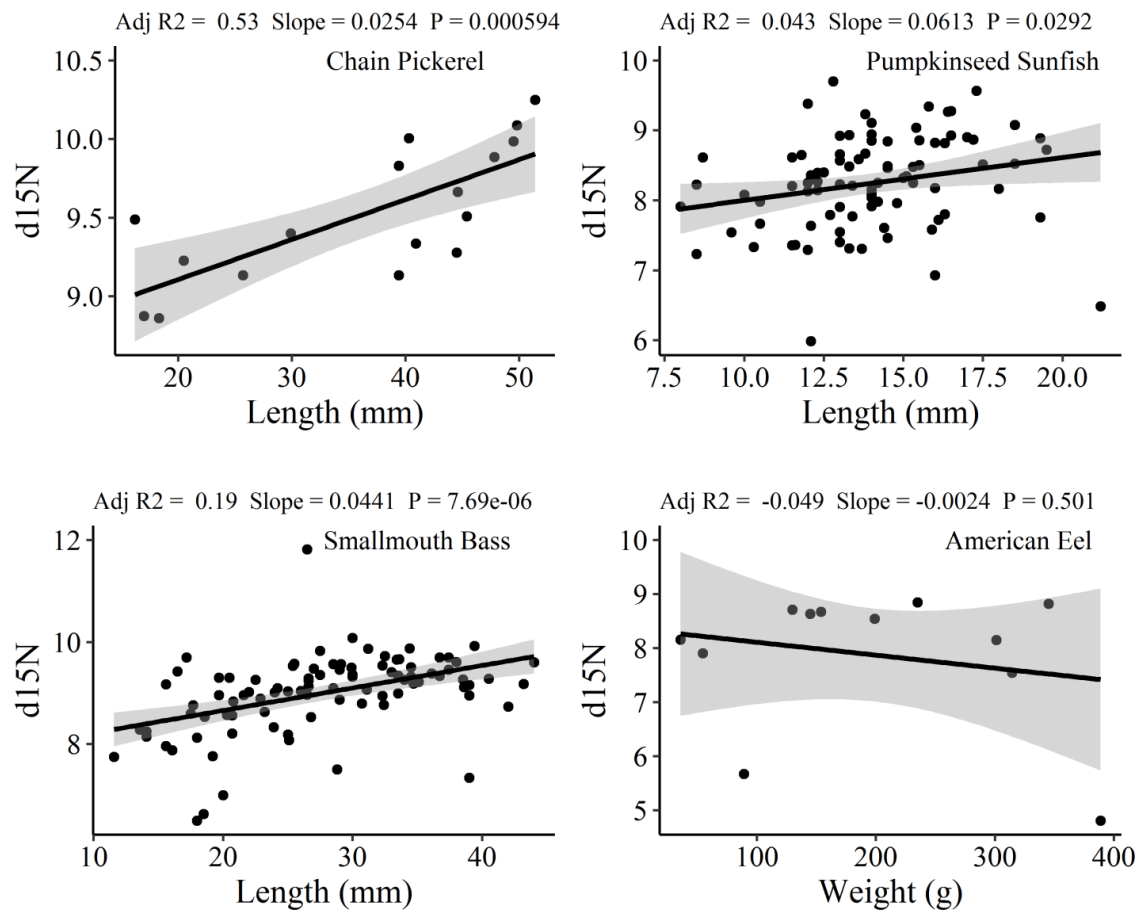


Figure A.2. Stable isotope biplots from the East Machias River in 2014 by site and season. Points represent mean values for each species found at a site with alewife (squares) and a site without alewife (circles). All plots include all data from both sites, but ellipses are drawn based on season (squares = 1, circles = 2, triangles = 3, diamonds = 4).

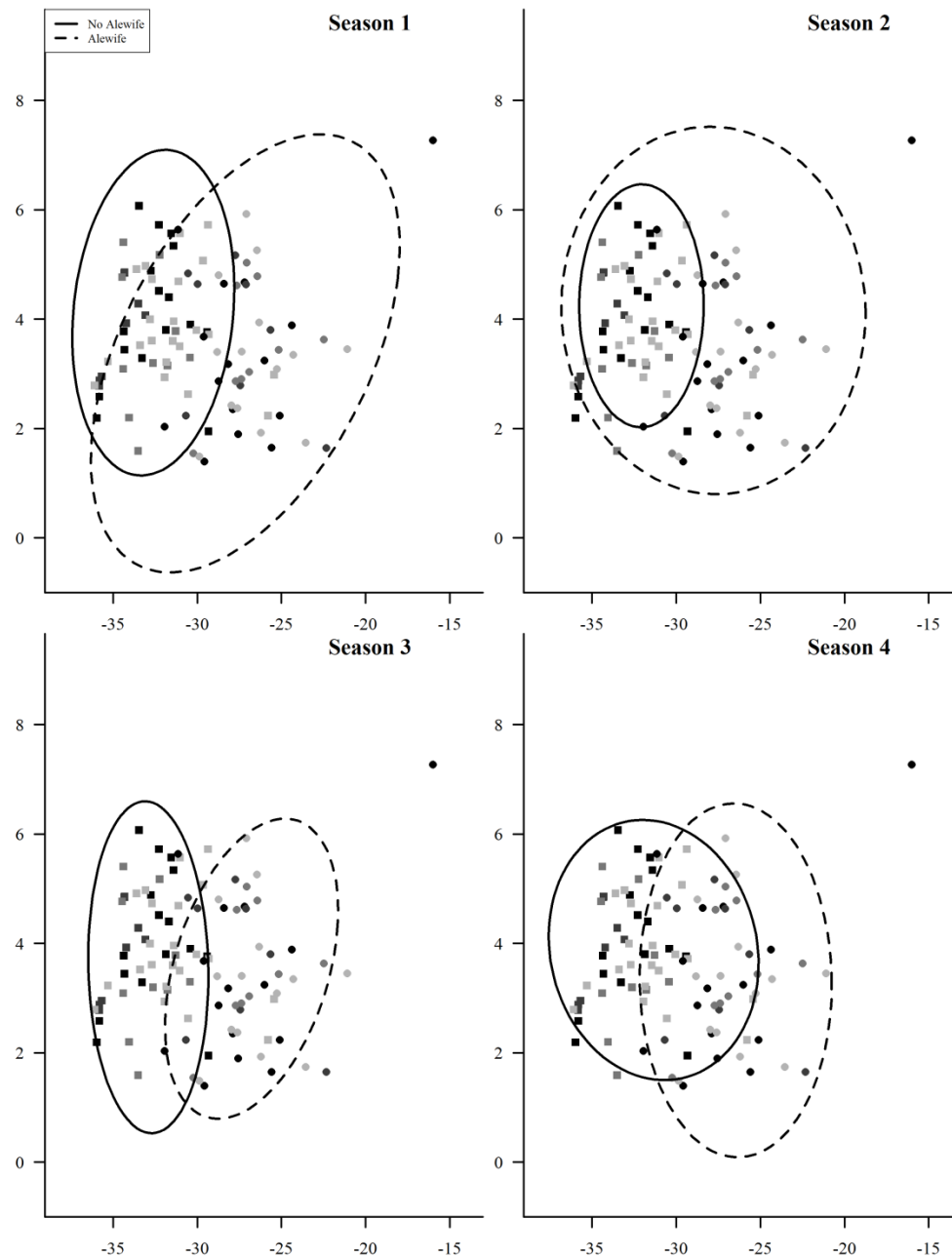
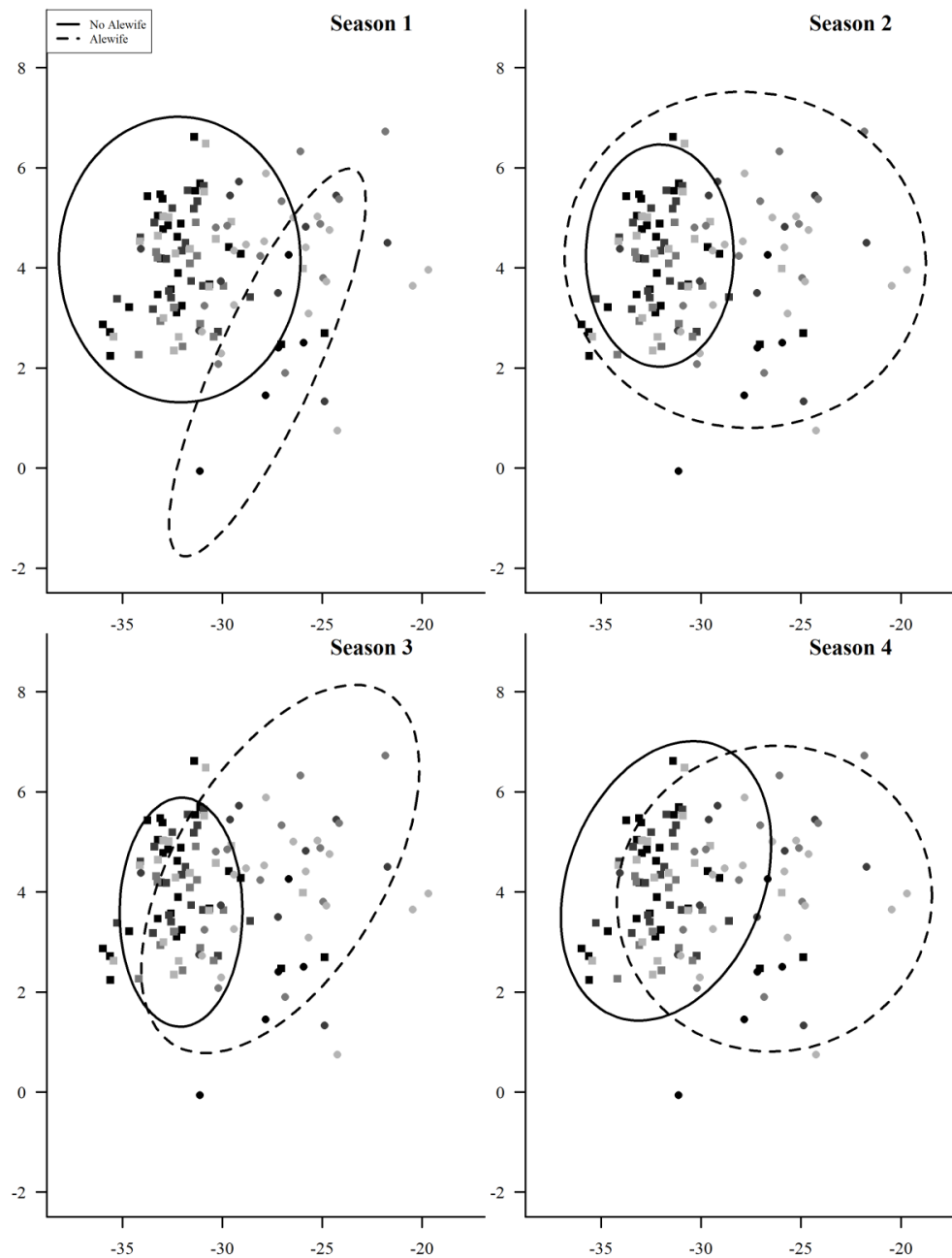


Figure A.3. Stable isotope biplots from the East Machias River in 2015 by site and season. Points represent mean values for each species found at a site with alewife (squares) and a site without alewife (circles). All plots include all data from both sites, but ellipses are drawn based on season (squares = 1, circles = 2, triangles = 3, diamonds = 4).



BIOGRAPHY OF THE AUTHOR

Betsy Barber was born on December 17, 1986 in Grand Island, Nebraska. She attended high school in Blair, Nebraska and graduated in 2005. After 18 years of never seeing the ocean, Betsy's childhood dream was to become a marine biologist. This pushed her to attend the University of Maine in Machias and graduate in 2009 with a Bachelor's degree in Marine Biology (summa cum laude). Betsy graduated from the University of New Brunswick at Saint John with a Master's Degree in marine biology. She then returned to Maine and joined the Department of Wildlife, Fisheries, and Conservation Biology in 2013. She is a member of the American Fisheries Society. Betsy is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in May 2018.