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Alewife (Alosa pseudoharengus) Contributions to Lake Phosphorus Budgets: Implications for Management

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Alewife (*Alosa pseudoharengus*) Contributions to Lake Phosphorus Budgets: Implications for Management

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Abstract

As human-made dams are removed and fish passage at dams is improved in support of restoration efforts, anadromous alewives (*Alosa pseudoharengus*) gain access to historic spawning grounds. As they migrate to spawn, adult alewives import marine derived nutrients to lakes and impoundments. Young of year alewives (juveniles) export nutrients as they emigrate to the sea. These nutrients support primary production and are incorporated into freshwater food webs. However, many lakes in New England are mesotrophic or eutrophic. Additional nutrients, specifically phosphorus (P), may exacerbate water quality issues. To examine these issues, I compared outputs of an alewife nutrient and population model to background lake P data from seven lakes in New England. My objective was to provide a nutrient analysis as an example for stakeholders, communities and organizations considering dam removal or improved fish passage and the restoration of alewife populations. Results demonstrated that alewives' impact on P levels was minimal under most scenarios. In 2017, alewives contributed less than 5% of mean epilimnetic P in four of seven lakes studied (China Lake, Highland Lake, Togus Pond, and Pawtuckaway Lake). Alewives contributed more P in Warwick and Webber Ponds, which translated to 3.6 – 11.19% of mean summer epilimnetic total phosphorus (TP) in Warwick Pond and 8.67 – 23.86% in Webber Pond. In Carr Pond, however, alewives contributed 11.43 – 93.67% of summer epilimnetic TP, which is potentially a large portion of the in-lake P budget. Alewife P import increased as adult escapement increased, and eventually adult import outweighed juvenile export, relative to lake size. Although the scale of P contributed by alewife was not extensive in the majority of the study lakes, it could be instructive to include alewife derived P as part of the flux of nutrients in management documents such as total maximum daily load (TMDL) reports.

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Introduction to Phosphorus Dynamics

An essential macronutrient for terrestrial, agricultural, and aquatic life, phosphorus (P) is required for formation of nucleic acids, the facilitation of cellular metabolism, and creating cell walls, all of which are essential to growth and reproduction (Elser 2012, Westheimer 1987). In aquatic ecosystems, bioavailable P supports primary production, such as algal and aquatic plant growth, and is subsequently incorporated throughout the food web (Childress et al. 2014, Naiman et al. 2002, Walters et al. 2009).

Anthropogenic activity has increased the availability and abundance of P in the aquatic environment (Carpenter et al. 1998, Elser 2012). In excess, P can cause eutrophication of freshwater ponds and lakes, increasing microbial activity and resulting in anoxic and hypoxic conditions that are detrimental to many aquatic organisms (Smith 2003, Watson et al. 2015). Phosphorus is considered the limiting nutrient in freshwater ecosystems, as the amount of P available in a system allows for and essentially controls the growth of primary producers (Elser 2012, Hecky & Kilham 1988, Wetzel 2001).

External sources of P originate outside of a given freshwater ecosystem, such as a river or lake, and can be derived from natural or anthropogenic sources. Natural sources of external P include soil weathering, runoff, atmospheric dry deposition, riparian vegetation, and migratory fish (Childress et al. 2014, Childress and McIntyre 2015, Fink et al. 2018). Anthropogenic sources of external P dominate lakes surrounded by urban or suburban development and include wastewater, industrial sources, agriculture, roads, tracks, and farmyards (Fink et al. 2018). Rain events have the potential to carry P from high P areas, that may be far away from a water source, into watersheds, and eventually to lakes.

Many factors affect the level of P sequestration and internal loading in lakes. Lake sediments contribute most internal P (Hoverson 2008). In stratified lakes with an oxygenated hypolimnion, P is bound by aluminum, iron (Amirbahman et al. 2003, Norton et al. 2008), and calcium complexes (Kaiserli 2002) and thus precipitates out to sediments, where it is unavailable to biota. In contrast, P may remain soluble and bioavailable to primary producers in stratified lakes with an anoxic hypolimnion contributing to recycling of P or internal loading (Nürnberg 2009, Nürnberg and Peters 1984).

Internal P dynamics are often quite complex and vary temporally among lakes depending on a multitude of abiotic and biotic factors. Underlying geology of a specific lake can also affect internal P dynamics; for example, lakes may have high naturally occurring levels of sulfur or aluminum (Heinrich et al. 2022, Kopáček et al. 2005). In lakes containing sulfur, sulfur competes with P for iron complexes, increasing internal P loading (Heinrich et al. 2022). The ratio of aluminum to iron and P in lake sediments, as well as bicarbonate-dithionite extractable (BD) fractions, influences internal P cycling (Kopáček et al. 2005). When [Al-$NaOH_{25}$] to [Fe-BD] ratios are greater than 3 and [Al-$NaOH_{25}$] to [P-NH_4Cl +P-BD] ratios are greater than 25, P is likely to be retained in sediments due to its insoluble association with [Al-$NaOH_{25}$] and thus is unlikely to be released in anoxic conditions (Kopáček et al. 2005). Alkaline and acidic pH levels may also lead to elevated P availability compared with neutral pH (Wu et al. 2014).

In a positive feedback effect, internal P release is correlated with lake trophic status; eutrophic lakes have higher internal P loading than mesotrophic or oligotrophic lakes do (Nürnberg et al. 1986). Warmer temperatures lead to increased microbial activity, which speeds decomposition at the sediment-water interface, consequently increasing organic P release (Wu et al. 2014). Lastly, greater microbial activity also reduces dissolved oxygen, which contributes to anoxic conditions, further increasing P release (Hupfer and Lewandowski 2008). Controlling P levels in lakes is compounded by delayed response to reduced external P load (Søndergaard et al. 2003, 2005) that results from internal P loading. These intricacies underscore some challenges associated with managing eutrophication and P in lakes.

Excess P has been directly linked to eutrophication (Correll 1998, Heisler et al. 2008). An abundance of P may lead to algal or phytoplankton blooms, which may negatively impact aquatic ecosystems by reducing water clarity and dissolved oxygen levels and increasing algal species capable of releasing cyanotoxins into the water (Davis et al. 2009, Watson et al. 2015, Zastepa et al. 2017). The eventual death of algal cells fuels bacterial decomposition in the hypolimnion, releasing excess P from dead algal cells. Increased bacterial activity leads to hypoxic or anoxic conditions that can trigger additional P release from the sediments, reducing oxygenated habitat for cold water fish

(Anderson et al. 2002, Paerl and Huisman 2009). These aspects of algal blooms may harm both wildlife and humans and contribute to loss of life, decreased aesthetic and economic value, and reduced biodiversity within lakes (Correll 1998, Smith et al. 2019, Watson et al. 2015, Yoshizawa et al. 1990).

Trophic status guides management of lake water quality and is generally calculated as a function of total phosphorus (TP), nitrogen (N), water clarity, and abundance of primary producers. Management actions are usually taken when lakes approach or become “eutrophic.” Although the criteria for eutrophy differ among states, regulating agencies in Maine, New Hampshire, and Rhode Island utilize similar parameters with slightly different values (Table 1). All three state agencies note that a combination of parameters is required to determine trophic status. High levels of TP indicate the likelihood of increasing eutrophication, prompting management action aimed at reducing TP.

Table 1. Trophic state indicators by state for Maine, New Hampshire, and Rhode Island.

Parameter	**Secchi disk (m)**	**Chlorophyll-a (ug/L)**	**Total P (ug/L)**	**TSI (trophic state indices)**
Oligotrophic				
Maine[1]	> 8	<1.5 ppb	< 4.5 ppb	0 - 25
New Hampshire[2]	> 4	< 3.3	< 8.0	No data
Rhode Island[3]	> 4	< 2.6 ppb	< 12 ppb	< 40
Mesotrophic				
Maine[1]	4 - 8	1.5 - 7 ppb	4.5 - 20 ppb	25 - 60
New Hampshire[2]	1.8 - 4	≤ 5.0	≤ 12.0	ND

Parameter	**Secchi disk (m)**	**Chlorophyll-a (ug/L)**	**Total P (ug/L)**	**TSI (trophic state indices)**
Rhode Island	2 - 4	2.6 – 7.2 ppb	12 – 24 ppb	40 - 50
Eutrophic				
Maine[1]	< 4	> 7 ppb	> 20 ppb	> 60 and/ or repeated algal blooms
New Hampshire[2]	< 1.8	≤ 11.0	≤ 28.0	ND
Rhode Island[3]	< 2	> 7.2 ppb	> 24 ppb	> 50

1. Maine Department of Environmental Protection (MEDEP; 2022)
2. New Hampshire Department of Environmental Services (NHDES; 2019)
3. Rhode Island Department of Environmental Management (RIDEM; 2010)

The Link Between P and Restored Populations of Migratory Fish

The inorganic nutrient and organic material flux and flow throughout ecosystems are essential to community structure, trophic cascades, and ecosystem productivity (Chapin et al. 2011). Diadromous fish, such as Pacific salmon (*Oncorhynchus* spp.*)*, Atlantic salmon (*Salmo salar*), American shad (*Alosa sapidissima)*, blueback herring (*A. aestivalis*), and alewives bring nutrients into freshwater systems as they migrate upstream, whereas anadromous juveniles transport nutrients as they move to the sea (Barber et al. 2018, Durbin 1979, Jonsson and Jonsson 2003, Naimen et al. 2002, Moore et al. 2011, Walters et al. 2009, West et al. 2010). Because of the role that P plays in lake primary productivity, there has long been an interest in migratory fish as external sources of P. This fertilization effect has been particularly well studied in Pacific salmon species that die on their spawning grounds (Naimen et al. 2002). Pacific salmon juveniles exported only 16% of nutrients, specifically P, brought into freshwater ecosystems by adults (Moore and Schindler 2004). These marine derived nutrients are incorporated into the freshwater food web (Macavoy et al. 2009, Samways et al. 2018, Vanni 2002, Walters et al. 2009). Thus, the presence of anadromous fish in freshwater ecosystems may increase primary production (Samways et al. 2018, Vanni 2002).

Members of the herring family (Clupeidae), alewives are migratory fish native to the Eastern seaboard and river systems of North America. Although some landlocked populations exist, alewives are predominantly anadromous; they spawn in freshwater lakes and spend their adulthood at sea (Hare et al. 2021). In New England, adults migrate upriver during spring to spawn, their eggs hatch approximately two weeks later, and young of year alewives (juveniles) and adults migrate out to sea in late summer or early fall.

Beginning in the mid-1800s, alewife populations declined in New England, largely due to overfishing and the extensive damming of rivers (Hall et al. 2012, Limburg and Waldman 2009). Historical estimates indicate that by the 1860s, alewife numbers had dropped from 50 million to 3 million in the northeast U.S. (Ames and Lichter 2013). Hall et al. (2012) estimated that between 1750 and 1900 the cumulative loss in alewife fisheries in Maine was as high as 11 billion fish.

In 2006, the National Oceanic and Atmospheric Administration (NOAA) listed alewife and blueback herring as Species of Concern (Hare et al. 2021). However, in 2013, the National Marine Fisheries Service (NMFS), of NOAA, determined that listing alewives as a threatened or endangered species was not necessary (NMFS 2013). In response to declining numbers, restoration efforts were implemented including improving fish ladders, removing dams, and re-establishing spawning runs through stocking gravid adults, as well as programs designed to reduce bycatch at sea (Opperman et al. 2011, Tuckey et al. 2011, Owen and Apse 2014). Preliminary data and field observations suggest these restoration efforts are having a positive impact on alewife populations (Hare et al. 2021).

The return of anadromous alewives to their native spawning lakes in New England has at times been controversial. In many lakes, alewives have been absent since the first full river mainstem dams were built in the 1800s (Hall et al. 2012), their numbers persisting only on those rivers that were not dammed. Stakeholders, such as lake shore owners, have voiced concerns regarding the reintroduction of anadromous alewife based on impacts of invasive land-locked alewife on zooplankton communities and associated algae blooms (Demi et al. 2015, Makarewicz 2000, Vigerstad and Cobb 1978), as well as their potential to import nutrients into lakes that might also drive algal blooms (Barber et al. 2018). However, in preliminary observations, lakes with spawning alewives have not seen an increase of algal blooms over time, although these instances are not well recorded in the literature. For example, Kircheis et al. (2002) found that the experimental reintroduction of alewives at 6 adults/acre reduced P levels and did not increase algal blooms in their study lake. More research is necessary to answer this question definitively.

Vanni et al. (2013) proposed three conditions to help establish whether migratory fish provide a net source or sink of nutrients. Migratory fish provide a sink when (1) more nutrients are retained by live biomass than deposited into the system, such as when growth and reproduction exceed mortality; (2) emigration exceeds immigration, including human harvesting; and (3) nutrients from dead fish are unavailable, e.g., removed by humans or by predators that then transport materials outside the system, or when they are sequestered in sediments. In a well-documented example, semelparous anadromous Pacific salmon provide a net nutrient flux into nutrient limited systems on the West Coast of North America (Naiman et al. 2002, Schindler et al. 2003). Unlike Pacific salmon, alewives are iteroparous and return to the ocean after spawning. However, alewife mortality in freshwater systems varies greatly. Alewives are commonly predated upon and harvested in New England. Consequently, alewives have the potential to be either a sink or source of nutrients.

Alewives may affect nutrient budgets by impacting phytoplankton dynamics both directly, via nutrient transport from the marine system (Barber et al. 2018, Durbin et al. 1979, Walters et al. 2009, West et al. 2010), and indirectly, by consuming herbivorous zooplankton, thereby releasing phytoplankton from predation in landlocked populations (Bradt and Chungu 1999, Brooks and Dodson 1965, Makarewicz 2000) and anadromous populations (Demi et al. 2015). Spawning adults potentially affect nutrient dynamics by providing a flux of marine-derived nutrients, whereas out-migrating juveniles potentially remove nutrients (Barber et al. 2018, Durbin 1979, Walters et al. 2009, West et al. 2010).

Alewives contribute phosphorus (P) and other nutrients to freshwater systems in the form of excrement, gametes, and carcasses. Nutrients from excrement may be immediately bioavailable for phytoplankton and larger plants (Vanni 2002), whereas nutrients from fish carcasses depend on decomposition and mortality rates (Boros et al. 2015, West et al. 2010). Debate exists around the interval between death and availability of nutrients from fish carcasses (Vanni et al. 2013). Walters et al. (2009) observed a carcass decomposition rate of one to two weeks. In microcosm experiments in the field, Boros et al. (2015) observed phytoplankton blooms one week after bluegill and gizzard shad carcasses were added. Thus, the flux of nutrients from alewives may not be immediately available for uptake by primary producers such as phytoplankton but may instead be gradual or delayed.

The percentage of alewives that die in freshwater also varies from system to system, across latitudes, and from year to year. Several authors estimated alewife mortality rates to be on average 57%, varying between 53% and 62%, during the spawning run at Bride Lake, a small Connecticut lake, based on the difference between escapement and the number of adults leaving the lake (West et al. 2010, Kissil 1974, Dalton et al. 2009). Durbin et al. (1979) found mortality rates to be between 30% and 40% in mesocosm experiments. Havey (1961) estimated mortality to be on average 83%, varying between 66% and 100%, at Love Lake, Maine (1973) and 41% at Long Pond, Maine. Northern latitudes may have lower mortality rates (J. Zydlewski, personal communication, March 2017), as alewives are semelparous in southern populations and iteroparous in northern populations (Pardue 1983). This variation in mortality indicates the potential for some discrepancy in the amount of carcass derived nutrient flux to a lake.

The iteroparous nature of northern populations of alewives leads adults to import nutrients when they return to freshwater spawning grounds, and both adults and juveniles to export nutrients when they return to the ocean (Barber et al. 2018, Walters et al. 2009, West et al. 2010). Both adult and juvenile alewives are incorporated into local freshwater and terrestrial food webs as they are consumed by fish (e.g., largemouth bass *(Micropterus salmoides);* M. Thurrell, personal observations) and birds (e.g., bald eagle *(Haliaeetus leucocephalus)*, common loon *(Gavia immer)*, osprey *(Pandion haliaetus)*, and great cormorants *(Phalacrocorax carbo)*; M. Thurrell, personal observations). Consequently, net contribution of alewife nutrients to lakes is difficult to quantify.

Alewives also impact lake nutrient budgets through feeding habits. Alewives are size-selective particulate and filter feeders that reduce the size and biomass of the dominant herbivorous zooplankton community within lakes (Demi et al. 2015, Makarewicz 2000, Vigerstad and Cobb 1978). Zooplanktivorous fish can trigger trophic cascades that lead to phytoplankton blooms under certain conditions (Bradt and Chungu 1999, Carpenter et al. 1985, Makarewicz 2000, Brooks and Dodson 1965). Zooplankton graze on phytoplankton and may keep algal species under control. Cascading effects of alewives on zooplankton and predation on phytoplankton may depend on the nutrient status of the lake. For example, trophic cascades were most detectable in oligotrophic systems, with decreasing effects with increasing trophic status, or as systems move from oligotrophic to mesotrophic or eutrophic (Demi et al. 2015).

Interest in lake water quality has spurred the formation of many volunteer-led lake monitoring programs or lake associations. Lake adjacent landowners take particular interest in lake water quality, as they are most likely to experience both direct and indirect effects of algae blooms. Multiple studies have been conducted on alewives as a source or sink of nutrients, although most were specific to the particular lake studied (Durbin et al. 1979; Walters et al. 2009; West et al. 2010). Lake associations are consequently interested in the impact of spawning alewives on lake water quality. These groups collect data regularly to better understand alewife interactions with water quality, with the goal of providing some clarity around alewife-water quality dynamics.

The objective of this study was to apply existing techniques for estimating nutrient budgets in a way that is approachable to community stakeholders, such as lake associations, to address concerns about anadromous fish and nutrients in lakes. To estimate the magnitude of alewife P contributions to summer TP values, I used information available to resourceful stakeholders or other groups interested in making informed, science-driven decisions, including TP, alewife population data, and modeled nutrient contributions from alewives (Barber et al. 2018). I completed a comprehensive study of seven lakes that estimated the impact of alewife-derived P in each system. This study should support and advise alewife restoration efforts in these lakes and provide examples for stakeholders to follow when evaluating consequences of dam removal, fish ladder installation, and fish passage improvement at dams.

To address this issue, I collected growing-season lake TP data. I used readily available alewife population data for lakes and a spawner recruit model created by Barber et al. (2018), which models population, mortality, and P flux due to mortality, gametes, excretion, immigration of adult alewives, and emigration of young of year and adult alewives.

Methods

Lake water quality data were collected at seven lakes to determine TP. To determine the magnitude of alewife-derived P in each lake, adult alewife population numbers were derived from either direct counts as fish entered the lake or stocking numbers. Juvenile alewife numbers were estimated using a model created by Barber et al. (2018) to determine P removed by juveniles. Alewife P contributions were also calculated using this model. Modeled alewife P was transformed to a concentration using a modified Vollenweider equation to compare the magnitude of estimated alewife-derived P to background lake phosphorus levels.

Study Sites

The seven study lakes were located in Maine, New Hampshire, and Rhode Island (Table 2). They varied in size and depth; the largest lake covered an area of 1593 ha (3837 ac) with a depth of 26 m and the smallest lake occupied an area of 22 ha (55 ac) with a depth of 6 m. The lakes ranged in trophic status from mesotrophic to eutrophic; thus water quality was already a concern to stakeholders. China Lake, Togus Lake, Webber Pond, Carr Pond, and Warwick Pond were considered eutrophic, whereas Highland Lake and Pawtuckaway Lake were considered mesotrophic (Jeff Dennis, MEDEP, Biologist, 2017; Phillip Edwards, RIDEM, Division of Fish & Wildlife Chief, 2017; Kevin Sullivan, Marine Biologist II, NH Fish and Game [NHFG], 2017; personal communications). All lakes had a minimum of one year of previously collected water quality data including TP data and associated environmental data (Table 2).

All lakes either had an active alewife run and fish count or were stocked by management agencies. Highland Lake and Webber Pond were dammed at the outlet of the lake with Denil fish ladders providing fish passage. Carr Pond was dammed 91 m from the pond's entrance and equipped with an Alaskan Steep Pass fish ladder. Warwick Pond was not dammed. At the time of this study, China Lake, Togus Pond, and Pawtuckaway Lake were dammed without fish passage and thus stocked with gravid adult alewives. Maine lakes were stocked by the Department of Marine Resources, and New Hampshire Lakes were stocked by NHFG. Alewife numbers ranged from 1,000 fish (0.78 fish/acre) stocked in Pawtuckaway Lake (2016) to 298,650 fish (242 fish/acre) counted entering Webber Pond.

Table 2. Physical characteristics of seven study lakes, 2017.

Waterbody	State	Latitude, Longitude	Area (ac)[1]	Area (ha)[1]	Max depth (m)[1]	Water quality[2]	Passage type[2,4]	Passage rate[5]	Number of fish (2017)[3]	Fish/ acre
China Lake	ME	44.43288, -69.56964	3937	1593	26.0	Eutrophic	No Passage	na	24849	6
Highland Lake	ME	43.77806, -70.35814	623	252	19.8	Mesotrophic	Denil Fish Way	96%	38106	61
Togus Pond	ME	44.32389, -69.65798	674	262	14.9	Eutrophic	No Passage	na	10000	16
Webber Pond	ME	44.40474, -69.65847	1233	486	12.5	Eutrophic	Denil Fish Way	96%	292677	244
Pawtuckaway	NH	43.086666, -71.13649945	784	317	15.2	Mesotrophic	No Passage	na	1000	1

Waterbody	State	Latitude, Longitude	Area (ac)[1]	Area (ha)[1]	Max depth (m)[1]	Water quality[2]	Passage type[2,4]	Passage rate[5]	Number of fish (2017)[3]	Fish/ acre
Carr Pond	RI	41.634417, -71.556514	55	22	5.8	Eutrophic	Alaskan Steep Pass	96%	58772	1065
Warwick Pond	RI	41.7228, -71.412906	86	35	7.9	Eutrophic	Open	100%	17874	209

1. Maine lake area and depth: Maine volunteer lake monitoring program (Lake Stewards of Maine 2018). New Hampshire lake area and depth: NHDES TMDL for Pawtuckaway (NHDES 2011). Rhode Island lake area and depth data: Elizabeth Herron, University of Rhode Island (URI) Watershed Watch, Program Director, email, 2016.
2. Trophic status and passage type data: Jeff Dennis, MEDEP, Biologist 2017; Phillip Edwards, RIDEM, Division of Fish & Wildlife Chief, 2017; and Kevin Sullivan, New Hampshire Fish and Game (NHFG), Marine Biologist II, 2017.
3. Fish count and stock data: Theo Willis, USM, Adjunct Professor, 2017; Phillip Edwards, RIDEM, Division of Fish & Wildlife Chief, 2017; Kevin Sullivan, NHFG, Marine Biologist II, 2017.

Waterbody	State	Latitude, Longitude	Area (ac)[1]	Area (ha)[1]	Max depth (m)[1]	Water quality[2]	Passage type[2,4]	Passage rate[5]	Number of fish (2017)[3]	Fish/ acre

4. Lakes without fish passage were stocked with gravid alewives trucked from another system.

5. Passage rate: Denil fishway (results for alewives: Bunt et al. 2011) and Alaskan Steep Pass fishway (Franklin et al. 2012).

Epilimnetic Total P

At each lake, I collected lake water samples to measure TP with the help of collaborators in NH and RI lakes. I focused on the epilimnion because I assumed alewives spend most of their time in that area. In eutrophic and mesotrophic lakes, the epilimnion has higher oxygen and light levels than the hypolimnion (Wetzel 2001), providing better habitat for alewife. For Maine and Rhode Island lakes, I collected epilimnetic water samples at the deep hole (the deepest part of the lake) in May, July, September, and October 2017. To make this study easily replicable by volunteer lake associations, I followed the Rhode Island Watershed Watch data collection protocols, including the timing and depths of sample collection (Green et al. 2021, Herron et al. 2020). Sample bottles were cleaned with P-free soap, acid washed in 10% HCl solution for a minimum of 3 h and rinsed in deionized water. We collected four 250 ml grab samples from the epilimnion (0.3 m below surface) by plunging the bottle to arm's depth. Within 1 h of collection, two samples were filtered through Whatman GF/F glass fiber filters (0.7 µm) for nitrate and phosphate analysis (See Appendix A). Two samples remained unfiltered for epilimnetic TP and nitrogen analyses (nitrogen data are included in Appendix A). We stored water samples on ice until frozen to slow decomposition (Green et al. 2021, Herron et al. 2020). Water samples were analyzed using an Astoria®-Analyzer Model 303A Segmented Continuous Flow Autoanalyzer at the URI Environmental Protection Agency certified water quality lab.

Water samples from Pawtuckaway Lake, NH, were collected at the deep hole and analyzed by NHDES.

I used the epilimnetic TP data (0.3 m) from the growing season (May, July, and September 2017) in calculations that compared modeled alewife-derived P to lake TP. One sample was collected per lake per sampling date.

Most lake monitoring programs collect 0.3 m grab samples. In Highland Lake samples were collected from additional depths, so I used these data to determine if 0.3 m grab data were representative of the epilimnion as a whole. The 2018 Highland Lake TP data set included individual samples taken at 1-m intervals from 0-10 m because the epilimnion ranged between 0 - 5 m and 0 - 9 m in depth throughout the growing season.

I performed a one-way ANOVA to compare the effect of unique lakes on TP values, to determine if epilimnetic TP was statistically significantly different between lakes when samples from May, July and September were used as replicates. I performed a two tailed t-test to determine if Highland Lake mean TP from 0-1 m was relatively similar to the mean TP from the epilimnion (0-9 m). I performed both tests using Microsoft Excel and used an alpha level of 0.05 for all statistical tests.

Net Nutrient Contributions from Alewives

I estimated the flux of nutrients from adult and juvenile alewives using a spawner recruit model developed by Barber et al. (2018) that incorporates population life cycle and nutrient data from Gibson and Myers (2003), Gibson (2004), Kissil (1974), Maine Department of Environmental Protection (MEDEP; 2014), ASMFC (2012), Bailey and Zydlewski (2013), Fisheries and Oceans Canada et al. (1981–2016), and Durbin et al. (1979). The deterministic model calculates the number of juveniles produced by a certain number of spawning adults based on the Beverton-Holt stock-recruitment curve (Barber et al. 2018). Juvenile production is density dependent based on lake area (Gibson and Myers 2003b).

The model assumed all habitat within a lake is equivalent in terms of likelihood to produce juvenile alewives, with more area equating to higher number of juveniles produced per year (Barber et al., 2018). Habitat choice (and habitat productivity) is likely more complex, but for the purpose of this study, this approach was the most efficient way to look at the issue.

In three study lakes (Carr, Warwick, and Webber Ponds), alewives had free access to additional habitat greater than the lake itself (i.e., upstream lakes, or river or estuarine habitat immediately downstream of the lake), which complicated analysis as I did not have P data for the additional habitat (Table 3). Thus, for these lakes I reduced the number of spawning adults assumed to deliver nutrients to these lakes by a percentage equal to the additional habitat (Table 3). Alewife counts for Carr Pond were adjusted from 72,664 to 58,772 due to 13 ac of additional viable habitat located upstream and downstream of the pond's 55.2 ac. The alewife count for Warwick Pond was adjusted from 27,552 to 17,874 fish to account for an additional 18.8 ac of viable habitat both upstream and downstream. The alewife count for Webber Pond was adjusted from 597,299 fish to 292,677 fish, assuming that 49% of the population spawn in Webber Pond and 51% spawn in the slightly larger Three Mile Pond.

Table 3. Adjustments for additional accessible habitat for Carr, Webber, and Warwick Ponds, for which I did not collect P data.

Waterbody	**Percentage of total habitat accessible**	**Additional habitat (ac)**	**Measured escapement (number of fish)**	**Adjusted escapement (number of fish)**
Webber	49%	1,174	597,299	292,677
Carr	81%	13	72,664	58,772
Warwick	64%	18.8	27,552	17,874

I used the spawner recruit model to estimate P flux from alewives using low, medium, and high juvenile alewife productivity, applying different stock-recruitment curves as a proxy for alewife productivity (Table 4). The following paragraphs describe parameters set in the model created by Barber et al. (2018). Stock recruitment parameters R_{asy} and alpha were calculated by Barber et al. (2018) using a spread, from 10th to 90th percentile, around the mean value from Gibson's meta-analysis (Gibson 2004 and unpublished data; Table 4). Juvenile numbers were calculated by Barber et al. (2018) using the number of eggs per adult female, recruits per acre (asymptotic recruitment level (R_{asy})), and alpha (α, alewife lifetime reproductive rate) which describes the slope of the Beverton-Holt stock-recruitment curve. R_{asy} describes the number of recruits that can be produced per acre of lake area (Barber et al. 2018). Alpha is the slope of the origin of the spawner recruit curve, here defined as the number of age 3 recruits that each individual spawner produces (Barber et al. 2018).

Juvenile export of TP was based on the modeled number of juveniles produced per system multiplied by mean wet weight of juveniles (3.5 g; Havey 1973) and P content per g of fish (0.0058 g P/g wet mass; West et al. 2010). Adult import of TP was calculated using number of adults multiplied by TP input from male and female gametes, excretion, and carcasses. Values for carcass, ovaries and testes mass were identified by year class and taken from Fisheries and Oceans Canada et al. (1981–2016) and Durbin et al. (1979). Each adult female was estimated to produce an average of 130,000 eggs (Barber et al. 2018). The sex ratio was assumed to be 50% (Barber et al. 2018). In-lake mortality was estimated to be 45%, averaged from Kissil (1974) and Durbin et al. (1979). Adults were assumed not to feed while spawning and to spend 14 days on spawning grounds (Kissil 1974, West et al. 2010).

Table 4. R_{asy} (number of recruits produced per acre of lake) and alpha values (slope of the origin of the spawner recruit curve) used in the model as a proxy for low, medium, and high juvenile alewife productivity, based on a spread around the mean value from Gibson's meta-analysis of 8 alewife populations (Barber et al. 2018; Gibson 2004).

Recruit Productivity	Relative to Mean Productivity*	Alpha	Rasy (age 3)
Low	10th percentage	0.0017	340.26
Medium	50th percentage	0.0019	582.659
High	90th percentage	0.0022	998.46
* Based on a spread, from 10th to 90th percentile, around the mean value from Gibson's meta-analysis of 8 alewife populations (Gibson 2004).			

The model accounted for passage rate of spawners through dams on upstream migration and of juveniles and adults passing dams on downstream migration by decreasing population numbers according to assumed passage rates. Passage rates were set for each system according to the type of fish passage (Table 2).

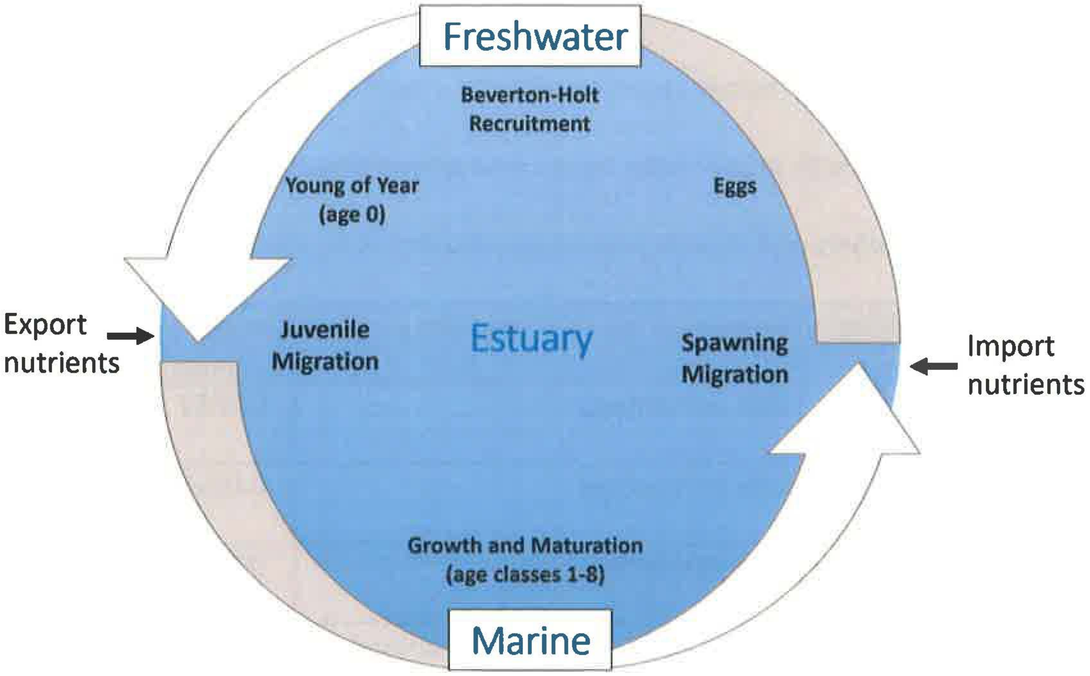

Figure 1. Figure modified from Barber et al. (2018), depicting components and steps of the deterministic population and nutrient model. Fish ages 2-8 years enter the spawning run, move from the ocean to spawning habitat and lay eggs. Survival to age 0 is determined by a Beverton-Holt spawner recruit curve. Nutrient flux is calculated by the model based on young of year alewife export (biomass) and adult alewife import (carcasses, gametes, excretion) (Barber et al. 2018).

To convert the amount of P contributed by fish to the equivalent concentration of TP in the water, I used two equations modified from Vollenweider (1976). Equation 1 accounts for sedimentation of P (i.e., as insoluble complexes) and thus gives a lower estimate of TP in the water column. Equation 2 does not account for sedimentation, thus giving a higher estimate of TP in the water column, as might occur if the lake has internal P cycling.

Equation 1: Low estimate of alewife contribution to lake P (measured as TP). This estimate assumes P is lost to sedimentation (Dillon and Rigler 1974, Vollenweider 1974, 1976). Note that 106 converts kilograms per m^3 into µg/L, and µg/L is equivalent to ppb for dilute solutions.

alewife P contribution (ppb) = alewife input (kg P)/ ((Vx106) (p+Vp))

where V is volume (m^3), and p is flushing rate (yr^{-1}).

Flushing rate data were available for Maine (Lake Stewards of Maine 2018) and New Hampshire lakes (NH DES 2011) but lacking for Rhode Island lakes. Flushing rate was determined for Warwick and Carr Ponds using the following equation (Gold et al. 2016): **flushing rate = 1/retention time**, where retention time = volume/ (Qnorm * watershed size * sec/yr). Qnorm is discharge normalized by watershed area and equals 0.021 (m^3/s*km^2) (Gold et al. 2016). Watershed size is expressed as km^2 and volume of lake is expressed as m^3. The conversion factor 0.031536 is used to convert from m^3 ·s −1 to km^3 ·year^{-1}.

Equation 2: High estimate of alewife contribution to lake TP. This estimate assumes that no P is sequestered in sediments (i.e., internal cycling is occurring, Dillon and Rigler 1974, Vollenweider 1974, 1976). Note that 106 converts kilograms per m^3 into µg/L, and µg/L is equivalent to ppb in dilute solutions.

Alewife P contribution (ppb) = alewife input (kg P)/ (Vx106)

where V is lake volume (m^3).

For each lake, I transformed the median value of mass (kg) of alewife-derived P provided by the model (Barber et al. 2018) to TP concentration using equations 1 and 2. Alewife P in ppb was then compared as a percentage of median summer in-lake epilimnetic P (May, July, Sep). In other words, the model was used to produce three different juvenile population outcomes based on three different stock-recruitment curves, and the median value was used to calculate alewife P contributions, which was then converted to a concentration and compared to in-lake TP.

To estimate the amount of P coming into the lake in 2017 via alewives, I used alewife run or stocking information from the following sources. Volunteers recorded adult alewives entering Highland Lake, Webber Pond, Carr Pond, and Warwick Pond. China Lake and Togus Pond were stocked by the Maine Department of Marine Resources (MEDMR). Pawtuckaway Lake was stocked by the New Hampshire Department of Fish and Game. Missed counts were estimated via linear extrapolation (Nelson 2006).

Results

Epilimnetic Total P

Epilimnetic TP was statistically significantly different between lakes when samples from May, July and September were used as replicates in a one-way ANOVA ($F_{6,20} = 11.8$, $p < 0.0001$). Mean TP was highest in Warwick Pond (Figure 2) and remained consistently high throughout summer (Figure 3). Highland Lake had the lowest mean TP

(Figure 2) and stayed consistently low during the growing season (Figure 3). For all lakes, TP did not appear to change in association with the arrival of adult alewives (between May and June) and departure of juveniles (between July and October) (Figure 3). In all lakes, TP appeared to be lower during summer (July), and higher in spring (May) and fall (October) (Figure 3).

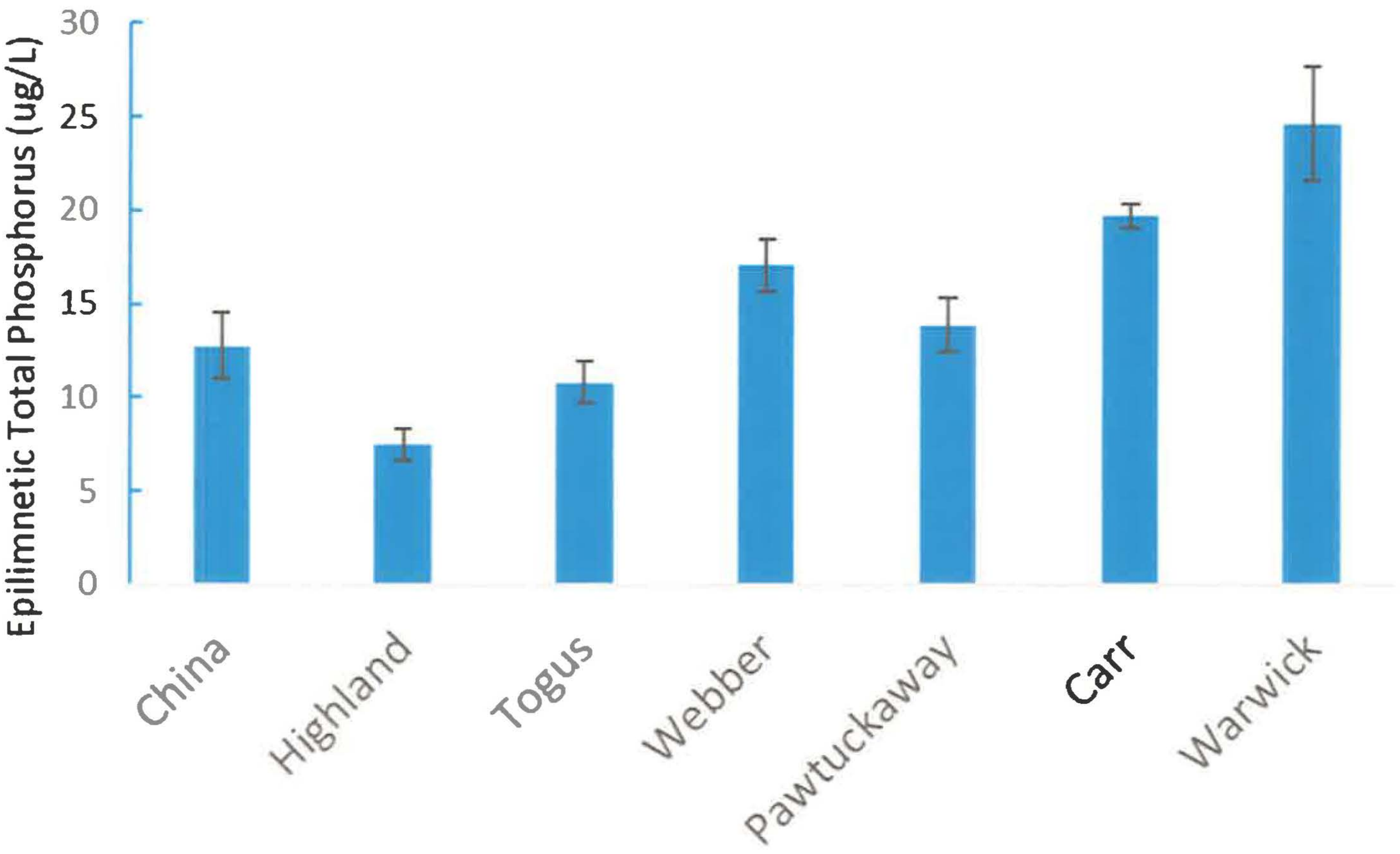

Figure 2. Mean (±SE) growing season epilimnetic TP (µg/L; n = 4) for seven study lakes located in Maine, New Hampshire, and Rhode Island (2017). October data were not available for Togus Pond (n = 3).

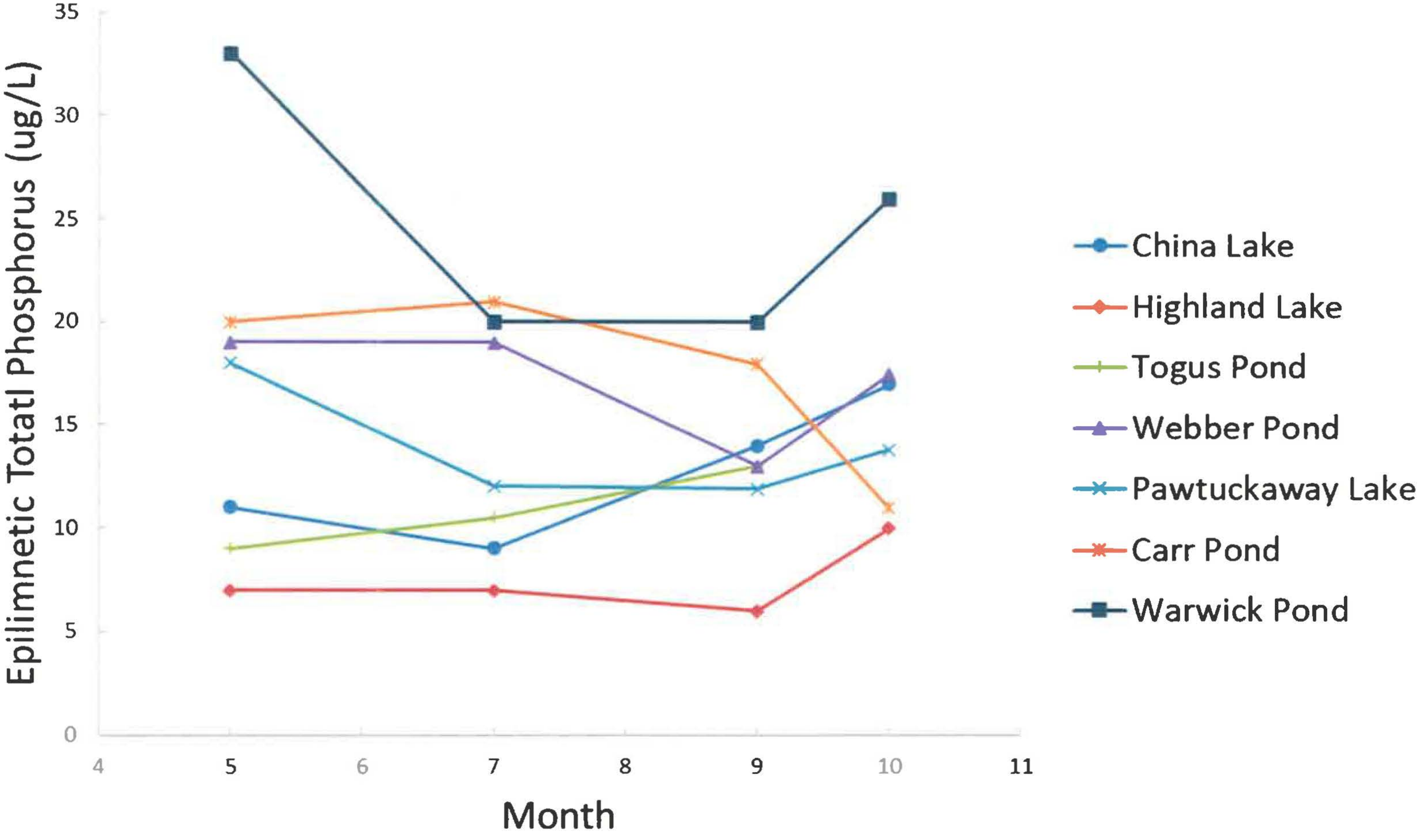

Figure 3. Trends in epilimnetic TP (μg/L) for seven lakes in Maine, New Hampshire, and Rhode Island, 2017. October data were not available for Togus Pond. Each data point is one sample.

Based on the more detailed Highland Lake TP data, the assumption that a 0.3m deep grab sample represents the epilimnion as a whole seems reasonable. In Highland Lake, the mean TP from 0-1 m (assumed to be most similar to 0.3 m) was relatively similar to the mean TP from the epilimnion (0-9 m) (two tailed t-test, $p = 0.8$). Across all sampling dates TP values never varied between the 0-1 m grab and the mean of the epilimnion by more than 1.5 ppb (Figure 4). The exception was one 0-1 m outlier at 11.55 ppb, with mean epilimnetic value of 9.18, a difference of 2.37 ppb.

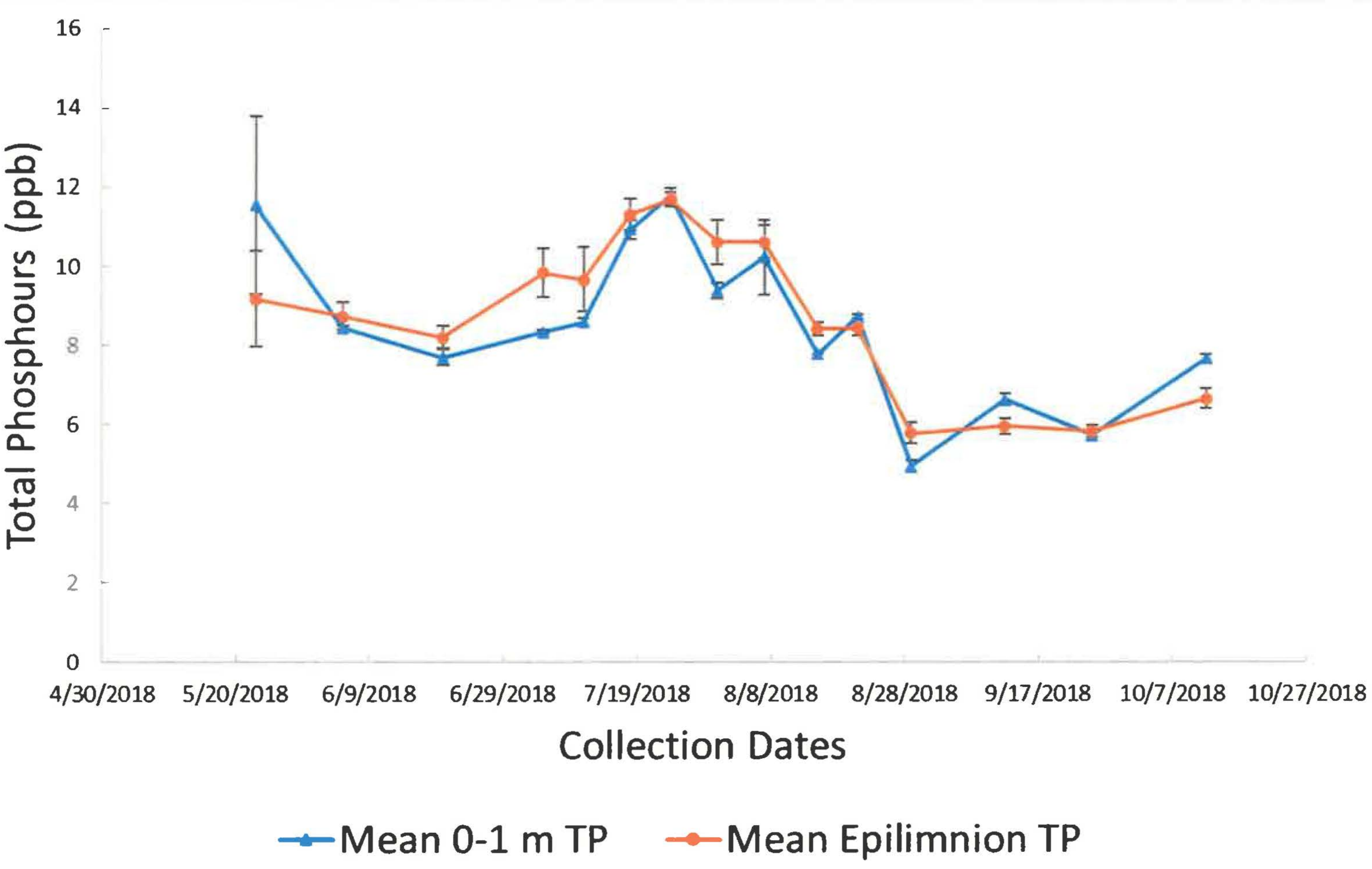

Figure 4. Mean (±SE) 0-1 m TP and mean epilimnetic TP (0-9 m) (±1 SE) collected from Highland Lake, Maine, 2018, to determine whether a 0.3 m (1 ft) sample is a useful proxy to estimate epilimnetic TP concentration.

Net Nutrient Contributions from Alewives

To better understand the amount of P entering and leaving a lake, I used the spawner-recruit nutrient model (Barber et al. 2018) to estimate the number of juvenile alewives produced in a lake for a given number of adult spawners. I used Highland Lake as an example to show how I used and interpreted the results (Figure 5). The model predicted a change in net P as escapement increased in all lakes. Net P export from each lake was correlated with increased production of juvenile alewives (as R_{asy} and Alpha increased, controlling the shape of the modeled stock recruitment curve (Figure 6)). As escapement continued to increase, export was curtailed as the P contributed by adults was greater in magnitude than that removed by juveniles (Figure 5). Eventually, juvenile population growth plateaued, and P contributed by adults continued to be greater in magnitude than that removed by juveniles (Figure 5).

In each lake I started the model at 100 spawners, and the model increased the population in yearly timesteps to 100,000 spawners under conditions of low, medium and high juvenile recruitment, or different stock-recruitment curves. Both upstream and downstream passage was assumed to be 96% (Bunt et al. 2011). For Highland Lake, when the model was set for medium juvenile recruitment, alewives removed P from the lake when escapement numbered fewer than approximately 40,000 fish (Figure 5). Above 40,000 fish, alewives provided a net influx of P in Highland Lake.

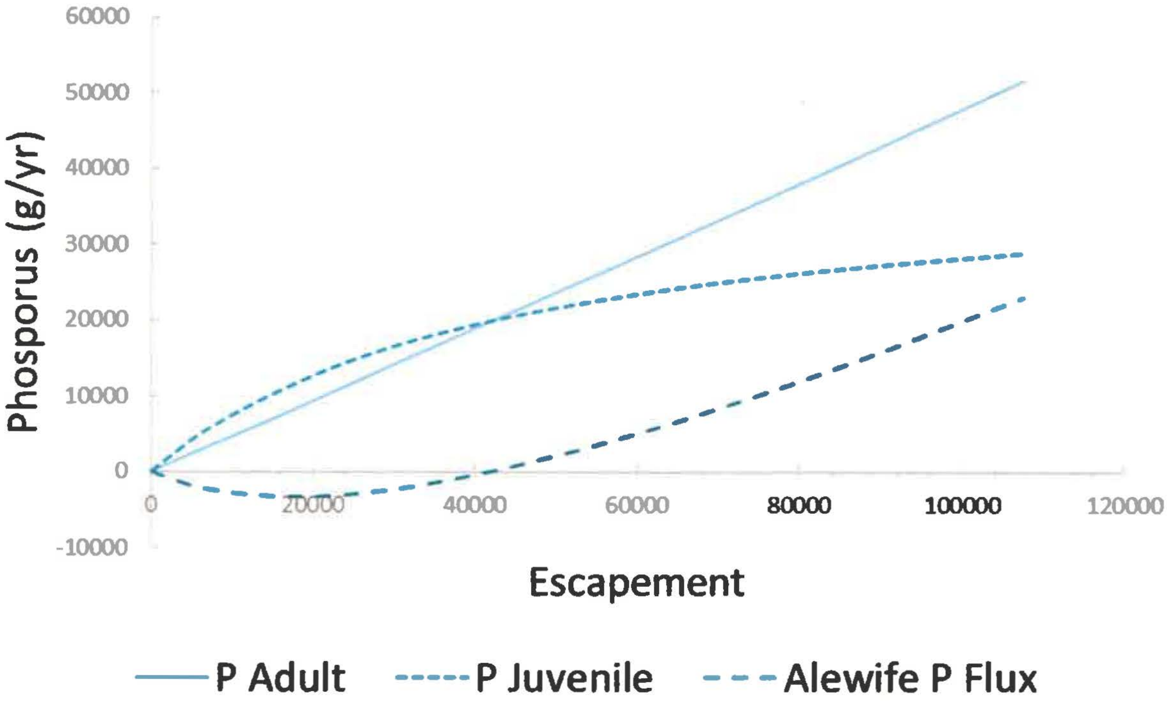

Figure 5. Modeled alewife nutrient contributions in Highland Lake. P imported by adults is indicated by a solid line, P exported by juveniles is indicated by a dotted line, and dashes indicate the net difference between adult and juvenile P. The model was set for medium juvenile recruitment and upstream/downstream passage rates of 96%. Historic escapement in Highland Lake ranges between 7,000 and 68,000 adult alewives.

Changing the shape of the stock recruitment curve shifted the magnitude of alewife P flux (Figure 6). In Highland Lake alewife-derived P ranged from a net influx of 5.84 kg/yr to a net reduction of 7.82 kg/yr (Table 5). Low recruitment rates, or fewer juveniles produced per adult spawner, removed the least P from the system (Figure 6). High recruitment rates, or more juvenile alewives produced per adult spawner, resulted in the highest amounts of P removed from the system (Figure 6). In Highland Lake, at high recruitment rates, up to approximately 80,000 spawners resulted in a net export of P from the system (Figure 6), whereas at low recruitment rates, up to 20,000 spawners resulted in a net export of P (Figure 6).

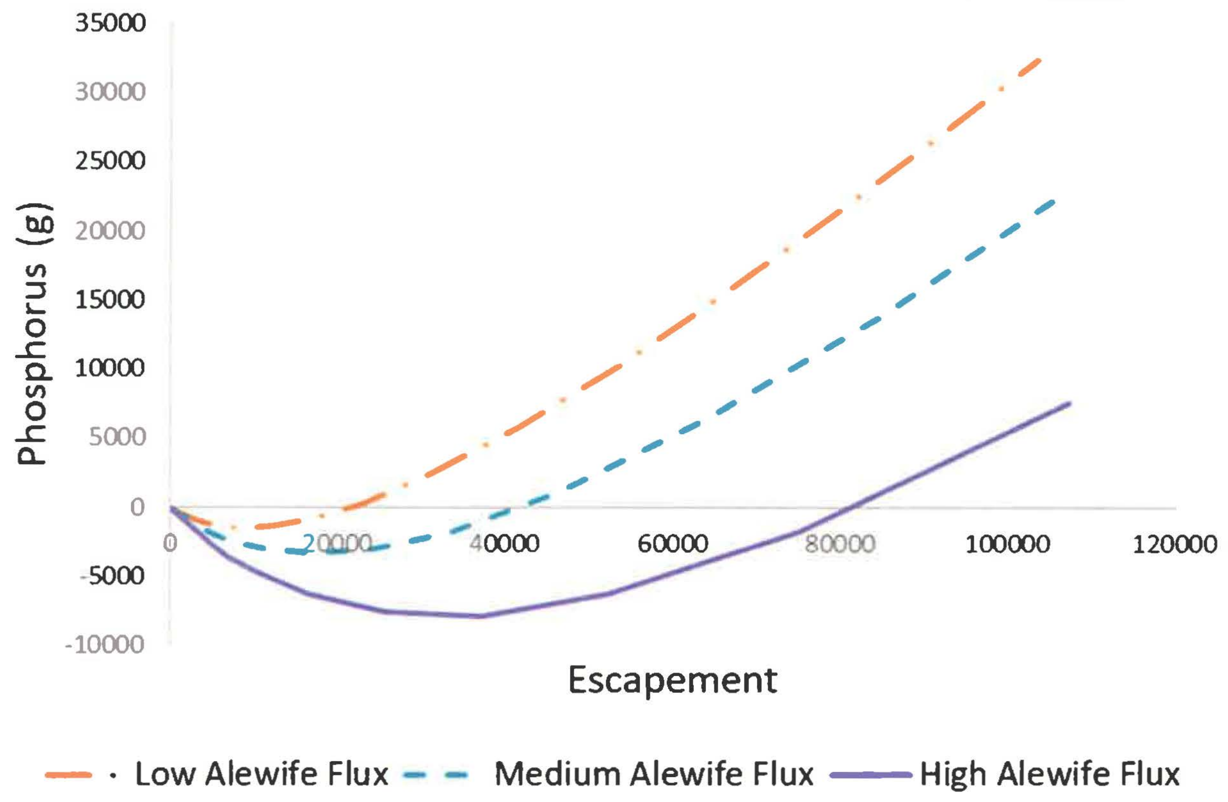

Figure 6. Total net P flux modeled at low, medium, and high juvenile alewife recruitment in Highland Lake. Values of R_{asy} and Alpha were varied to simulate low, medium, and high juvenile recruitment. R_{asy} represents the asymptote or the number of recruits that can be produced per acre and Alpha corresponds to the slope of the Beverton-Holt stock-recruitment model (Barber et al. 2018) and is the log of lifetime reproductive rate or the number of age 3 recruits that each spawner produces.

Alewives imported more TP than they exported in three of seven lakes across all three stock-recruitment relationships. In Webber Pond, Warwick Pond, and Carr Pond, adult alewives brought in more P than juveniles exported (Tables 5 and 6) and thus were a net influx or source of P to the system. For China Lake, Pawtuckaway Lake, and Togus Pond, juvenile export was greater than adult import across all three stock-recruitment relationships, and thus alewives were a net sink of P, removing more P than they brought in (Tables 5 and 6). Highland Lake showed a net influx at low recruitment and a net export at medium and high recruitment (Tables 5 and 6).

Table 5. Net (static) alewife TP flux to lakes based on 10th (low), 50th (medium), and 90th (high) juvenile recruitment. The model (Barber et al. 2018) was used to calculate number of spawners and associated net TP flux. Net TP values are displayed for the modeled number of adult spawners closest to actual spawner counts. Passage rates were standardized for comparison and set at 96% for upstream and downstream passage. Alewife counts are from 2017. Negative numbers indicate a net export of TP from the lake.

		Low Recruitment		**Medium Recruitment**		**High Recruitment**	
Waterbody	**Actual Escapement (2017)**	**Modeled escapement**	**TP (kg/yr)**	**Modeled escapement**	**TP (kg/yr)**	**Modeled escapement**	**TP (kg/yr)**
China	24849	27134	-6.97	26686	-10.14	27251	-14.39
Highland	38106	41689	5.84	33387	-1.77	37286	-7.82
Togus	10000	8621	-1.54	11411	-3.13	10148	-4.76
Webber	292677	294251	109.49	320582	93.64	317153	54.24
Pawtuckaway	1000	831	-0.30	930	-0.44	1080	-0.67

		Low Recruitment		Medium Recruitment		High Recruitment	
Waterbody	Actual Escapement (2017)	Modeled escapement	TP (kg/yr)	Modeled escapement	TP (kg/yr)	Modeled escapement	TP (kg/yr)
Carr	58772	58765*	26.75	58765*	25.41	58765*	23.19
Warwick	17874	18019	6.33	17932	4.52	18236	2.23
* For Carr Pond the model was forced by starting escapement at 50000 fish. The model capped fish numbers at 13000, 22000, and 40000 for 10th, 50th, and 90th productivity, respectively, far lower than the 60,000 alewives counted at the fish ladder.							

Because the model used a one-year time step, numbers of adult alewives predicted by the model did not always match observed numbers of adult alewives entering or stocked in a system. Regardless of the stock-recruitment relationship, the modeled number of adults returning to Carr Pond was always less than the observed number of returning adults (Table 5). The model returned similar, although not precise, count data for all other systems.

The significance of imported or exported P depends on the concentration of TP already present in the lake. To compare modeled alewife P to lake TP, I converted modeled alewife P in kg to a concentration, ppb or µg/L, using Equation 1, which assumes P is lost to sediments, and Equation 2, which assumes that lakes experience internal recycling of P (Table 6). Alewives removed P from China Lake, Togus Pond, and Pawtuckaway Lake under low, medium (Figure 7), and high stock recruitment scenarios, whether accounting for sedimentation or not (Table 6). Highland Lake experienced a very low (0.07 to 0.45 ppb) net export of P at medium (Figure 7) and high stock recruitment relationships, whether accounting for sedimentation or not (Table 6). At low juvenile recruitment, i.e., low R_{asy} and Alpha values, Highland Lake experienced 0.22 to 0.34 ppb influx of P from alewives (Table 6). Webber, Carr, and Warwick Ponds had a net positive influx of P at low, medium (Figure 7), and high stock recruitment parameters and whether sedimentation was accounted for or not (Table 6). Carr Pond showed the highest influx at 19.39 ppb when not accounting for sedimentation, using the lowest recruitment parameter values (Table 6).

Table 6. Alewife P flux converted to concentration, or in-lake P, in µg/L. Sedimentation accounts for some alewife P being incorporated into sediments, whereas no sedimentation does not. Low, medium, and high P indicate juvenile recruitment levels. A negative number indicates net export of P from the lake.

	Sedimentation			**No Sedimentation**		
Waterbody	**Low P**	**Med P**	**High P**	**Low P**	**Med P**	**High P**
China	-0.07	-0.10	-0.14	-0.10	-0.14	-0.20
Highland	0.22	-0.07	-0.29	0.34	-0.1	-0.45
Togus	-0.06	-0.13	-0.20	-0.11	-0.23	-0.34
Webber	1.72	1.47	0.85	4.74	4.06	2.35
Pawtuckaway	-0.01	-0.01	-0.01	-0.03	-0.044	-0.07
Carr	2.36	2.25	2.05	19.39	18.42	16.82
Warwick	1.23	0.88	0.43	3.81	2.72	1.34

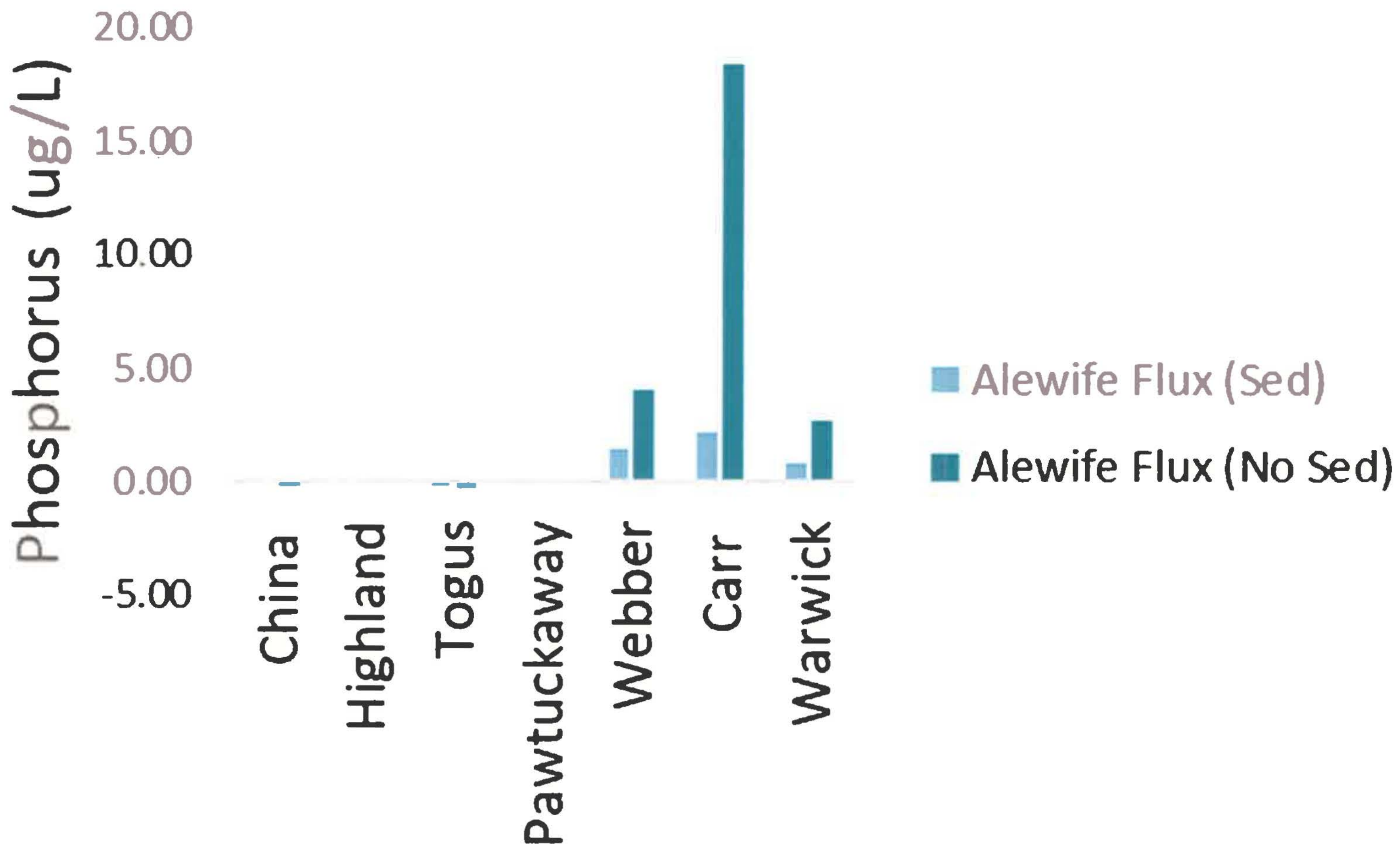

Figure 7. Alewife P flux converted to concentration, or in-lake P, in µg/L, at medium juvenile recruitment, accounting for sedimentation or not.

To better understand the significance of net P values, I converted ug/L to a percentage of the mean summer epilimnetic TP for each lake (Table 7). For example, I calculated % mean summer epilimnetic TP for Highland Lake, assuming low productivity and not accounting for sedimentation as:

Adult alewife P = 19.91 kg P/ 17.3 $10^6 m^3 (0.7 + \sqrt{0.7})$ = 0.75 µg/L

Juvenile alewife P = 14.08 kg P/ 17.3 $10^6 m^3 (0.7 + \sqrt{0.7})$ = 0.53 µg/L

Total flux of P = 0.75 ppb – 0.53 ppb = 0.22 µg/L

Mean epilimnetic TP in Highland Lake = 6.67 µg/L

Total alewife P as a percentage of summer TP in Highland Lake = (0.22/ 6.67) x 100% = 3.29%

The percent increase or decrease in TP (µg/l) associated with alewife import or export indicates that, for 4 of 7 lakes (China Lake, Highland Lake, Togus Pond, Pawtuckaway Lake), alewives provided a net export of TP or below ~5% of the existing epilimnetic TP (Table 7). These results hold for both sedimentation, which assumes some loss of TP to sediments, and high no sedimentation, which assumes no loss of TP to sediments, or when internal P recycling occurs. In contrast, alewives result in a relative increase in TP concentrations in Webber, Carr, and Warwick Ponds across all scenarios (Table 7).

Table 7. Alewife P flux as a percentage of summer epilimnetic P. Low, medium, and high P (%) indicate juvenile recruitment levels. A negative number indicates a net export of P from the lake.

Waterbody	Sedimentation			No Sedimentation		
	Low (%)	Med (%)	High (%)	Low (%)	Med (%)	High (%)
China	-0.59	-0.85	-1.21	-0.85	-1.10	-1.43
Highland	3.29	-1.00	-4.41	5.06	0.34	-5.22
Togus	-0.60	-1.22	-1.85	-1.02	-1.69	-3.09
Webber	10.14	8.67	5.02	27.90	23.86	13.82
Pawtuckaway Lake	-0.04	-0.06	-0.09	-0.22	-0.31	-0.48
Carr Pond	12.03	11.43	10.44	98.62	93.67	85.50
Warwick Pond	5.05	3.60	1.78	15.65	11.19	5.52

Discussion

Migratory fish may provide a sink under three conditions: (1) when more nutrients are retained by live biomass than are deposited into the system, (2) when emigration exceeds immigration, and (3) when nutrients from dead fish are unavailable (Vanni et al. 2013). This paradigm proved accurate in most study lakes with some refinements. Lakes had a net export of P when reproduction and growth of juvenile alewives outpaced P contributed from mortality, excretion, and gametes from adult alewives. Export was higher when emigration of juvenile alewives exceeded immigration of adult spawners. However, as run size increased, juvenile numbers were constrained by density dependent growth, and adult import began to outweigh juvenile export. Finally, removing carcasses, either through commercial harvest or through predation, should be effective at reducing P input.

The potential impact of alewives on P levels during the growing season in New England lakes varies widely. However, across the majority of scenarios P contributions from alewives were minimal. Based on the number of spawning adults in 2017, alewives contributed less than 5% of mean epilimnetic TP in four of seven lakes studied in the summer (China Lake, Highland Lake, Togus Pond, and Pawtuckaway Lake). In these lakes, alewives did not contribute to P nutrient balance. In comparison, looking at medium values, alewives contributed more P in Warwick and Webber ponds, translating from 3.6 – 11.19% of mean summer epilimnetic TP in Warwick Pond and 8.67 – 23.86% in Webber Pond. In Carr Pond, however, alewives contributed 11.43 – 93.67% of summer epilimnetic TP, which is potentially a large portion of the in-lake P budget. These ranges in P contributions depend on the shape of the alewife stock recruitment curve (Gibson 2004). Smaller or net negative overall contributions of P occur when juvenile productivity is higher, and thus juvenile emigration removes more P than imported by adult spawners.

In all lakes, as numbers of spawning adults rose, juveniles began to experience density dependence, and juvenile productivity plateaued, such that the net alewife-derived P input to the lake increased as adult numbers increased and was no longer balanced by juvenile emigration. In Highland Lake this plateau occurred above 40,000 adults. Numbers of alewives returning to spawn in Highland Lake fluctuated between 7,000 and 68,000 fish between 2014 and 2018 (Wilson, unpublished data), suggesting that in some years alewives provide a net influx of P and in other years they remove P. As productivity of the system stabilized due to constraints of habitat size, net import of P increased, correlated with increased escapement. This density dependent constraint on P export was true across all lakes.

Although the magnitude of the alewife P flux was largely dependent on alewife run size, the size of the receiving lake also played a role. In smaller lakes with higher escapement, spawning alewives resulted in a larger net influx of nutrients. In larger lakes, alewives either contributed negligible levels of P or provided a net reduction in TP levels, as juvenile emigration removed larger quantities of P than adults imported. Thus, as was shown in Highland Lake, up to a certain escapement, alewives provide a net export of TP from the lake. The asymptotic density dependent nature of juvenile alewife population growth curtails the ability for continued export at larger escapement levels.

In lakes with a smaller run size, increasing escapement could potentially produce more juveniles and thus have a larger reduction in TP. Variation in the number of juveniles per acre and juveniles per spawner impacted P balance. Increasing the number of eggs per spawner and the number of juvenile alewives raised per acre allowed for greater productivity of juveniles, which led to higher net negative reduction in TP within systems. In a study of 29 lakes, density dependence plateaued at approximately 1000 adults/ha (Devine et al. 2021). However, Carr Pond had over twice that density, whereas Webber Pond and Warwick Pond had nearly half of this estimate. The remaining lakes fell far below these values.

The model assumed all habitat was equal relative to production of juveniles, regardless of trophic status. I expected that lakes with higher lake primary productivity would provide more food resources and support higher somatic growth rate of juvenile alewives (Devine et al. 2021). Juvenile alewives feed on phytoplankton and zooplankton (Demi et al. 2015, Kircheis et al. 2002), and higher primary production would mean greater food availability, which in turn supports larger juvenile alewives (Devine et al. 2021). Thus, I expected eutrophic lakes to support larger numbers of recruits per adult per hectare than mesotrophic or oligotrophic lakes do. Eutrophic lakes such as China Lake, Togus Pond, Webber Pond, Carr Pond, and Warwick Pond may provide more food and thus result in larger juveniles compared to mesotrophic or oligotrophic lakes. In my calculations, increased numbers of juveniles resulted in greater P reduction, as seen in the Highland Lake model comparing three productivity scenarios. The relative size of juveniles should have a similar effect in P reduction, because nutrients stored in body mass are proportional to greater population numbers. Consequently, higher lake P levels potentially result in higher P reduction.

Carr Pond was the smallest lake in this study. The model capped Carr Pond at 23,000 adult alewives entering the lake for medium productivity (50th percentage) and 40,000 adults for high productivity rates (90th percentage); yet 60,000 returning alewives were counted at the fish ladder (Phillip Edwards, RIDEM, Division of Fish & Wildlife Chief, 2017, personal communication). Alewives generally return to lakes in which they spawned previously, suggesting that these numbers originated in Carr Pond or in surrounding habitat. In Carr Pond, spawning also may occur in nearby saline habitat (DiMaggio et al. 2015, 2016), or in upstream habitat of Mattatuxet River. Alternatively juvenile alewives may emigrate earlier than typical to nearby habitat, including Lower and Upper Ponds, the Narrow River Estuary, and Pettaquamscutt Cove (Phillip Edwards, RIDEM, Division of Fish & Wildlife Chief, 2017, personal communication, Hare et al. 2021), consequently expanding their nursery habitat. This additional habitat would allow Carr Pond to support more juvenile fish than expected and explain the larger run size.

Another limit of the study is that the model uses data from historical studies in specific systems (Durbin et al. 1979, Gibson and Meyers 2003, Gibson 2004, Havey 1973, Kissil 1974, 1969). Estimates of P removed by juvenile alewives are calculated using an average size or mass per juvenile. However, juvenile alewives differ in size at date of departure, depending on food source, availability, and when they leave natal spawning grounds (Devine et al. 2021, Gahagan et al. 2010). Moreover, juvenile alewives leave in pulses, correlated with higher water levels, greater fish length, and overall physical condition (Gahagan et al. 2010). Juveniles remaining in the lake may be released from density dependence when a significant number of conspecifics leave earlier in summer. As a result of these variables, P export may be greater than calculated by the model.

Compared to the complete mortality of Pacific salmon after spawning, alewife mortality in lakes post spawning is relatively low, which means that the amount of alewife carcass-derived nutrients is relatively lower versus those contributed to freshwater systems by Pacific salmon (West et al. 2010). The model assumed spawning mortality to be between 37.5% (Durbin et al. 1979) and 57.4% (Kissil 1974). However, studies indicate that alewife mortality rates vary between 30 and 80% (Dalton et al. 2009, Durbin et al. 1979, Havey 1961, Kissil 1974, West et al. 2010). This wide disparity in mortality indicates that P contributed by alewife carcasses can vary greatly, which may not be captured in the model.

The model also uses a time period of 14 days as the average length of stay for an adult spawning alewife (Barber et al. 2018, Kissil 1969). However, length of stay for a spawning adult can be up to 82 days (Hare et al. 2021, Kissil 1974). The length of stay in the spawning habitat may depend on external variables such as water level in exit structures or outlets (Tommasi et al. 2015; M. Thurrell, personal observation), with higher water being the primary driver for emigrations (Kissil 1974). In Highland Lake, some adults are still present in the lake as late as October, although most fish leave earlier if rains are sufficient past the breeding period (Stewart et al. 2021). Thus, both the amount of P contributed either via excretion or mortality and the amount of P sequestered by adult alewives may vary.

The model assumes that adult alewives do not feed in spawning lakes (Barber et al. 2018). However, longer residence times in freshwater suggest that adult alewives feed while in freshwater (Rosset et al. 2017), a behavior observed by Willis (2009) and Stewart et al. (2021). Anadromous alewives are efficient zooplanktivores, often reducing the abundance of larger sized zooplankton during summer when they are late residents (Brooks and Dodson 1965, Demi et al. 2015). However, unlike lakes with landlocked alewives, zooplankton communities recover after juveniles leave the system (Post et al. 2008). Because zooplankton graze on some species of phytoplankton responsible for algae blooms, alewives can potentially increase the prevalence of nuisance algal blooms through trophic cascades (Bradt & Chungu 1999). In contrast, due to feeding in spawning lakes, adults likely remove additional freshwater-derived P, not accounted for in the model, when they migrate to the ocean. Overall, the impacts of alewives on P budgets and associated algal blooms are a combination of import and export from adults and juveniles and food web manipulation.

Seasonal timing of the alewife run also may impact the lake P budget. Immigrating adults arrive in spring (May–June) and contribute P through excretion, mortality, and gametes during the clear water phase (Hare et al. 2021, Kissil 1969). Adult alewives consume zooplankton, incorporating some freshwater P in the process. Juvenile alewives also accumulate freshwater P as they grow. Nutrients sequestered in biomass are then removed during emigration. Therefore, the immediate effect of emigration might be a reduction in zooplanktivory and subsequent increase in phytoplankton grazing as zooplankton communities recover. In the longer term, the effect of removal of lake P by alewives may be cumulative reductions in TP over many years. Longer term studies are needed to address this question.

Creating a nutrient budget for a lake is challenging because estimating the number of out-migrating juvenile alewives or young of year alewives at seven lakes was beyond the scope and capacity of this study. Although electronic fish counters, trapping, or visual counts can be used to census immigrating adults, these methods are not appropriate for counting juvenile alewives accurately. Catching juvenile alewives would require tremendous effort and is generally discouraged due to the likelihood of high mortality rates. As a result, researchers have encountered challenges in creating nutrient budgets with alewives. Other researchers have approached this problem by estimating juvenile alewife abundance in lakes using seine nets (e.g., Devine et al. 2021), but this metric of fish abundance does not account for early migrations out of the lake.

This study used the most accessible and minimal data set necessary to produce a picture of lake P dynamics. I used epilimnetic TP as a measure of total lake P because these data were readily available across all lakes in this study and are easily collected by volunteers. A more complete analysis would measure P at multiple discrete depths in the epilimnion, metalimnion, and hypolimnion. Direct measurements of external watershed loading and an evaluation of internal lake loading could be used to develop a comprehensive lake nutrient budget to compare with alewife results. Such a complete and nuanced analysis of sources of lake P would aid managers in fine tuning decisions around P mitigation. Because of high variability across lakes, as illustrated in this study, specific data from a given lake should be used to inform management decisions.

Management Implications

Alewife spawning runs have been proposed as an aspect of P control on some eutrophic lakes (Kircheis et al. 2002). If the assumption that juvenile productivity is density dependent is correct (that is, their growth is restricted by an asymptotic maximum), then spawning access could be controlled to maximize production of juveniles and therefore reduction of P in lakes. However, the suggestion that we limit adult access to spawning grounds to reduce P requires several important considerations:

1. Alewives' impact on TP levels was minimal under most scenarios.
2. To make a significant reduction in P, large numbers of juveniles are required relative to adults, and reliable downstream passage must be provided.

3. Reducing the number of spawners as a method of P management does not remove other sources of P, such as agricultural and industrial sources, which are likely to be greater in magnitude than that contributed by alewives.

4. Managing the number of spawning adult alewives has larger ecological implications. Alewives have only recently begun making a comeback, and population numbers are still low. Access to historical spawning habitat is at or near a historical low, and risk of mortality is currently high during their residence at sea (e.g., bycatch, Hasselman et al. 2016). Alewives represent one of only a few marine forage fish for which humans directly control access to spawning grounds. Other marine forage fish, such as Atlantic herring, occur at extremely low population numbers. Alewives comprise a native component of lake, river, and nearshore marine ecosystems, that for decades have been prevented from reaching spawning grounds by dams and poor passage structures. As a natural component of these systems, alewives should be included as an allocation in lake P budgets such as the Total Maximum Daily Load plan (TMDL) along with the rest of aquatic systems (i.e., background P).

5. If numbers of returning adults are controlled, consideration about which age classes to harvest must be included. Older and larger fish are more likely to be repeat spawners, which both scientists and regulators consider important for spawning run persistence over time (Waldman et al. 2016).

6. Managers need a better understanding of which portions of the run should be prevented from spawning, suggesting that more active and regional management is required.

7. Alewives provide forage for commercially important fish species in marine ecosystems and are harvested as high quality local lobster bait in Maine.

8. Alewives are consumed by many of the same species that prey on Atlantic salmon. Alewife migration occurs at the same time as Atlantic salmon migration, and thus alewives are ecologically important as distraction or cover prey to the restoration of Atlantic salmon in New England.

9. Work should focus on lakes with higher alewife escapement, such as Carr Pond, which could be designated to provide stock, i.e., gravid adult alewives transported to new spawning habitats to start new natal spawning runs.

10. Anadromous alewives cross many political and institutional boundaries during their life cycles, necessitating the cooperation of many entities, including multiple municipalities, state and federal agencies. For example, in Maine, alewives are considered a marine fisheries resource (NOAA Fisheries) and are managed by the MEDMR, even when using freshwater habitats, where they interact with freshwater species (managed by Maine Department of Inland Fisheries and Wildlife), and potentially influence water quality and nutrient dynamics (monitored and regulated by the MEDEP). Other stakeholders include lake associations, towns, and dam owners.

Conclusion

In conclusion, in the majority of systems studied, alewives provided a net negative or negligible amount of P. Alewife impact on lake nutrient budgets varied depending on variables such as lake size, escapement, juvenile productivity, and mortality. If escapement is low compared to the size of the lake, alewife P is negligible. Up to a certain magnitude of escapement, alewives provided a net export of P, largely due to juveniles sequestering P prior to leaving the lake, and this export outweighed import from spawning adults. As escapement increased, alewives began to provide a net import of P. Alewives may be used to manipulate P levels through controlling escapement. Finally, alewife P is generally many orders of magnitude smaller than other external sources of P, such as agricultural derived P.

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APPENDIX A. Water Quality Data for Maine Lakes

*Data for Rhode Island and New Hampshire lakes available upon request from New Hampshire Fish and Game and Rhode Island Watershed Watch.

Site	Date	Station Location	Latitude	Longitude	Avg Secchi (m)	Sample Size (mL)	Depth From Surface (m)	Method	Filter (um)	Treatment	Parameter Type	N (mg/L)[1]	P (ug/L)[1]
Highland Lake	5/13/2017	Deep hole	43.77806	-70.35814		125	19	Van dorn	0.7	Frozen	NO3/PO4	0.044	4
Highland Lake	5/13/2017	Deep hole	43.77806	-70.35814		125	19	Van dorn	0.7	Frozen	NO3/PO4	0.038	4
Highland Lake	5/13/2017	Deep hole	43.77806	-70.35814		125	19	Van dorn	NA	Frozen	TN/TP	0.216	6
Highland Lake	5/13/2017	Deep hole	43.77806	-70.35814		125	19	Van dorn	NA	Frozen	TN/TP	No data	No data
Highland Lake	5/13/2017	Deep hole	43.77806	-70.35814		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
Highland Lake	5/13/2017	Deep hole	43.77806	-70.35814		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
Highland Lake	5/13/2017	Deep hole	43.77806	-70.35814		125	0.3048	Surface grab	NA	Frozen	TN/TP	0.206	7
Highland Lake	5/13/2017	Deep hole	43.77806	-70.35814		125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Togus Pond	5/21/2017	Deep hole	44.32389	-69.65798		125	15	Van dorn	0.7	Frozen	NO3/PO4	0.022	9
Togus Pond	5/21/2017	Deep hole	44.32389	-69.65798		125	15	Van dorn	0.7	Frozen	NO3/PO4	No detection	12
Togus Pond	5/21/2017	Deep hole	44.32389	-69.65798		125	15	Van dorn	NA	Frozen	TN/TP	0.414	39
Togus Pond	5/21/2017	Deep hole	44.32389	-69.65798		125	15	Van dorn	NA	Frozen	TN/TP	No data	No data
Togus Pond	5/21/2017	Deep hole	44.32389	-69.65798		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
Togus Pond	5/21/2017	Deep hole	44.32389	-69.65798		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	3
Togus Pond	5/21/2017	Deep hole	44.32389	-69.65798		125	0.3048	Surface grab	NA	Frozen	TN/TP	0.191	9
Togus Pond	5/21/2017	Deep hole	44.32389	-69.65798		125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
China Lake	5/23/2017	Deep hole	44.43288	-69.56964		125	26	Van dorn	0.7	Frozen	NO3/PO4	No detection	5
China Lake	5/23/2017	Deep hole	44.43288	-69.56964		125	26	Van dorn	0.7	Frozen	NO3/PO4	No detection	6
China Lake	5/23/2017	Deep hole	44.43288	-69.56964		125	26	Van dorn	NA	Frozen	TN/TP	0.352	23
China Lake	5/23/2017	Deep hole	44.43288	-69.56964		125	26	Van dorn	NA	Frozen	TN/TP	No data	No data
China Lake	5/23/2017	Deep hole	44.43288	-69.56964		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	5

Site	Date	Station Location	Latitude	Longitude	Avg Secchi (m)	Sample Size (mL)	Depth From Surface (m)	Method	Filter (um)	Treatment	Parameter Type	N (mg/L)[1]	P (ug/L)[1]
China Lake	5/23/2017	Deep hole	44.43288	-69.56964		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	5
China Lake	5/23/2017	Deep hole	44.43288	-69.56964		125	0.3048	Surface grab	NA	Frozen	TN/TP	0.3	11
China Lake	5/23/2017	Deep hole	44.43288	-69.56964		125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Webber Pond	5/23/2017	Deep hole	44.40474	-69.65847		125	10	Van dorn	0.7	Frozen	NO3/PO4	No detection	6
Webber Pond	5/23/2017	Deep hole	44.40474	-69.65847		125	10	Van dorn	0.7	Frozen	NO3/PO4	No detection	7
Webber Pond	5/23/2017	Deep hole	44.40474	-69.65847		125	10	Van dorn	na	Frozen	TN/TP	0.26	14
Webber Pond	5/23/2017	Deep hole	44.40474	-69.65847		125	10	Van dorn	NA	Frozen	TN/TP	No data	No data
Webber Pond	5/23/2017	Deep hole	44.40474	-69.65847		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	5
Webber Pond	5/23/2017	Deep hole	44.40474	-69.65847		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	6
Webber Pond	5/23/2017	Deep hole	44.40474	-69.65847		125	0.3048	Surface grab	NA	Frozen	TN/TP	0.374	19
Webber Pond	5/23/2017	Deep hole	44.40474	-69.65847		125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Highland Lake	7/16/2017	Deep hole	43.77806	-70.35814		125	20	Van dorn	0.7	Frozen	NO3/PO4	0.139	5
Highland Lake	7/16/2017	Deep hole	43.77806	-70.35814		125	20	Van dorn	0.7	Frozen	NO3/PO4	0.148	5
Highland Lake	7/16/2017	Deep hole	43.77806	-70.35814		125	20	Van dorn	NA	Frozen	TN/TP	0.3	7
Highland Lake	7/16/2017	Deep hole	43.77806	-70.35814		125	20	Van dorn	NA	Frozen	TN/TP	No data	No data
Highland Lake	7/16/2017	Deep hole	43.77806	-70.35814		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	6
Highland Lake	7/16/2017	Deep hole	43.77806	-70.35814		125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	6
Highland Lake	7/16/2017	Deep hole	43.77806	-70.35814		125	0.3048	Surface grab	NA	Frozen	TN/TP	0.194	7
Highland Lake	7/16/2017	Deep hole	43.77806	-70.35814		125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Togus Pond	7/18/2017	deep hole	44.32389	-69.65798	4.7	125	14	Van dorn	0.7	Frozen	NO3/PO4	No detection	13
Togus Pond	7/18/2017	Deep hole	44.32389	-69.65798	4.7	125	14	Van dorn	0.7	Frozen	NO3/PO4	No detection	11

Site	Date	Station Location	Latitude	Longitude	Avg Secchi (m)	Sample Size (mL)	Depth From Surface (m)	Method	Filter (um)	Treatment	Parameter Type	N (mg/L)[1]	P (ug/L)[1]
Togus Pond	7/18/2017	Deep hole	44.32389	-69.65798	4.7	125	14	Van dorn	NA	Frozen	TN/TP	0.309	44
Togus Pond	7/18/2017	Deep hole	44.32389	-69.65798	4.7	125	14	Van dorn	NA	Frozen	TN/TP	No data	No data
Togus Pond	7/18/2017	Deep hole	44.32389	-69.65798	4.7	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	7
Togus Pond	7/18/2017	Deep hole	44.32389	-69.65798	4.7	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	7
Togus Pond	7/18/2017	Deep hole	44.32389	-69.65798	4.7	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.3235	10.5
Togus Pond	7/18/2017	Deep hole	44.32389	-69.65798	4.7	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
China Lake	7/19/2017	Deep hole	44.43288	-69.56964	7.645	125	22	Kemmerer	0.7	Frozen	NO3/PO4	0.156	17
China Lake	7/19/2017	Deep hole	44.43288	-69.56964	7.645	125	22	Kemmerer	0.7	Frozen	NO3/PO4	0.184	14
China Lake	7/19/2017	Deep hole	44.43288	-69.56964	7.645	125	22	Kemmerer	NA	Frozen	TN/TP	0.434	26
China Lake	7/19/2017	Deep hole	44.43288	-69.56964	7.645	125	22	Kemmerer	NA	Frozen	TN/TP	No data	No data
China Lake	7/19/2017	Deep hole	44.43288	-69.56964	7.645	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	nd
China Lake	7/19/2017	Deep hole	44.43288	-69.56964	7.645	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	nd
China Lake	7/19/2017	Deep hole	44.43288	-69.56964	7.645	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.327	9
China Lake	7/19/2017	Deep hole	44.43288	-69.56964	7.645	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Webber Pond	7/19/2017	Deep hole	44.40474	-69.65847	1.825	125	6.5	Kemmerer	0.7	Frozen	NO3/PO4	No detection	3
Webber Pond	7/19/2017	Deep hole	44.40474	-69.65847	1.825	125	6.5	Kemmerer	0.7	Frozen	NO3/PO4	No detection	4
Webber Pond	7/19/2017	Deep hole	44.40474	-69.65847	1.825	125	6.5	Kemmerer	NA	Frozen	TN/TP	0.373	18
Webber Pond	7/19/2017	Deep hole	44.40474	-69.65847	1.825	125	6.5	Kemmerer	NA	Frozen	TN/TP	No data	No data
Webber Pond	7/19/2017	Deep hole	44.40474	-69.65847	1.825	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	5
Webber Pond	7/19/2017	Deep hole	44.40474	-69.65847	1.825	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	5
Webber Pond	7/19/2017	Deep hole	44.40474	-69.65847	1.825	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.452	19

Site	Date	Station Location	Latitude	Longitude	Avg Secchi (m)	Sample Size (mL)	Depth From Surface (m)	Method	Filter (um)	Treatment	Parameter Type	N (mg/L)[1]	P (ug/L)[1]
Webber Pond	7/19/2017	Deep hole	44.40474	-69.65847	1.825	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Highland Lake	9/17/2017	Deep hole	43.77806	-70.35814	6.65	125	18	Kemmerer	0.7	Frozen	NO3/PO4	No detection	4
Highland Lake	9/17/2017	Deep hole	43.77806	-70.35814	6.65	125	18	Kemmerer	0.7	Frozen	NO3/PO4	No detection	5
Highland Lake	9/17/2017	Deep hole	43.77806	-70.35814	6.65	125	18	Kemmerer	NA	Frozen	TN/TP	0.255	nd
Highland Lake	9/17/2017	Deep hole	43.77806	-70.35814	6.65	125	18	Kemmerer	NA	Frozen	TN/TP	No data	No data
Highland Lake	9/17/2017	Deep hole	43.77806	-70.35814	6.65	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	0.055	4
Highland Lake	9/17/2017	Deep hole	43.77806	-70.35814	6.65	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	0.052	4
Highland Lake	9/17/2017	Deep hole	43.77806	-70.35814	6.65	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.24	6
Highland Lake	9/17/2017	Deep hole	43.77806	-70.35814	6.65	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Togus Pond	9/21/2017	Deep hole	44.32389	-69.65798	6.61	125	13	Kemmerer	0.7	Frozen	NO3/PO4	No detection	6
Togus Pond	9/21/2017	Deep hole	44.32389	-69.65798	6.61	125	13	Kemmerer	0.7	Frozen	NO3/PO4	No detection	5
Togus Pond	9/21/2017	Deep hole	44.32389	-69.65798	6.61	125	13	Kemmerer	NA	Frozen	TN/TP	0.57	42
Togus Pond	9/21/2017	Deep hole	44.32389	-69.65798	6.61	125	13	Kemmerer	NA	Frozen	TN/TP	No data	No data
Togus Pond	9/21/2017	Deep hole	44.32389	-69.65798	6.61	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	5
Togus Pond	9/21/2017	Deep hole	44.32389	-69.65798	6.61	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	5
Togus Pond	9/21/2017	Deep hole	44.32389	-69.65798	6.61	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.286	13
Togus Pond	9/21/2017	Deep hole	44.32389	-69.65798	6.61	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
China Lake	9/24/2017	Deep hole	44.43288	-69.56964	2.325	125	24	Kemmerer	0.7	Frozen	NO3/PO4	0.096	11
China Lake	9/24/2017	Deep hole	44.43288	-69.56964	2.325	125	24	Kemmerer	0.7	Frozen	NO3/PO4	0.101	10
China Lake	9/24/2017	Deep hole	44.43288	-69.56964	2.325	125	24	Kemmerer	NA	Frozen	TN/TP	0.398	18
China Lake	9/24/2017	Deep hole	44.43288	-69.56964	2.325	125	24	Kemmerer	NA	Frozen	TN/TP	No data	No data

Site	Date	Station Location	Latitude	Longitude	Avg Secchi (m)	Sample Size (mL)	Depth From Surface (m)	Method	Filter (um)	Treatment	Parameter Type	N (mg/L)[1]	P (ug/L)[1]
China Lake	9/24/2017	Deep hole	44.43288	-69.56964	2.325	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
China Lake	9/24/2017	Deep hole	44.43288	-69.56964	2.325	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
China Lake	9/24/2017	Deep hole	44.43288	-69.56964	2.325	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.394	14
China Lake	9/24/2017	Deep hole	44.43288	-69.56964	2.325	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Webber Pond	9/24/2017	Deep hole	44.40474	-69.65847	3.41	125	10	Kemmerer	0.7	Frozen	NO3/PO4	No detection	12
Webber Pond	9/24/2017	Deep hole	44.40474	-69.65847	3.41	125	10	Kemmerer	0.7	Frozen	NO3/PO4	No detection	16
Webber Pond	9/24/2017	Deep hole	44.40474	-69.65847	3.41	125	10	Kemmerer	NA	Frozen	TN/TP	0.727	68
Webber Pond	9/24/2017	Deep hole	44.40474	-69.65847	3.41	125	10	Kemmerer	NA	Frozen	TN/TP	No data	No data
Webber Pond	9/24/2017	Deep hole	44.40474	-69.65847	3.41	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
Webber Pond	9/24/2017	Deep hole	44.40474	-69.65847	3.41	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
Webber Pond	9/24/2017	Deep hole	44.40474	-69.65847	3.41	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.36	13
Webber Pond	9/24/2017	Deep hole	44.40474	-69.65847	3.41	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Highland Lake	10/15/2017	Deep hole	43.77806	-70.35814	5.65	125	18	Kemmerer	0.7	Frozen	NO3/PO4	No detection	6
Highland Lake	10/15/2017	Deep hole	43.77806	-70.35814	5.65	125	18	Kemmerer	0.7	Frozen	NO3/PO4	No detection	3
Highland Lake	10/15/2017	Deep hole	43.77806	-70.35814	5.65	125	18	Kemmerer	NA	Frozen	TN/TP	0.245	4
Highland Lake	10/15/2017	Deep hole	43.77806	-70.35814	5.65	125	18	Kemmerer	NA	Frozen	TN/TP	No data	No data
Highland Lake	10/15/2017	Deep hole	43.77806	-70.35814	5.65	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
Highland Lake	10/15/2017	Deep hole	43.77806	-70.35814	5.65	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	3
Highland Lake	10/15/2017	Deep hole	43.77806	-70.35814	5.65	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.214	10
Highland Lake	10/15/2017	Deep hole	43.77806	-70.35814	5.65	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data

Site	Date	Station Location	Latitude	Longitude	Avg Secchi (m)	Sample Size (mL)	Depth From Surface (m)	Method	Filter (um)	Treatment	Parameter Type	N (mg/L)[1]	P (ug/L)[1]
Togus Pond	10/17/2017	Deep hole	44.32389	-69.65798	2.85	125	13	Kemmerer	0.7	Frozen	NO3/PO4	No detection	17
Togus Pond	10/17/2017	Deep hole	44.32389	-69.65798	2.85	125	13	Kemmerer	0.7	Frozen	NO3/PO4	No detection	33
Togus Pond	10/17/2017	Deep hole	44.32389	-69.65798	2.85	125	13	Kemmerer	NA	Frozen	TN/TP	1.025	77
Togus Pond	10/17/2017	Deep hole	44.32389	-69.65798	2.85	125	13	Kemmerer	NA	Frozen	TN/TP	No data	No data
Togus Pond	10/17/2017	Deep hole	44.32389	-69.65798	2.85	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No data	No data
Togus Pond	10/17/2017	Deep hole	44.32389	-69.65798	2.85	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No data	No data
Togus Pond	10/17/2017	Deep hole	44.32389	-69.65798	2.85	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Togus Pond	10/17/2017	Deep hole	44.32389	-69.65798	2.85	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
China Lake	10/21/2017	Deep hole	44.43288	-69.56964	2.26	125	24	Kemmerer	0.7	Frozen	NO3/PO4	No detection	10
China Lake	10/21/2017	Deep hole	44.43288	-69.56964	2.26	125	24	Kemmerer	0.7	Frozen	NO3/PO4	No detection	10
China Lake	10/21/2017	Deep hole	44.43288	-69.56964	2.26	125	24	Kemmerer	NA	Frozen	TN/TP	0.384	30
China Lake	10/21/2017	Deep hole	44.43288	-69.56964	2.26	125	24	Kemmerer	NA	Frozen	TN/TP	No data	No data
China Lake	10/21/2017	Deep hole	44.43288	-69.56964	2.26	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
China Lake	10/21/2017	Deep hole	44.43288	-69.56964	2.26	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	4
China Lake	10/21/2017	Deep hole	44.43288	-69.56964	2.26	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.479	17
China Lake	10/21/2017	Deep hole	44.43288	-69.56964	2.26	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data
Webber Pond	10/21/2017	Deep hole	44.40474	-69.65847	2.31	125	9	Kemmerer	0.7	Frozen	NO3/PO4	No detection	4
Webber Pond	10/21/2017	Deep hole	44.40474	-69.65847	2.31	125	9	Kemmerer	0.7	Frozen	NO3/PO4	No detection	3
Webber Pond	10/21/2017	Deep hole	44.40474	-69.65847	2.31	125	9	Kemmerer	NA	Frozen	TN/TP	0.307	16
Webber Pond	10/21/2017	Deep hole	44.40474	-69.65847	2.31	125	9	Kemmerer	NA	Frozen	TN/TP	No data	No data
Webber Pond	10/21/2017	Deep hole	44.40474	-69.65847	2.31	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	7

Site	Date	Station Location	Latitude	Longitude	Avg Secchi (m)	Sample Size (mL)	Depth From Surface (m)	Method	Filter (um)	Treatment	Parameter Type	N (mg/L)[1]	P (ug/L)[1]
Webber Pond	10/21/2017	Deep hole	44.40474	-69.65847	2.31	125	0.3048	Surface grab	0.7	Frozen	NO3/PO4	No detection	6
Webber Pond	10/21/2017	Deep hole	44.40474	-69.65847	2.31	125	0.3048	Surface grab	NA	Frozen	TN/TP	0.3745	17.5
Webber Pond	10/21/2017	Deep hole	44.40474	-69.65847	2.31	125	0.3048	Surface grab	NA	Frozen	TN/TP	No data	No data

1. Detection Limit: no detection <0.02 mg N/l or <3ug P/l

APPENDIX B. Final Approval

THE UNIVERSITY OF SOUTHERN MAINE
DEPARTMENT OF BIOLOGICAL SCIENCES

Date: 11/5/2022

We hereby recommend that the thesis of entitled:

Alewife (*Alosa pseudoharengus*) Contributions to Lake Phosphorus Budgets:

Implications for Management

Be accepted as partial fulfillment of the requirements for the degree of

Master of Science in Biology

Signatures

Author: Meg Farley Thurrell Date: 11/5/2022

Advisory Committee:

Date: 11/8/2022
(Graduate Advisor)

Date: 6 November 2022

Date: 11/8/2022

Date:

Date:

Chair of the Department of Biological Sciences:

Date: 11/8/2022

Dean of the College of Science, Technology and Health

Date: 12/18/2022