Implications of Anadromous Alewife (*Alosa pseudoharangus*) Restoration in Freshwater Systems of Maine

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The purpose of this report is to describe scientific findings and potential effects of anadromous Alewife restoration to freshwater systems of Maine. This report is a work in progress and should not be considered an official policy paper issued by NMFS. Any comments and questions regarding any of the information in this draft are welcomed and should be directed to Rory Saunders at (207) 866-4049 or Rory.Saunders@noaa.gov.

Abstract: Habitat restoration and increased connectivity of watersheds via dam removal and fish passage in Maine has allowed for anadromous Alewives to migrate upstream to their historic spawning areas for the first time in hundreds of years. However, the effects of anadromous Alewives (Alosa pseudoharengus) on freshwater systems that have become established since dam construction are debated. Existing literature concerning Alewife diet and feeding ecology, landlocked Rainbow Smelt (Osemerus mordax) diet and life history, and interactions between Alewives and cold-water fish were reviewed. Alewives significantly influence zooplankton community structure and decrease zooplankton average size. Alewives and Smelt both prefer large Cladocera and Copepoda. However, dietary overlap may be minimal within those taxa. Existing literature is not conclusive on potential trophic cascading effects of Alewives on plankton communities. Landlocked Rainbow Smelt are important winter forage for landlocked Atlantic Salmon, but have also shown to feed significantly on Alewives in the spring. Literature concerning landlocked Atlantic Salmon feeding in the presence of both species is dated and sparse. The effects of Alewife restoration on freshwater systems is well documented concerning zooplankton. However, more information is needed to determine direct effects on Rainbow Smelt.

ALEWIVES

Post, D.M., Palkovacs, E. P., Schielke, E.G., & Dodson, S. I. (2008). Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology, 89*(7), 2019-2032.

Post et al. (2008) investigated how variation in life history (anadromy vs. landlocked) affects zooplankton and phytoplankton diversity and abundance. The study includes measuring of zooplankton community structure, algal biomass, and spring total phosphorous throughout a range of lakes containing either anadromous, landlocked, or no Alewives. The main findings include:

1. Anadromous Alewives affected lake zooplankton community structure on a seasonal basis. Landlocked Alewives continually alter zooplankton community structure year-round.
2. Large Cladocerans are greater in abundance in anadromous lakes until young-of-year (YOY) Alewife gape size is large enough to consume them. Once YOY

Alewives can feed on them, large Cladocerans are mostly extirpated until YOY Alewife emigrate in the fall.

3. The presence of anadromous Alewives was positively correlated with phytoplankton biomass. Presence of anadromous Alewives were associated with higher phytoplankton biomass per unit of spring total phosphorous compared to landlocked Alewives.

Demi, L. M,, Simon, K. S., Coghlan, S.M. Jr., Saunders, R. & Anderson, D. (2012). Anadromous alewives in linked lake-stream ecosystems: do trophic interactions influence stream invertebrate communities? *Freshwater Science*. 31(3), 973-985.

This research focuses not only on the effects of anadromous Alewife on lake seston (including zooplankton and phytoplankton) but also the outflow of this seston to streams and the potential impacts on stream invertebrate communities. Because anadromous Alewives have been shown to affect zooplankton and phytoplankton biomass and community structure, the outflow of this seston may be reflected in outflow streams of lakes and ponds. Available seston will likely impact the abundance and diversity of filter feeding invertebrates such as net-spinning caddisflies (Trichoptera: Hydropsychidae). The main findings include:

1. Little influence of anadromous Alewives on stream filter-feeders in outflow streams. Lack of influence is likely due to lake seston not being equally represented in stream seston.
2. Alewife did not induce any cascading effects resulting in the increase of algal biomass in this study. This contrasts with the findings of other studies.
3. Alewife displayed size-selective predation and altered lake zooplankton and seston size. However, they did not induce cascading effects throughout the food web.
4. Uncertainty: Why were no trophic cascading effects observed as they have been in other studies? How is this possible when zooplankton average size is decreased?

Demi, L., Simon, K., Anderson, D., Coghlan, S., Saros, J., & Saunders, R. (2015). Trophic status may influence top–down effects of anadromous alewife *Alosa pseudoharengus* (Actinopterygii, Clupeidae) in lakes. *Hydrobiologia, 758*(1), 47-59.

In this study, the seasonal impacts of anadromous Alewife on zooplankton and phytoplankton communities was observed throughout lakes of varying trophic status to test the effect of trophic status on these top-down trophic cascades detailed in previous literature. This research offers interesting points on systems where Alewife are also experiencing predation pressure and the impacts that may have on plankton communities. The main findings include:

1. Intense size selection on Cladocerans by YOY Alewife in every lake where Alewives were present.

2. Alewife nutrient import, and the release of zooplankton from food limitation can allow biomass of zooplankton to remain stable with predation, or increase depending on trophic status.
3. Effects of Alewife predation weakened with increasing trophic status. This was attributed to potentially higher rates of predation on YOY Alewife by a greater abundance of piscivorous fish.
4. Uncertainty: Why does trophic status influence trophic cascading effects? How can this study attribute this to fish density and not nutrient availability?

Brooks, J.L. & Dodson, S.I. (1965). Predation, body size, and composition of plankton. *Science, 150*(3692), 28-35.

This classic study demonstrates the effects of landlocked Alewife on zooplankton size and community structure. Zooplankton were sampled in lakes not containing Alewives as well as Crystal Lake where landlocked Alewives were introduced. This research demonstrates the selectivity of Alewife by size and location. The change in zooplankton over time in Crystal Lake has become a standard reference for size-selective predation by Alewife since its publication. The main findings include:

1. Alewife size-selective predation significantly reduces or eliminates large lake zooplankton, allowing for small sized species to grow significantly in abundance.
2. Alewife predation favors pelagic zooplankton, allowing for the dominant species to be both of small size and littoral at least in the small lakes and ponds in Connecticut.
3. Larger lakes such as Lake Cayuga experienced the same effects of size-dependent predation by Alewives, while some large zooplankton persist at greater depths.
4. Uncertainty: How does this intense size selectivity influence the availability of prey for other zooplanktivores? Are they capable of shifting to feed on smaller zooplankton or is it direct competition?

Palkovacs, E. P., Dion, K. B., Post, D. M., & Caccone, A. (2008). Independent evolutionary origins of landlocked alewife populations and rapid parallel evolution of phenotypic traits. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/18179439

This research investigates the genetic divergence of landlocked Alewives from anadromous Alewives, as well as potential scenarios of divergence for landlocked populations of Alewives. The study also incorporates the evolutionary rates of phenotypes as populations transition between life histories. The authors utilize mitochondrial DNA and microsatellites to determine phenotypic divergence as well as divergence time. The main findings include:

1. Landlocked Alewife populations independently diverge from an ancestral core of the anadromous population.
2. Landlocked populations arose from 5,000-300 years ago. Dam construction since colonial settlement likely facilitated this genetic and life history divergence.

3. Traits favoring smaller zooplankton size may commonly evolve in multiple species during the transition from anadromy to freshwater residence.
4. Uncertainty: What is the rate of natural land-locking? Can this occur with one year of blocked downstream passage or does continuously blocked passage drive this life history shift away from migration? Do the forms co-exist? Does restoration of fish passage lead to changes back to anadromous forms?

Janssen, J. & Brandt, S. B. (1980). Feeding Ecology and Vertical Migration of Adult Alewives (*Alosa pseudoharengus*) in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences.* 37, 177-184.

In this study the vertical migrations of landlocked Alewives were observed using acoustic monitoring as well as trawling for micro-crustaceans and Alewives. This researched showed the migrations of Alewives being closely related to the vertical presence of *Mysis* and the time of day. Differences in daily migrations by adult and juvenile Alewives were compared and some explanations for these differences were presented. The main findings include:

1. Alewives remained near the bottom of the water column during the day and migrated to midwater in the night with the upper limit of their migration being determined largely by the presence of *Mysis* and the location of the thermocline.
2. Abundance of zooplankton compared to *Mysis* in Alewife diets suggests that filter feeding is only advantageous in high concentrations of zooplankton and that *Mysis* were selected visually by Alewives as a function of size.
3. Alewives that fed exclusively in the lower parts of the *Mysis* layer had greater sized prey items in their stomachs supporting size selective predation on *Mysis* and filter feeding on zooplankton.
4. Uncertainties: Do these vertical migrations allows for overlap with (and predation on) YOY Alewife or Rainbow Smelt that occupy the epilimnion or concentrate around the thermocline?

Weis, J. J., & Post, D. M. (2013). Intraspecific variation in a predator drives cascading variation in primary producer community composition. *Oikos, 122*(9), 1343-1349.

This research focuses on how the variation in life history of Alewives (landlocked vs anadromous) affects zooplankton and phytoplankton community and body size. This study utilizes in-lake mesocosms to control the presence and life history type of the Alewife treatment. The mesocosms allow for control of the experiment in a way that full lake experiments cannot replicate. The main findings include:

1. Lower rates of herbivory were observed among anadromous Alewives, as well as a statistically significant cascading effect on phytoplankton community composition.
2. Alewife presence and life history altered phytoplankton community structure, but phytoplankton biomass and diversity did not differ significantly.
3. Cascading effects took place in the absence of Daphnia which could have increased the magnitude of trophic cascades.

4. Uncertainties: Do lower rates of predation by anadromous alewives reduce the incidence and magnitude of trophic cascading? This would contradict findings by Post et al. 2008, and support findings by Demi et al. 2012 and Demi et al. 2015.

SMELT

Parker-Stetter, S. L., Thomson, J. L., Rudstam, L. G., Parrish, D. L., Sullivan, P. J. (2007). Importance and Predictability of Cannibalism in Rainbow Smelt. *Transactions of the American Fisheries Society*. 136: 227-237.

In this study, the effects of cannibalism and the cyclical nature of (landlocked) Rainbow Smelt populations is studied as well as predictability of cannibalism rates based on temperature profile and location of year classes within the water column. The researchers utilized hydroacoustic monitoring of YOY and 1+ Rainbow Smelt as well as trawling to confirm hydroacoustic data and gather diet information for 1+ Rainbow Smelt in Lake Champlain. The main findings include:

1. Thermal stratification provides a spatial buffer for YOY Rainbow Smelt from cannibalistic 1+ Rainbow Smelt. Periods with weak thermoclines showed the greatest level of cannibalistic 1+ Rainbow Smelt through diet analysis.
2. Experienced density (Age 0 Rainbow Smelt density and spatial overlap between year classes) was the best predictor for the level of cannibalism compared to just spatial niche overlap and just Age-0 density.
3. Gape size of age-1+ fish is a limiting factor for the rate of cannibalism. The authors suggest future studies incorporate size dependency in experienced density predictions of cannibalism.

Rupp, R. S. (1959). Variation in the Life History of the American Smelt in Inland Waters of Maine. *Transactions of the American Fisheries Society.* 88(4), 241-252.

This study summarizes data from multiple sources to demonstrate the variation within and among lakes concerning Rainbow Smelt life history. Rupp (1959) discusses many factors that may explain this variation and potential internal and external stimuli that may contribute to these differences. Overall, the paper lays a good foundation for future studies of run timing, spawning habitat, and size at spawning for Smelt in Maine lakes and ponds. The main findings include:

1. Run timing of Rainbow Smelt is variable between lakes, but remains consistent within lakes through time. Run timing is not exclusively linked to water temperature.
2. Spawning habitat is variable within and among lakes for Smelt. Rupp (1959) provides numerous examples of spawning in alternative habitats including large rivers and beaches.
3. Due to the variation experienced between lakes it is likely that environmental variation shapes variation in life history with some indication of genetically isolated populations that are evolving independently to their specific lake or pond.
4. Uncertainties: Does run timing of Rainbow Smelt allow for juvenile emergence into the lake when thermal stratification exists, as this provides a buffer from

cannibalism? How is run timing and juvenile hatching linked to lake thermal stratification?

Henderson, B. A. and Nepzy S. J. (1989). Factors affecting recruitment and mortality rates of rainbow smelt (Osmerus mordax) in Lake Erie, 1963-85. Journal of Great Lakes Research. 15(2): 357-366.

In this study, the authors investigate the potential effects of cannibalism, piscivorous fish stocking, and commercial harvest on recruitment of Rainbow Smelt to yearling (age-1+) stage. The study incorporated two distinct areas of Lake Erie and compared age-0+ density to age-1+ densities, age-1+ diet, and parasitism to population trends in recruitment between year classes. The main findings include:

1. Survival to the age-1+ stage depends on the number of age-1+ individuals in the year before. Recruitment to age-1+ is based on cannibalism of age-0+ by the previous year class.
2. A very small rate of cannibalism was observed in the diet study of age-1+ fish. Only 2% of fish showed direct evidence of cannibalism in their diet, but the cyclical effects of cannibalism were still observed suggesting low rates of cannibalism can cause these effects.
3. Cyclical trends in year classes were not observed in the later years of the study. This could be due to piscivorous fish predation, commercial harvest, decreasing size of all Smelt year classes or a combination of these factors.
4. Uncertainties: Are Smelt “their own worst enemy” or does this cyclical population cycle have an ecological or evolutionary function in Rainbow Smelt’s native habitats? Does this allow them to avoid predation by another species? Can this increase density during favorable years and decrease in unfavorable years?

Stritzel-Thomson, J.L., Parrish, D. L., Parker-Stetter, S. L., Rudstam, L. G., Sullivan, P. J.(2011).Growth rates of rainbow smelt in Lake Champlain: effects of density and diet. *Ecology of Freshwater Fish*. 20: 503-512.

This study analyzed the growth rates of age-0 and age-1 Rainbow Smelt in Lake Champlain related to density and cannibalism. Previous studies by the same group of researchers have shown that low rates of cannibalism can cause cyclical annual population fluctuations. This study builds upond the previous research by testing “biologically plausible explanations for growth rates” using Akaike Information Criterion (AIC). The main findings include:

1. As Age-0 Smelt density increased, growth rate decreased. Growth of YOY Smelt is density dependent in Lake Champlain.
2. Cannibalism is correlated with a faster growth rate in age-1 Smelt. There is a positive correlation between age-1 growth and age-0 density.
3. Increased density of age-0 Smelt results in slower growth. Slower growth often makes fish more vulnerable to predation as they have a smaller body size for a longer period of time.

4. Uncertainties: How does lower density impact competition with other zooplanktivores such as alewives? Can a few large individuals compete better than many small individuals?

Parker-Stetter, S. L., Witzel, L. D., Rudstam, L. G., Einhouse, D. W. and Mills, E. L. 2005. Energetic consequences of diet shifts in Lake Erie rainbow smelt (*Osmerus mordax*). *Canadian Journal of Fisheries and Aquatic Sciences*. 62: 145-152.

In this research, the authors were seeking to explain decreasing size of Rainbow Smelt in Lake Erie from the 1960s through the 1990s. With decreasing Smelt body size, declines in *Cladocera* populations took place in Lake Erie. However, others have attributed the decline in Rainbow Smelt size to spiny water fleas (*Bythotrephes longimanus and Bythotrephes cederstroemi)* being introduced to the system. The authors attempted to explain whether the decline in *Cladocerans*, or the introduction of *Bythotrephes* contributed to the decline in Rainbow Smelt body size. The main findings include:

1. Energy density in the summer diet of Smelts was not altered between the 1960s to the 1990s.
2. Summer diet of Smelts shifted throughout the sampling period. However, these changed cannot explain the continuing decline in individual growth rates.
3. Indigestible spines of *Bythotrephes* likely occupy stomach space of Rainbow Smelt and take up space which would normally be occupied by nutrient rich food allowing for greater growth rates.
4. Uncertainties: Can Smelt diet shifts to smaller individuals of the same species retain equal energy densities in the face of competition? Where is the threshold that energy expended outweighs energy consumed (and Smelt are effectively outcompeted)?

Baby, M. C., Bernatchez, L. and Dodson, J. J. (1991). Genetic structure and relationships among anadromous and landlocked populations of rainbow smelt, *Osmerus mordax*, Mitchill, as revealed by mtDNA restriction analysis. *Journal of Fish Biology.* 39(Supplement A): 61-68.

In this research the authors were seeking to compare the genetic similarity (or dissimilarity) of anadromous, landlocked, and dwarfed Rainbow Smelt. The authors used mitochondrial DNA, analyzed them using gel electrophoresis and compared the similarity of nucleotides between groups. This research is important in distinguishing how landlocked and dwarfed populations arise, and how they should be managed moving forward. The main findings include:

1. Genetic distinction between anadromous and landlocked forms of Rainbow Smelt, with an overlap of around 23% similarity.
2. Dwarfed Smelt held more genetic similarity when compared to landlocked Smelt vs. anadromous Smelt.

3. All anadromous populations held distinct genetic differences except for two spawning tributaries of the St. Lawrence River because of the use of the same larval retention area.
4. Uncertainties: Could introduced landlocked populations theoretically exist naturally throughout their range? How do sea run Smelt and Alewives interact in the estuarine environment and can we learn anything from those interactions?

Rothschild, B. J. (1961). Production and Survival of Eggs of the American Smelt, *Osmerus Mordax* (Mitchill), in Maine. *Transactions of the American Fisheries Society.* 90(1): 42-48.

This research project aims at understanding the spawning behavior, as well as survival of Rainbow Smelt eggs in a tributary of Branch Lake, Maine. The study was carried out by placing black tiles on the stream bottom which Smelt eggs would then adhere to. Rothschild used a tile with one half being cleared of eggs daily and the other half remaining as a control to estimate survival of eggs. This study design disturbs the eggs more than they would experience naturally, so survival estimates are likely lower in the paper's findings. The main findings include:

1. Mean egg survival was estimated at 24% of total production (collected 1-15 days before hatching).
2. Egg survival increased with distance from the stream mouth. Eggs that were deposited further up the stream had better survival.
3. Peak numbers of Smelt present in the brook was not correlated with peak egg deposition.
4. Uncertainties: How did this sampling design not impact the control Smelt eggs? Is this a reliable or consistent measure of Smelt egg survival and production compared to other, newer literature?

Siefert, R. E. (1972). First Food of Larval Yellow Perch, White Sucker, Bluegill, Emerald Shiner, and Rainbow Smelt. *Transactions of the American Fisheries Society.* 101(2): 219-225.

This study aimed at understanding the first food intake of larval fish of multiple different species. Entire digestive tracts of the fish were examined to determine diet. This research is important as it allows us to understand what food is available to larval fish at this critical period of survival. All fish were captured from northeastern and north-central Minnesota. The main findings include:

1. First feeding Smelt digestive tracts contained *Cyclops bicuspidatus*, copepod nauplii, diatoms, and non-motile green algae.
2. Cladocerans were minor food items in the first food of Rainbow Smelt, while they make up the majority of the diet for adult fish.
3. Large overlap of first food between fish species was observed. This is due to the size and speed restrictions for fish prey at this larval stage.

Lantry, B. F. and Stewart, D. J. (1993). Ecological Energetics of Rainbow Smelt in the Laurentian Great Lakes: An Interlake Comparison. *Transactions of the American Fisheries Society.* 122: 951-976.

In this paper Lantry and Stewart utilize a complex bioenergetics modeling technique to estimate population size, age, and growth coefficients of Rainbow Smelt between the five Great Lakes. This baseline information on consumption and production coupled with diet and age class abundance has not been compiled previously. While the modeling is extensive, parameter estimations are well justified and fall within or near existing estimations from previous literature. It is important to understand how the variability between lakes will affect Smelt population structure and abundance as it relates to salmonid predation and trophic interactions. The main findings include:

1. Piscivory by Smelts increases with individual fish size, and Smelt diet shifts from zooplankton early in life to large invertebrates and fish at older ages.
2. Preferred temperatures of varying age classes of Smelt compared with temperature preferences of salmonid predators may allow for greatest predation on age-2 and older Smelt due to spatial buffering of water temperature.
3. Populations with less variation in spawning age classes, combined with environmental stochasticity in spawning conditions may account for large variations in recruitment of age-0 Smelt.
4. Uncertainties: Can Smelt capable of feeding on small fish predate YOY Alewife? Could Alewife be both a competitor and a prey item for Smelt? How could this impact adult Smelt survival into the winter as a food source for game fish?

INTERACTIONS

Sayers, R. E., Moring, J.R., Johnson, P.R., Roy, S.A., (1989). Importance of Rainbow Smelt in the Winter Diet of Landlocked Atlantic Salmon in Four Maine Lakes. *North American Journal of Fisheries Management* 9: 298-302.

This research focused on the seeming dependence of landlocked Atlantic salmon on Rainbow Smelt as winter forage. The study utilized angler captured fish (using Rainbow Smelt as bait) in four cold-water lakes in Piscataquis County, Maine. Fish stomachs were collected and a diet analysis was performed utilizing classification and enumeration of forage items in each fish. The study incorporates three lakes with an abundance of Rainbow Smelt, and one lake lacking in Rainbow Smelt abundance. The main findings include:

1. Rainbow Smelt was the primary winter forage for landlocked Atlantic salmon in the four lakes sampled.
2. Poor growth rates were observed by salmon that did not feed on Rainbow Smelt compared to those that did (lakes where Smelt was abundant vs. depleted).
3. Landlocked Atlantic salmon stomach contents may be a reliable method for estimating relative abundance of Rainbow Smelt within a lake system.

4. Uncertainties: How do we know that this relationship is exclusive to Smelt? Would the same relationship be shown if Alewives were the prey item in the study?

Speirs, G. D. (1974) Food Habits of Landlocked Salmon and Brook Trout in a Maine Lake after Introduction of Landlocked Alewives. *Trans American Fisheries Society* No. 2: 396-399.

This research focuses on Echo Lake, Maine, and the effects of landlocked Alewife introduction on sport fish diet. The study utilizes stomach contents of Brook Trout and landlocked Atlantic Salmon to study the seasonality of forage types in the fish following the introduction of landlocked Alewives to the system. The main findings include:

1. The presence of Alewives limits the abundance of large zooplankton available for salmon forage.
2. YOY Alewives consisted of 37 and 58% of salmon stomach volume in the summers of 1969 and 1970, respectively.
3. The percent volume of Smelt consumed by salmon and brook trout was lower in Echo Lake compared to the state average, while percent volume of other fish consumed remained consistent with the state average.
4. Uncertainties: Is this decreased Smelt consumption due to the presence of alewives as alternative forage, or are there less Smelt due to alewives?

Fisher, J. P., Fitzsimons, J. D., Combs Jr, G. F., & Spitsbergen, J. M. (1996). Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic salmon and Great Lakes lake trout. *Transactions of the American Fisheries Society*, *125*(2), 167-178.

This project investigated the effects of reproductive failure rates and potential mechanisms underlying poor fry survival in Atlantic salmon of the Finger Lakes as well as Lake trout of the Great Lakes. Landlocked Alewives have been introduced to these systems and have become the most abundant forage fish available to native and invasive sport fish alike. Due to the abundance of thiaminase in landlocked Alewives, it is proposed that the fish are experiencing a thiamine deficiency. To better understand the limiting vitamins affecting fry survival and “Cayuga syndrome”, eggs were exposed to varying vitamin treatments by injection or ambient exposure. The main results include:

1. All individuals exposed to thiamine subsidies in their development experienced significantly higher survival past the fry stage.
2. Differences in thiamine concentrations of eggs from differing lakes positively correlate with the abundance of landlocked Alewives in the respective lakes.
3. Due to the pelagic feeding habits of Atlantic salmon, they may be more affected by a thiamine deficiency as a side effect of an almost exclusive diet of landlocked Alewives.
4. Uncertainties: How does the rate of thiaminase differ in landlocked alewives vs. anadromous alewives? Is the same pattern observed with anadromous alewives as salmon cannot feed on them year-round?

Lackey, R. T. (1969). Food Interrelationships of Salmon, Trout, Alewives, and Smelt in a Maine Lake. *Transactions of the American Fisheries Society*. 4: 641-646.

This research builds upon the numerous research papers concerning landlocked Alewife introduction to Echo Lake, Maine in 1966. Lackey attempts to reveal interactions of Alewives and Smelt as the primary forage fish for Landlocked salmon. Through diet analysis, Lackey demonstrates both the forage of salmon as well as the zooplanktivory of Alewife and Smelt in Echo Lake. Lackey's main findings line up well with previous papers on the same subject. The main findings include:

1. Salmon fed on Alewives only in the spring, while Smelt were consumed throughout the spring, summer, and fall. However, other fish and benthic invertebrates were consumed throughout the year.
2. Salmon did not forage on the 1967 year class of Alewives proportional to their abundance. Lackey noted "It is not entirely clear why salmon did not utilize 1967 brood year alewives more heavily, since this year class was apparently available in significant numbers."
3. The diet of echo lake salmon had a disproportionate number of invertebrates (about one third of the total diet) compared to other Maine populations.
4. Uncertainties: Does the disproportionate use of Alewives to their abundance show a preference for Smelt? While there is plenty of forage fish for salmon, why did they feed on so many benthic invertebrates?

Simonin, P. W., Parrish, D. L., Rudstam, L. G., Pientka, B., Sullivan, P. J. (2016). Interactions between Hatch Dates, Growth Rates, and Mortality of Age-0 Native Rainbow Smelt and Nonnative Alewife in Lake Champlain. *Transactions of the American Fisheries Society.* 145: 649-656.

This study seeks to determine if the interactions between hatch dates growth rates, and mortality of Rainbow Smelt and Alewives influence their competition for food resources and ability to prey on larvae (of their own or the other species). This study builds off previous research by Parker-Stetter et al. in Lake Champlain using hydroacoustics to monitor Smelt and Alewife density, locations, and mortality. However, this paper gives the first insights into how hatch timing and growth rates of the species factors into their density and spatial presence. The main findings include:

1. Rainbow Smelt hatch earlier in the year (from late May through early July) while Alewives hatched later in the year (from mid-June through early August).
2. Alewife growth rates were higher than Smelt, and early hatching individuals of each species grew slower than late hatching individuals.
3. When age-0 Smelt were declining at the greatest rate, age-0 Alewives were increasing in abundance at their greatest rate.
4. Rainbow Smelt have hatched late historically to avoid high rates of cannibalism, with increasing Alewife predation in summer may also shift hatch dates of Smelt earlier in the spring.

5. Uncertainties: How does Alewife predation on Smelt impact hatch timing to avoid cannibalism? Is there a happy medium where the timing of Smelt hatching minimizes both cannibalism and predation?

Smith, S. H. (1970). Species Interactions of the Alewife in the Great Lakes. *Transactions of the American Fisheries Society*. 4: 754-765.

In this paper, Smith provides a good overview of the establishment of landlocked Alewives in the Great Lakes, their current and potential positive and negative interactions with other native and introduced species, and a way forward after introduction. Smith provides the only scenario in which salmonid predators can effectively reduce Alewife stocks while also allowing native forage fish to recover. Smith would inevitably predict the collapse of the Alewife populations in the Great Lakes. The main findings include:

1. Some evidence of Smelt population increases following the initial large pulse of Alewife population growth.
2. Introduction of salmonid predators can accomplish the Alewife reduction and transition back to native forage fisheries. However, Smith warns of fishery collapses without careful management.
3. Anecdotal evidence of large Alewives feeding on larval Smelt, while not reflected in diet studies (rapid breakdown of larval Smelt in stomachs?).
4. Uncertainties: Why did this path forward of Alewife eradication inevitably lead to widespread fishery collapses? How can we apply this to Alewife restoration?

Kircheis, F. W., Trial, J. G., Boucher, D.P., Mower, B., Squires, T., Gray, N., O'Donnell, M., Stahlnecker, J. (2002). Analysis of Impacts Related to the Introduction of Anadromous Alewives into a Small Freshwater Lake in Central Maine, USA. *Maine Department of Inland Fisheries and Wildlife*.

This research effort, which spanned multiple government agencies and over a decade of work resulted in one of the most comprehensive studies of anadromous Alewife re-introduction in Maine. Kircheis et al. (2002) considered many components of the food web including nutrient flows, water clarity, thermal stratification, and dissolved oxygen levels. The study takes place in three phases, the first being three years of sampling to gain background information, the second being three years of sampling during the stocking of anadromous Alewives, and the third being three years of sampling following the cease of Alewife stocking. What results is a comprehensive look into the dynamic, and sometimes unexpected effects of anadromous Alewife introduction to a lake system in central Maine. While the findings of the study are numerous, the main takeaways can be summarized as follows:

1. The introduction of anadromous Alewives to Lake George had no effect on the average length or weight of the sport fish present in the system (brown trout, smallmouth bass, chain pickerel, white perch, and other minor fisheries).
2. YOY Rainbow Smelt and YOY Alewife both appeared to almost exclusively target *Cladocera* and *Copepoda.* However, similarity analysis showed no significant overlap in YOY Alewife and YOY Rainbow Smelt diet.

3. YOY Rainbow Smelt grew faster in the presence of Alewives. This is likely due to the planktivory of YOY Alewives releasing the Smelt's preferred taxa of *Cladocera* and *Copepoda* from competition and a decrease in the density of YOY Rainbow Smelt during Alewife stocking.
4. Total phosphorous was expected to increase in the presence of Alewives due trophic cascading effects of their planktivory. However, total phosphorous decreased in the presence of Alewives suggesting YOY Alewife are a source of phosphorous sequestration at a rate high enough to mitigate trophic cascading effects on phytoplankton communities.
5. Uncertainties: Can we observe true effects of alewives at this density? Were Rainbow Smelt densities altered by sampling? Does phosphorous sequestration explain the lack of trophic cascading effects?

LIFE HISTORY TABLE

Table 1. Life history attributes of landlocked and sea-run Alewife as well as Rainbow smelt.

Life History etc.	Landlocked Alewife	Sea-run Alewife	Landlocked Rainbow Smelt
Spawn timing	Late spring, 12 – 16 ºC	L. spring/ E. summer 12.8 - 15.5 ºC[2]	Shortly after ice-out 4 – 10 ºC[4]
Outmigration Timing	N/A	Immediate post-spawn (overlap)[2]	N/A
Lake/Pond residency	Year-round	May/June - July-October[2]	Year-round
Spawn location	Vegetation, rough substrate, or detritus	75% Silt, Detritus, Vegetation[6]	Tributary streams or gravelly beaches[4]
Incubation	6 days	3-6 days (temp. dependent)[2]	10 days
Size at hatching	5 mm	2.5 - 5mm	5 mm
Body size July 1st	20 mm (unhatched – 30 mm)		40 mm (20 – 60 mm)
Body size Oct 1st	70 mm (30 – 120 mm)		70 mm (40 – 90 mm)
Adult body size		279-305mm[2]	
YOY location	Pelagic – near surface	Pelagic - near surface	Pelagic – near thermocline
YOY preferred temp	16 – 20 ºC		18 – 24 ºC
Adult location	Pelagic - hypolimnion		Pelagic - hypolimnion
Adult preferred temp			
Juvenile diet	Cladocera/ Copepoda[5]	Cladocera/ Copepoda[3]	Cladocera/Copepoda[3]
Adult diet	Zooplankton, Larval Fish	Benthic Inverts, Larval fish (Perch)[3]	Larval fish (including smelt)
Juvenile predators			
Adult predators			
Fry sampling methods			
Juvenile sampling methods	Trawling/ Hydroacoustics[1]		Trawling/ Hydroacoustics [1]
Adult sampling methods			

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