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1 **Title:** Whole-lake food web model indicates alewife invasion fueled lake trout restoration and
2 altered patterns of trophic flow Lake Champlain

3

4 **Authors:**

5 Justin S. Lesser^{1*}, Rosalie Bruel^{2,3}, Benjamin Marcy-Quay¹, Amelia T. McReynolds¹, Jason D.
6 Stockwell¹, J. Ellen Marsden¹

7

8 ¹ Rubenstein Ecosystem Science Laboratory, University of Vermont, Burlington, VT

9 ² Pôle RandD “ECLA”, Aix-en-Provence, France

10 ³ OFB, Aix-en-Provence, France

11

12 *JSL: Justin.Lesser@uvm.edu

13 RB: Rosalie.Brue1@ofb.gouv.fr

14 BMQ: Benjamin.Marcy-Quay@uvm.edu

15 ATR: Amelia.McReynolds@uvm.edu

16 JDS: Jason.Stockwell@uvm.edu

17 JEM: Ellen.Marsden@uvm.edu

18

19 ***Corresponding Author:**

20 Justin S. Lesser

21 Rubenstein Ecosystem Science Laboratory

22 University of Vermont

23 3 College St.

24 Burlington, VT 05401

25 Justin.Lesser@uvm.edu

26

27

28 **Abstract**

29 Food web responses to invasion can be context-dependent and therefore difficult to predict
30 based only on invasion histories. Alewives (*Alosa pseudoharengus*) had generally negative
31 impacts on the native fish communities of the Laurentian Great Lakes after they invaded in the
32 19th century and were thus expected to negatively impact the Lake Champlain food web after
33 entering the lake in 2003. We evaluated the impact of alewives on the Lake Champlain food web
34 by compiling 25 years of biomass, abundance, and diet data and constructing an Ecopath with
35 Ecosim model of the coldwater food web. Model projections indicated that, contrary to the Great
36 Lakes experience, biomass of native predators increased, mortality rates decreased, and overall
37 trophic level of the pelagic fish community decreased after alewife entered the system.
38 Consequently, the amount of primary production supporting predator biomass increased in
39 response to the addition of prey fish production. The model suggests that alewife invasion in
40 Lake Champlain could have altered food web structure by transferring more energy to tertiary
41 consumers via pelagic pathways at the expense of other energy pathways and “jump started”
42 wild lake trout recruitment by expanding the forage base. In contrast to the Great Lakes response
43 to alewife invasion, Lake Champlain may represent an alternate trajectory for alewife invasion
44 and demonstrates that alewife impacts are context-dependent.

45

46 **Keywords**

47 Food webs, species invasions, Ecopath with Ecosim, trophic flow, Lake Champlain

48 **Introduction**

49 Food webs are complex networks of trophic relationships that can respond to stressors in
50 context-specific and unexpected ways. Species invasions are one such stressor that can alter
51 fluxes of energy and thus impact ecosystem structure and function (Rodriguez, 2006; Rooney et
52 al., 2006). Invaders can shunt resources away from historical pathways used by native species
53 and alter the pathways of production available to predators (Hogan et al., 2007; Johnson et al.,
54 2005). For example, after invasive smallmouth bass (*Micropterus dolomieu*) reduced littoral prey
55 fish abundance in Canadian Shield lakes, native lake trout (*Salvelinus namaycush*) became
56 dependent on pelagic zooplankton prey, with a subsequent decline in trophic level (Vander
57 Zanden et al., 1999). Invasive species may also alter energy flow by linking primary production
58 to native predators through fewer trophic steps and thus increase the system's ability to support
59 predator biomass; consumption of invasive round goby (*Neogobius melanostomus*) rapidly
60 increased body size of Lake Erie watersnakes (*Nerodia sipedon insularum*) (King et al., 2006).
61 The food web response to a particular invader is often dependent on multiple drivers interacting
62 at a particular time and place, and may therefore be complex, unique, and sometimes unexpected
63 compared to similar invasions in other systems (Bowler et al., 2022). Likewise, the consequences
64 of a non-native species entering a system cannot necessarily be inferred from invasion of
65 apparently similar systems because minor variations in physical, environmental, and trophic
66 context can induce diverse responses in food webs. For example, system productivity, habitat
67 depth, and invasive predator size can influence the degree of trophic niche overlap between
68 native predators and invasive lionfish (*Pterois volitans*) in coral reef systems (O'Farrell et al.,
69 2014).

70 The food webs of the Laurentian Great Lakes have been significantly altered by the invasion
71 and establishment of more than 185 aquatic invasive species over the past 150 years (Sturtevant
72 et al., 2019). Alewives (*Alosa pseudoharengus*), a typically anadromous fish native to the
73 Atlantic Ocean, invaded all five Great Lakes between 1860 and 1955 (Smith, 1970) and are
74 firmly established as a key component of the food webs in four of the Great Lakes. They
75 consume pelagic zooplankton and serve as prey for many lake predators (Madenjian et al.,
76 2008b; O'Gorman and Stewart, 1999). Alewives are hypothesized to interfere with native lake
77 trout restoration in the Great Lakes by preying on lake trout free embryos and inducing thiamine
78 deficiency in lake trout eggs (Harder et al., 2018; Krueger et al., 1995; Madenjian et al., 2008b;

79 O’Gorman and Stewart, 1999). Overall, impacts of alewife on other native fish species in the
80 Great Lakes appear to be context-dependent and species-specific, spanning a continuum from
81 minimal (e.g., non-native rainbow smelt, *Osmerus mordax* and native yellow perch, *Perca*
82 *flavescens*) to severely negative (e.g., Atlantic salmon, *Salmo salar*, and lake trout; Madenjian et
83 al., 2008). However, alewife are important to many management agencies because they are the
84 primary prey for introduced Chinook salmon (*Oncorhynchus tshawytscha*) and other predators
85 (Brandt, 1986; Clark Jr et al., 2017; O’Gorman and Stewart, 1999) that support multi-billion
86 dollar recreational fisheries (Melstrom and Lupi, 2013). Consequently, recent declines in Great
87 Lakes alewife populations are of concern to these management agencies (O’Gorman and
88 Stewart, 1999).

89 The Lake Champlain food web is less complex and contains fewer established invasives than
90 the Great Lakes (~50 species, Marsden and Hauser, 2009), but is comparable in many ways in
91 terms of physical and chemical properties (Myer and Gruendling, 1979; Smeltzer et al., 2012)
92 and ecological structure (Ball et al., 2015; Bruel et al., 2021; Marsden and Langdon, 2012;
93 Mihuc et al., 2012). The prey base for piscivores is species-poor, historically comprised chiefly
94 of native rainbow smelt and a small population of cisco (*Coregonus artedi*). The capture of seven
95 alewives in Lake Champlain in 2003 caused serious concern among managers due to the long
96 history of negative alewife impacts in similar systems such as the Great Lakes and the Finger
97 Lakes, NY. By 2007, the alewife population had expanded dramatically, followed by a large die-
98 off in 2008 (Marsden and Hauser, 2009). However, despite the continued prevalence of alewife
99 in the Lake Champlain food web (Simonin et al., 2019), their expansion in Lake Champlain has
100 not had the same overall negative impact on lake trout restoration efforts as observed in the Great
101 Lakes. Lake trout stocking in Lake Champlain began in 1973 with annual stocking of 105,000-
102 325,500 per year until a major cut in stocking in the mid-1990s and supported a large population
103 but with no wild recruitment (Ellrott and Marsden 2004). However, lake trout began to exhibit
104 wild recruitment starting in 2012 and wild cohorts have been consistently observed since that
105 time (Marsden et al. 2018, Wilkins and Marsden 2021), *after* alewife became established in Lake
106 Champlain (Marsden et al., 2018). Thus, the food web of Lake Champlain appears to be a
107 significantly different context for alewife invasion and impact than the Great Lakes, prompting
108 questions about the applicability of predictions shaped by the Great Lakes alewife experience to
109 other freshwater systems.

110 We modeled the coldwater food web of Lake Champlain's largest basin (Marsden and
111 Langdon, 2012) to determine the extent to which trophic relationships can explain trends in
112 consumer biomass before, during, and after the invasion of alewives, and to evaluate the
113 hypothesis that alewife benefited lake trout recovery in Lake Champlain. We used the Ecopath
114 with Ecosim (EwE) approach (Christensen and Pauly, 1992; Christensen and Walters, 2004;
115 Walters et al., 1997) to build a Lake Champlain food web model based on known trophic
116 relationships after alewives were added to the system (Ecopath). We assumed that Lake
117 Champlain functions similarly to the Great Lakes. We then replicated yearly dynamics of the
118 system for 25 years and simulated alewife invasion during this time to evaluate their potential
119 contribution to what we know about the system's current structure (Ecosim), asking the question,
120 "If Lake Champlain functions similarly to the Great Lakes, what was the impact of alewife on
121 the food web?" Finally, we compared the model's predictions to three long-term datasets
122 (rainbow smelt, *Mysis diluviana*, lake trout) and used the model's hypothetical food web to
123 identify potential knowledge gaps of Lake Champlain food web dynamics, identify the impacts
124 alewives may have had on the system, and pose questions for future research and management.

125 **Methods**

126 *Site description*

127 Lake Champlain is a large freshwater lake (26 km³, 1130 km²) located among Vermont, New
128 York (USA), and Québec (CAN, Figure 1). The lake comprises five distinct basins which differ
129 in size, nutrient levels, and total volume (Marsden and Langdon, 2012; Myer, 1979; Smeltzer et
130 al., 2012). Water exchange and fish passage are possible between basins but are limited to
131 shallow (< 7 m), narrow (19 to 225 m) connections through human-made causeways (Marsden
132 and Langdon, 2012, Euclide et al., 2019; Figure 1). Our model specifically focused on the
133 contiguous Main Lake (21 km³, 699 km²), which extends from Crown Point (NY) in the south to
134 Rouses Point (NY) in the north (Figure 1). This section contains the largest volume and the
135 deepest areas of the lake (122 m) and has moderate to low productivity relative to other lake
136 basins (Myer, 1979; Smeltzer et al., 2012).

137 *Ecopath mass-balance modeling*

138 We used the mass-balanced model EwE (version 6.3, Christensen and Pauly, 1992;
139 Christensen and Walters, 2004; Walters et al., 2000; software and documentation available at

140 <http://www.ecopath.org/>). The model describes the biomass flows among groups in the food web
141 using the following equation:

$$B_i * (P/B)_i * EE_i = \sum_j B_j * (Q/B)_j * DC_{ij} + BA_i + Y_i + E_i$$

142
143 where B_i is the biomass for group i , j represents all predators on group i , $(P/B)_i$ is the
144 production/biomass ratio of group i , EE_i is the ecotrophic efficiency, which represents the
145 proportion of group i production consumed by predators that is used for biomass
146 accumulation BA_i or exported from the system through fishery harvest Y_i and net
147 migration E_i (emigration–immigration). B_j and $(Q/B)_j$ represent the biomass and
148 consumption/biomass ratio of predator j , and DC_{ij} is the fraction of prey i in the diet of
149 predator j . Units are expressed in $\text{g/m}^2/\text{yr}$ wet weight for flows (BA , Y , and EE), g/m^2 for biomass
150 (B), $1/\text{yr}$ for P/B , and g/g/yr for Q/B . BA was set to zero because we assumed the food web was
151 in a stable state, we assumed no migration into/out of the system for any group, and included no
152 fishery harvest mortality because no coldwater commercial fishing takes place on Lake
153 Champlain, charter fishing is limited, and coldwater angling is mostly a catch-and-release fishery
154 (Marsden and Langdon, 2012).

155 Our model represents the coldwater portion of the food web (Marsden and Langdon, 2012).
156 We initialized the model with 25 taxonomic/functional groups of which four were multi-stanza
157 groups (Table 1). Groups in Ecopath require 3 of 4 inputs (B , P/B , Q/B , and EE). For many
158 single stanza groups, P/B and Q/B ratios were initialized with data from other Ecopath models of
159 the Great Lakes (Kao et al., 2018, 2016, 2014) or of similar, nearby large lakes (Lake Simcoe,
160 Goto et al., 2020, Table 1). When needed, our protocol for choosing values was to first look for
161 suitable values in Kao et al., 2016 (Lake Huron), then in Kao et al., 2018 (Lake Michigan), and
162 finally in Kao et al., 2014 (Lake Huron - Saginaw Bay) or Goto et al. 2020 (Lake Simcoe). In
163 using these values, when needed, we assumed Lake Champlain is similar to lakes Huron,
164 Michigan and Simcoe in terms of its physical, chemical, and ecological properties (Marsden and
165 Langdon, 2012; Myer and Gruendling, 1979; Smeltzer et al., 2012) and its invasion history
166 (Marsden and Hauser, 2009). The numerous direct comparisons with the Great Lakes to
167 understand its function also supports our assumption (e.g., Bruel et al., 2021; Chiapella et al.,
168 2022.; Facey et al., 2012; Herbst et al., 2013; Knight et al., 2018; Marsden and Hauser, 2009;
169 Simonin et al., 2012). Consequently, our EwE model was based on the *a priori* assumption that

170 Lake Champlain functions similarly to the Great Lakes, which aligns with the initial concerns of
 171 managers when alewife were discovered in Lake Champlain. We tested our model's sensitivity
 172 to parameter uncertainty by (1) varying alewife EE (and therefore biomass) down to 0.4 to assess
 173 the its impact on lake trout biomass and zooplankton biomass and alewife derived predation
 174 mortality (see Supplementary material, Table S3, Figures S3A-C) and (2) by using the Monte
 175 Carlo parameter estimation method to create and compare model outputs to a best fit model that
 176 accounted for overall parameter uncertainty (see Supplementary material, Table S4A-B, Figures
 177 S4A-G). The model was balanced by adjusting diet compositions and input parameters according
 178 to guidance from outside experts and with agreement of all authors. For detailed information
 179 about Ecopath model parameterization, see supplementary material.

180 *Ecosim time-dynamic modeling*

181 After the Ecopath model was balanced, we used Ecosim to simulate the dynamics of the food
 182 web during 1995-2020. We chose this period because it began after an initial period of
 183 experimental sea lamprey control (commenced in 1990, Young et al., 2021) and a concomitant
 184 intentional reduction in lake trout stocking in 1994 (Marsden and Langdon, 2012). In the Ecosim
 185 model, biomass B of a group i changes with time as:

$$\frac{dB_i}{dt} = G_i \sum_j Q_{ji} - \sum_j Q_{ij} - E_i - (M0_i + F_i) * B_i$$

186 where G_i is the gross conversion efficiency, Q_{ji} is consumption of prey j by predator i ; Q_{ij} is
 187 consumption of prey i by predator j , E_i is the net migration rate, $M0_i$ is the non-predatory natural
 188 mortality rate of group i , and F_i is the fishing mortality rate of group i . Consumption is modeled
 189 based on foraging arena theory, in which prey biomass is divided into a predation-vulnerable
 190 fraction and non-vulnerable fraction (Christensen and Walters, 2004) using the equation:

$$Q_{ji} = \frac{p_{ji} v_{ji} B_i B_j}{2v_{ji} + p_{ji} B_j} S_{ji} M_{ji}$$

192 where p_{ji} is the predation rate on group i by unit biomass of group j , v_{ij} is the vulnerability
 193 parameter, B_i and B_j are biomass for groups i and j , S_{ji} are long-term forcing functions to model
 194 invasion effects, and M_{ij} are user-defined mediation functions for indirect effects on Q_{ij} .
 195 Definitions of forcing shapes (S_{ij}) used to modify v_{ij} in our model are described below and visual
 196 representations are shown in in Figure S2. Before analysis, the model was allowed to stabilize
 197

198 for one year (1995) for prey species (i.e., rainbow smelt, alewife, *Mysis*, slimy sculpin (*Cottus*
199 *cognatus*), and troutperch (*Percopsis omiscomaycus*)) and two years (1995 and 1996) for
200 predator species (i.e., lake trout, burbot (*Lota lota*), yellow perch (*Perca flavescens*), and walleye
201 (*Sander vitreus*)).

202 Very few changes to the system occurred between 1995 and 2020, therefore, we believe the
203 system remained as close to a “steady state” as would be possible for a real food web during the
204 modelled time span. *Bythotrephes longimanus* and *Cercopagis pengoi* were detected in 2014 and
205 2018, respectively, but impacts to the food web of Lake Champlain have not been quantified.
206 The most notable changes were alewife invasion and sea lamprey control efforts, which we
207 account for in in our model. Alewife invasion was simulated using a modified version of method
208 2 from Langseth et al. (2012). High artificial fishing pressure on alewife was added on the first
209 two iterations of the simulation as a means to drop the relative biomass of alewife to essentially
210 zero. Then, fishing pressure was incrementally removed starting in 2003 until 2007, when it was
211 fully removed to increase alewife biomass to the initial Ecopath model levels. This pattern
212 simulated the invasion history of alewife (Marsden and Hauser, 2009). Alewife/prey and
213 predator/alewife relationships were modified during the pre-invasion period using forcing
214 functions to modify vulnerability parameters (detailed below, Figure S2A-B).

215 Sea lamprey are an important part of the Ecosim model because they are a large source of
216 mortality on pelagic coldwater predators in the Great Lakes (Madenjian et al., 2008a) and
217 suppressing sea lamprey populations is a primary objective for fisheries managers in Lake
218 Champlain (Young et al., 2021). Therefore, we included forcing functions to model the history of
219 those control efforts in Lake Champlain. An acceptable level of control was achieved in Lake
220 Champlain in three phases; an “experimental” phase from 1990-1998 which was converted to a
221 long-term management phase in 2002, with a “partial” phase occurring in between (1999-2001;
222 Young et al., 2021). We modeled this effort using fishing pressure as a surrogate for control
223 activities that reflected the known impacts of each phase on lamprey populations. The
224 experimental control phase (model years 1995-1998) included seasonal use of tributary barriers
225 and trapping to block migrating spawners and a 4-yr cycle of larval lampricide application
226 (Young et al., 2021). During the partial control phase these efforts were slightly reduced, so
227 ‘fishing’ pressure was reduced accordingly in the model. Sea lamprey wounding increased in the
228 years immediately following the initialization of the long-term phase; additional sea lamprey

229 spawning populations had become established and adaptive management responses were needed
230 to achieve full population control (Young et al., 2021). This phase in our model (Figure S1A)
231 was therefore captured by starting with yearly ‘fishing’ pressure similar to the experimental
232 phase in pattern (i.e., pressure applied in the spring) but reduced in magnitude (less than what
233 was applied in the experimental phase), increasing yearly to reflect the adaptation of the program
234 and eventual reduction in lamprey wounding that approached management goals (Young et al.,
235 2021). This method produced estimates of lamprey biomass that matched well with population
236 model estimates from 1995-2005 (Sum of Squares (SS)= 0.335, Christensen et al., 2005, Figure
237 S1B, Howe et al., 2012).

238 *Forcing functions*

239 We included forcing functions that modify the vulnerability of prey to their predators
240 (Langseth et al., 2012). For alewife-prey interactions, we included a forcing function that
241 eliminated the vulnerability of alewife prey to alewife during the years when alewife were not
242 present in the system, then immediately returned the vulnerability to 1.0 during the first year of
243 their invasion (2003, Figure S2A). For alewife-piscivore interactions, we used a forcing function
244 that eliminated the vulnerability of alewife during the years when alewife were absent from the
245 system, then increased quickly to 1.0 to simulate predators quickly adapting to consume alewife
246 as prey, as occurred in the Great Lakes (Madenjian et al., 2008b, Figure S2B).

247 Yellow perch (*Perca flavescens*) diet was separately forced to match observed and estimated
248 diet patterns. Preliminary diet analysis in Lake Champlain indicates that alewife comprise the
249 vast majority of coldwater pelagic prey in yellow perch diets (Lesser et al. *unpublished data*),
250 similar to observations before and after alewife invasions in the Great Lakes (Truemper et al.,
251 2006). We did not have yellow perch diet data specific to Lake Champlain prior to alewife
252 invasion, so we assumed this pattern of yellow perch diet switching observed in the Great Lakes
253 applied to Lake Champlain. We included forcing functions that replaced rainbow smelt with
254 alewife as alewife invasion progressed, reducing rainbow smelt from the diet of yellow perch
255 within two years of the alewife invasion (Figures S2D-E).

256 *Time series*

257 To assess model performance, we compared model biomass projections of three species to
258 long-term annual biomass datasets. Two datasets were based on field surveys – *Mysis* (1996-
259 2014; Ball et al., 2015) and rainbow smelt biomass estimates (1995-2015; Bruel et al., 2021,

260 Pientka and Staats 2018). Both species are important prey in the Lake Champlain food web.
261 Additionally, estimates of age 2+ lake trout biomass were compared to population modeling
262 estimates of annual lake trout biomass for the model period. These estimates were created by
263 applying age-specific survival rates to annual stocking records to produce abundance-at-age
264 estimates for each year in the study period. Three different sets of survival estimates were used
265 depending on the time period: (1) for 1980-1987, survival estimates were taken from Plosila and
266 Anderson (1985), who estimated low adult (ages 5+) survival using synthetic cohort analysis
267 applied to lake trout caught in standardized gillnet surveys and aged using a combination of
268 hatchery fin clips and scales; (2) for 1988-2000, survival estimates were taken from Marsden et
269 al. (2003) who used an updated version of the same dataset to assess the impact of sea lamprey
270 control, finding that control had a positive impact on survival of early-adult (ages 3-4) and adult
271 fish; and (3) for 2000-2022, survival estimates were taken from Hemmelgarn et al. (2022) who
272 used standardized bottom trawl surveys and a combination of hatchery fin clips and maxillary
273 age estimates to estimate survival for juveniles (ages 1-3), early-adult, and adult lake trout. Adult
274 survival was much greater over 2000-2022 compared to earlier periods (Hemmelgarn et al.,
275 2022). The transition point between the first two estimates was set at the midpoint between the
276 years for which they produced estimates, while the choice of 2000 as a transition between the
277 second and third set was based on the observation of a marked increase in contemporary catches
278 from the 2000 cohort forward (Marcy-Quay, *unpublished data*). As no historical records of
279 juvenile survival were available, survival rates for all years were set to the values estimated by
280 Hemmelgarn et al. (2022). Estimates of abundance for all years were then transformed to
281 estimates of biomass using the length-at-age and weight-length relationships estimated by
282 Hemmelgarn et al. (2022). All datasets were assessed for goodness-of-fit based on RSME of
283 long-term data to predicted output (Kao et al. 2016), and by visual comparison to the model-
284 derived food web dynamics.

285 *Predator trophic level and energy transfer calculation*

286 To assess the impact of alewife invasion on the energy dynamics of the Lake Champlain food
287 web, we first calculated an energy pathway-specific trophic level for fish prey communities
288 belonging to the pelagic and benthic pathways. “Pelagic” prey consisted of rainbow smelt and
289 alewife, while “benthic” prey included troutperch and slimy sculpin. We averaged the Ecopath-
290 calculated trophic level of all prey within each pathway (pelagic or benthic), weighted by the

291 proportion of the combined Ecopath-derived biomass that each species occupied. For predators
292 (lake trout, walleye, yellow perch, and burbot), pathway-specific trophic levels were calculated
293 similarly, except averages were weighted by the percent that each fish prey contributed to the
294 predators' diets and 1.0 was added to account for the trophic step from prey to predator. For
295 walleye, we used an "other" pathway rather than a "benthic" pathway; walleye consume larger
296 proportions of yellow perch than other modeled predators, and yellow perch represent an
297 important link between cold and warmwater lake habitats. The walleye "other" pathway also
298 included slimy sculpin (benthic). Fish prey that contributed ~1% or less to consumer diets, the
299 percent of the diet attributed to the "other/inverts" entry in the model (Table 1), which could not
300 be reliably assigned to a trophic level, and benthic invertebrates were excluded as prey from this
301 analysis. Next, we calculated the amount of primary production required for each predator at
302 each timestep by taking the total primary production from the model (phytoplankton and detritus,
303 Table 1) and multiplying by a 10% trophic transfer efficiency (Lindeman, 1942) raised to the
304 number of calculated trophic steps. This calculation was done for each model timestep so that
305 changes could be analyzed over time as alewife entered the system.

306 **Results**

307 *Prey Species*

308 The model projections of rainbow smelt, troutperch, and slimy sculpin biomass remained
309 constant during the periods before, during, and after alewife invasion (Figure 2A). Rainbow
310 smelt projections matched long-term data reasonably well (RSME=0.60; Figure 2A). The lack of
311 rainbow smelt response to alewife invasion in the model was consistent with the absence of a
312 temporal trend in the long-term data in the Main Lake basin ($F_{1,19}=0.12$, $p > 0.05$; see also Bruel
313 et al., 2021). Alewife biomass fluctuated in step with rainbow smelt biomass after their entrance
314 into the system (Figure 2A). Pelagic fish community trophic level dropped from an average of
315 3.95 in 2000 to a minimum of 3.60 in 2006, averaging 3.62 in the period after alewife invasion
316 (2008+) while benthic fish community trophic level remained constant at (Figure 2B).

317 Model projections for *Mysis* biomass remained relatively stable across the entire time range
318 and was consistent with long-term data, although the fit between model results and long-term
319 data was not as good as rainbow smelt (RSME=8.62; Figure 2C). The modeled lack of a
320 response to alewife invasion was consistent with a lack of a significant temporal trend in the
321 long-term data ($F_{1,18} = 3.399$, $p > 0.05$; see also Ball et al., 2015). The model projections did not

322 capture the observed decline in *Mysis* starting in 2012, well after alewife establishment but
323 concurrent with the first year of lake trout natural recruitment.

324 *Lake Trout*

325 EwE model projections of stocked age 2+ lake trout biomass doubled after alewife invasion
326 despite constant stocking levels. The EwE estimates matched population model estimates of age
327 2+ lake trout biomass well (RSME=0.019; Figure 3A). Stocked lake trout age 2+ annual
328 mortality (Z) decreased over the course of the model window, starting at 0.96/year in the period
329 prior to alewife invasion, dropping to a minimum of 0.51/year immediately after the invasion,
330 and then averaging 0.73/year after alewife were established as a prominent part of the food web
331 (Fig. 3C).

332 Model-predicted piscivorous lake trout diet was impacted by alewife invasion. Before alewife
333 entered the system, age 2+ lake trout diet averaged 68% rainbow smelt, with a smaller fraction of
334 their diet coming from prey sources such as *Mysis* and other fishes/invertebrates (Figure 3B).
335 The average percent of rainbow smelt in the diet decreased to 39% after alewife invasion, but
336 lake trout reliance on pelagic fishes (rainbow smelt plus alewife) increased to 86% of diet
337 (Figure 3B), mirroring contemporary diet studies of lake trout in Lake Champlain (Marsden et al
338 2022). This change was accompanied by a decrease in the contribution of prey items from other
339 energy pathways (slimy sculpin, troutperch, benthic invertebrates, and other prey sources; Figure
340 3B). Lake trout “pelagic-pathway” trophic level decreased from 4.96 to 4.64 after alewife
341 invasion and energy consumed via the pelagic pathway doubled, while “benthic-pathway”
342 trophic level and energy consumed via the benthic pathway remained constant throughout
343 (Figure 3D).

344 *Other major predators*

345 Modeled yellow perch biomass estimates remained relatively constant throughout the
346 simulation period (Figure 4A). Diet forcing (see Methods) switched yellow perch coldwater fish
347 consumption from rainbow smelt- to alewife-dominated (Figure 4B), consistent with
348 observations in Lake Champlain and the Great Lakes (Truemper et al., 2006; Lesser *unpublished*
349 *data*). The lower trophic level for alewife predicted by the model caused a corresponding drop in
350 yellow perch pelagic-pathway trophic level from 4.96 to 4.51 and a 2.5-fold increase in energy
351 consumption via the pelagic pathway (Figure 4C).

352 Estimated burbot biomass increased over the modeled period in response to alewife invasion
353 (Figure 5A). Alewife became a large percentage of burbot diet following their invasion (average
354 25% after 2008). However, this switch was not at the expense of rainbow smelt, which increased
355 from 14% to 19%. The switch coincided with a reduction in consumption of “other” items,
356 which included invertebrates and fishes not captured in this model (28% to 19%) and benthic
357 prey (46% to 30%) (Figure 5B). Burbot “pelagic-pathway” trophic level decreased from 4.96 to
358 4.64 after alewife invasion, and energy consumed via the pelagic pathway doubled, while
359 “benthic-pathway” trophic level and energy consumption remained constant (Figure 5C).

360 Total (stocked + wild) modeled walleye biomass increased over the modeled period in
361 response to alewife invasion (Figure 6A). Alewife became a high percent (20%) of walleye diet
362 following their invasion; this increase coincided with small reductions in consumption of yellow
363 perch (21% to 17%) and benthic prey (13% to 9%) and a larger reduction in “other” items (51%
364 to 36%; Figure 6B). Walleye “pelagic-pathway” trophic level decreased from 4.96 to 4.63 after
365 alewife invasion, and energy consumed via the pelagic pathway doubled, while “other-pathway”
366 trophic level and energy consumed via the other pathways remained constant (Figure 6C).

367 **Discussion**

368 Our EwE model of Lake Champlain suggests that alewives had a series of neutral to positive
369 impacts on the native fish community, contrary to the experience of alewife invasions in the
370 Great Lakes. The arrival of alewives in Lake Champlain was alarming to managers, given the
371 negative impacts of alewives on native fish communities and restoration efforts in the Great
372 Lakes (Madenjian et al., 2008b; Rudstam et al., 2011) and smaller lakes in New York (e.g.,
373 Finger Lakes, Fisher et al., 1996; Otsego Lake, Harman et al., 2002). Our model predicted no
374 major concurrent native species declines, but instead predicted increased native predator
375 production. Based on simple trophic relationships, these predictions reasonably replicated
376 available long-term biomass trends in three important food web components (stocked age 2+
377 lake trout, *Mysis*, and rainbow smelt). Additionally, overall trophic level (and therefore, the
378 number of steps between primary production and consumer biomass) of the pelagic fish
379 community decreased with the invasion, suggesting that energy became more efficiently
380 transferred up the food web via the pelagic pathway. The wide range of this impact, from
381 obligate coldwater fishes (lake trout, burbot) to fishes found across multiple lake habitats (yellow
382 perch, walleye), emphasizes the significance of alewife on the entire Lake Champlain food web.

383 Our model results highlight how ecological context can influence the trajectory of an invasion
384 and therefore the challenges of predicting the impact of an invasive in a new location based on
385 previous invasions.

386 Our model indicated little to no negative change in biomass dynamics of modeled native
387 species after alewife invaded Lake Champlain, suggesting the coldwater food web of the Main
388 Lake remained stable after alewife entered the system. Alewife were unable to outcompete other
389 planktivores for resources in the Main Lake (but see Bruel et al., 2021 for impacts on rainbow
390 smelt in other basins). Prey populations in the Main Lake of Lake Champlain appear to have
391 been stable (Ball et al., 2015; Bruel et al., 2021), supporting our model outputs. Declines in non-
392 native rainbow smelt populations rarely correlated with increases in alewives in the Great Lakes
393 (Madenjian et al., 2008b), suggesting low competition in those systems as well. The main
394 response of rainbow smelt to alewife is a change in their habitat occupancy; in larger, deeper
395 systems, rainbow smelt tend to be deeper in the water column after invasion than before
396 invasion, mitigating apparent competition for zooplankton prey through spatial separation
397 (Simonin et al., 2019, 2012). *Mysis* in the Main Lake could also act as an additional resource for
398 rainbow smelt; the presence or absence of other trophic links can explain native species
399 persistence or extirpation in the presence of invaders (Jackson et al., 2013; Valdovinos et al.,
400 2018). This explanation is consistent with declines in rainbow smelt populations following
401 appearance of alewife in shallower basins of Lake Champlain, where spatial separation by depth
402 is not possible and where other resources such as *Mysis* are not available (Bruel et al., 2021).
403 Although our model results do not strongly match the long-term datasets of rainbow smelt and
404 *Mysis* in Lake Champlain, much of the deviation between empirical data and model results
405 reflects substantial annual variability in the populations of these prey species. The variability in
406 the *Mysis* and rainbow smelt datasets may be sampling variability or perhaps may signal a
407 response to annual fluctuations in environmental variables acting on recruitment success directly
408 or on the resources on which they rely. Additionally, long-term *Mysis* biomass estimates from
409 Ball et al. (2015) originate from *Mysis* densities sampled in the water column during the day;
410 O'Malley et al. (2018) demonstrated that these densities may not be accurate as ecosystem-level
411 estimates because larger, benthic *Mysis* compose a significant proportion of the daytime *Mysis*
412 community. Thus, the variability may actually be indicative of changes in *Mysis* behavior. The
413 deviation of the *Mysis* projections from the *Mysis* observations occurs from 2012 onward, when

414 *Mysis* biomass declined. This decline was well after the establishment of alewife but co-occurs
415 with the start of natural recruitment of lake trout, suggesting a possible top-down impact of wild
416 juvenile lake trout feeding on *Mysis* (Marsden et al. 2022).

417 The modeled response of lake trout to alewife in Lake Champlain contrasts with the overall
418 severe negative impact of alewives on lake trout in the Great Lakes (Madenjian et al., 2008b),
419 indicating that food web predictions based on experience with alewives in the Great Lakes may
420 not be applicable to Lake Champlain or possibly to other lakes. Alewives are hypothesized to
421 negatively impact lake trout and Atlantic salmon in the Great Lakes through two mechanisms
422 affecting early life stages. First, if alewife are present and abundant at lake trout spawning sites
423 when lake trout free embryos are feeding above the substrate, alewife may impose direct
424 predation on the free embryos, compete with free embryos for zooplankton forage, and interfere
425 with foraging (Krueger et al., 1995). However, alewife populations in Lake Champlain do not
426 seem to overlap with lake trout embryos to the same degree as they do in the Great Lakes; in
427 fact, lake trout embryos were more likely to be consumed by large populations of nearshore
428 species found concurrently at spawning sites, such as rock bass (*Ambloplites rupestris*) and
429 yellow perch, than by alewife (Riley and Marsden, 2009). Second, consumption of alewife,
430 which contain thiaminase, is hypothesized to induce Thiamine Deficiency Complex (TDC) in
431 salmonid free embryos (Harder et al., 2018; Madenjian et al., 2008; O’Gorman and Stewart,
432 1999). However, symptoms of thiamine deficiency and mortality in Lake Champlain were not
433 observed in embryos originating from hatchery-raised, alewife-consuming lake trout (Ladago et
434 al., 2020), and the recent, sustained recruitment of lake trout indicates that TDC is not a major
435 factor in early mortality (Wilkins and Marsden 2021). Several factors are involved in thiamine
436 reduction, including abundance of alewife in the diet, lipid content of the prey, and thiaminase
437 content of the prey. Thiaminase in Lake Champlain alewife declined four-fold between 2006 and
438 2012 (Ladago et al. 2020), suggesting lower potential for alewife to induce TDC in Lake
439 Champlain consumers, but no recent data on thiamine levels or activity in prey species are
440 available.

441 Both our food web model and the results of population modeling suggest that age 2+ lake
442 trout biomass began to increase in Lake Champlain during 2003-2007, concurrent with alewife
443 invasion. In this interval the increase in biomass did not include wild recruits, which did not
444 appear until the 2012 year-class (Marsden et al. 2018). In the absence of alewife-induced TDC

445 and alewife predation on lake trout embryos, and because neither the oxythermal habitat nor the
446 nutrient level changed during this period in the Main Lake basin (Bruel et al., 2021), the addition
447 of alewife to lake trout diet appears to be the predominant factor driving the positive lake trout
448 population response to alewives in Lake Champlain. Alewives are an important component of
449 age 2+ lake trout diets in both the Great Lakes and Lake Champlain (Madenjian et al., 2008b;
450 Simonin et al., 2018) and have higher caloric content than rainbow smelt (Flath and Diana,
451 1985). A shift by age 2+ lake trout to consume alewife at the expense of rainbow smelt could
452 increase the overall energy consumption per unit effort by lake trout. Additionally, alewives tend
453 to consume more zooplankton and fewer *Mysis* than rainbow smelt; because *Mysis* also rely on
454 zooplankton, rainbow smelt exist at a slightly higher trophic level than alewives. Thus, rainbow
455 smelt consumption represents more trophic transfers, relative to alewife, before energy from
456 basal resources is incorporated by lake trout populations. Alewives, therefore, may provide a
457 more direct route to primary sources of production for adult lake trout through fewer trophic
458 steps than rainbow smelt, increasing the amount of energy available to support age 2+ lake trout
459 biomass. Model results also predicted smaller declines in age 2+ lake trout consumption of other
460 prey items (troutperch, slimy sculpin, and *Mysis*) relative to those predicted for rainbow smelt.
461 These diet items derive their biomass from other basal resource pools, so a change in the
462 proportion of these species in lake trout diets may signal that energy flow in the deepwater Lake
463 Champlain food web has been fundamentally altered by alewives. The degree to which Lake
464 Champlain's food web currently relies on alewife mirrors more recent trends in the Great Lakes;
465 though alewife were historically associated with hindering predator restoration (i.e., lake trout),
466 recent alewife declines in the Great Lakes have been a concern for managers because they are an
467 important prey for Chinook salmon and other predator species that support economically
468 valuable fisheries (O'Gorman and Stewart, 1999).

469 Invasive prey can be an abundant resource for native predators (Jackson et al., 2013; King et
470 al., 2006). The addition of alewife as a new prey coincided with lower age 2+ lake trout mortality
471 in our model, both as a single extreme pulse in the year immediately following alewife
472 proliferation, and in subsequent years. Higher adult survival would result in an increased
473 spawning stock, suggesting that establishment of alewife in Lake Champlain "jump-started" the
474 recruitment of wild lake trout that began in 2012 (Marsden et al., 2018). Alewife are a lipid-rich
475 prey (Flath and Diana, 1985), more so than other available prey items in Lake Champlain (Futia

476 et al., 2019), and unlike rainbow smelt, their lipid concentration is directly related to body size
477 (Madenjian et al., 2000). Lipid stores are an important determinant of lake trout fecundity and
478 higher egg quality (energy content) because they promote higher free embryo survival and
479 recruitment of more offspring (Henderson and Wong, 1998). Higher lipid content in wild relative
480 to stocked lake trout in Lake Champlain also indicates that the population benefitted from the
481 influx of lipid-dense alewife (Sorrentino et al., 2020). Additionally, alewife are an important
482 component of age-1 lake trout diets as wild lake trout switch from invertivory to piscivory
483 (Marsden et al., 2022), so an increase in small prey available to age-1 lake trout likely benefitted
484 their survival and growth at this vulnerable stage.

485 A food web-based prediction of positive relationship between salmonids and alewife is not
486 unique to Lake Champlain. Bioenergetics models have also predicted positive effects of alewife
487 on salmonid growth rates in Great Lakes, despite the prevailing paradigm of a negative
488 relationship (Kitchell and Crowder, 1986; Rand et al., 1994; Rand and Stewart, 1998; Stewart et
489 al., 2010). Food web models indicate that recent alewife declines in Lake Huron resulted in
490 decreased growth rates of salmonids and proposed that the alewife collapse was caused by a
491 combination of increased salmonid predation and decreased lower trophic level production (e.g.,
492 Kao et al. 2016), suggesting a positive effect of alewife on salmonids in the Great Lakes.
493 However, despite these findings, a negative alewife-salmonid relationship has been the accepted
494 paradigm historically (Harder et al., 2018; Krueger et al., 1995; Madenjian et al., 2008b;
495 O’Gorman and Stewart, 1999). The discrepancy between food web models and field
496 observations in the Great Lakes highlight a limitation of food web models in predicting the
497 impacts of invasive species because the mechanisms of their impact may not always be the result
498 of trophic dynamics. For salmonids, the lack of early survival due to alewife-induced TDC in the
499 Great Lakes cannot be predicted by existing EwE models unless a negative effect of alewife on
500 lake trout recruitment is specifically built into the model. TDC does not seem to have had the
501 same severity in Lake Champlain as in the Great Lakes and was not incorporated into our model;
502 this is likely the primary reason our model shows a positive alewife-salmonid relationship. A
503 trophic relationship between alewife and lake trout free embryos likely exists (see above) and is
504 incorporated in Great Lakes models. However, the relationship is not sufficient to replicate
505 negative impacts in the Great Lakes and further highlights the importance of dynamic rather than
506 energetic impacts in determining the direction of alewife-salmonid relationship in Great Lakes

507 systems (Solomon et al., 2011). Extremely intense but short-term periods of consumption (i.e.
508 alewife consuming lake trout embryos during the short time they overlap spatially in the water
509 column) can still result in low energetic or food web linkage strength (Solomon et al. 2011). The
510 dynamic impact of alewife consumption of lake trout free embryos (losing younger lake trout age
511 classes) may have a high impact on lake trout populations even if the actual loss of yearly lake
512 trout production due to alewife consumption is proportionally minimal because the lake trout are
513 very small when consumed. One caveat to the apparent disagreement between modern models
514 and historic observations in the Great Lakes is idea of expecting a modern food web to react in a
515 specific way based on a historic paradigm; the systems modelled in recent papers have had 50-
516 100 years to reform and incorporate alewife since their invasion. Therefore, the direction of the
517 alewife-salmonid relationship may have changed such that it can now be captured by a food web
518 model. So, while Lake Champlain food web model may not be directly comparable to the
519 modern Great Lakes, as the systems are at different points along their invasion trajectories, food
520 web models may be appropriate to capture invasive impacts via trophic mechanisms in Lake
521 Champlain and the modern Great Lakes. Additionally, conclusions about the “salmonid”
522 response to alewife between systems may be too general; Chinook salmon are also exotic to the
523 Great Lakes and therefore may respond to alewife differently than native salmonids such as lake
524 trout.

525 The results of our food web model raise interesting questions about the mechanisms of energy
526 flow in the current Lake Champlain food web relative to pre-invasion conditions. The
527 establishment and proliferation of alewives in Lake Champlain, apparently without a
528 corresponding decrease in biomass of other food web components in the Main Lake, leads to the
529 question: where did the extra production required to maintain alewife populations come from? In
530 a stable, maximally efficient food web, one would expect the incursion of a large population of a
531 new mid-trophic level species to come at the expense of another component. A simple
532 explanation is that the lack of consistent and expansive long-term datasets means we were not
533 able to capture concurrent species declines. However, long-term data for rainbow smelt indicates
534 no significant declines in the Main Basin of Lake Champlain in coldwater species related to
535 alewife invasion (Bruehl et al., 2021). Alternatively, the Lake Champlain food web may have had
536 a pool of under-used productivity that was available for alewife to exploit and propagate through
537 the food web. A characteristic of the Lake Champlain food web is a lack of large populations of

538 any of the coldwater pelagic coregonines that are present in the Great Lakes (i.e., *Coregonus*
539 spp.) except for a small population of cisco (*Coregonus artedi*), so an open niche appears to have
540 been available for alewife (Marsden and Langdon, 2012). Alewife populations in coldwater
541 zones could also be receiving an energy subsidy from other portions of the system or other lake
542 regions outside the spatial bounds of this model, such as in the Northeast Arm where alewife do
543 appear to be negatively impacting rainbow smelt (Bruel et al., 2021). Anecdotal reports of
544 declines in warmwater forage fishes such as cyprinids may be due to alewife competition in
545 nearshore areas, though this requires further study. Additional alternatives are possible; our
546 model is a hypothesis that highlights the need for a continued assessment of the energy pathways
547 supporting alewife biomass in the lake.

548 Model results for non-salmonid predators suggest that the presence of alewives in Lake
549 Champlain had the potential to fundamentally alter the degree to which many predators across
550 ecological zones of the lake rely on pelagic or benthic energy pathways. Burbot, yellow perch,
551 and walleye represent predator species that exist in distinct capacities within the lake. Burbot
552 captured in the deepest depths of the lake are obligate deepwater residents. Walleye and yellow
553 perch are representative of the “coolwater” food web, foraging in a wide range of habitats
554 including deep coldwater (modeled here) and shallow warmwater food webs (Marsden and
555 Langdon, 2012). All these species consume alewife as a major portion of their diet (Simonin et
556 al., 2018; Lesser *unpublished data*; McReynolds *unpublished data*), and model results suggest
557 that these diet shifts caused an increase in pelagic-derived prey reliance that shifted the relative
558 contribution of benthic vs. pelagic energy pathways to their biomass. Alewife are found within
559 the deepwater boundaries represented by our model, but are also regularly captured in the
560 summer during nearshore community sampling (Pientka, 2021) and are a primary diet item of
561 warmwater predator species such as smallmouth bass (Lesser *unpublished data*). Thus, the
562 apparent impact of alewife on predator biomass dynamics and energy flow may have
563 fundamentally altered many other features of the food web throughout the lake, such as
564 connectivity between distinct food web zones outside the bounds of our model. The change in
565 energy flow related to alewife consumption may now be a feature of the food webs across all
566 habitat zones of Lake Champlain, and the implications of this shift in energy pathways requires
567 further exploration, including field survey data to examine changes in growth and survival.

568 Our model, as constructed, is a relatively simple and hypothetical representation of the Lake
569 Champlain food web. Unfortunately, adequate historical data do not exist to empirically
570 parameterize a number of the model compartments and many of the parameters used from other
571 systems may not accurately represent Lake Champlain. Therefore, the scope of our findings may
572 be limited. Nevertheless, all models must start somewhere. Additionally, we recognize that
573 results from our model could be expected simply because of the structure of the initial Ecopath
574 portion model and how the invasion was modeled (i.e., by removing a food web component and
575 then having it return to the food web), and therefore our model is a “simple” representation of the
576 food web. We contend that our model, although imperfect, still provides insights on the
577 functioning of the Lake Champlain system after alewife invasion and can be used as a starting
578 point on which to build and improve (Grimm and Railsback, 2005). The available data we used
579 were reasonable to construct a foundational model supported by parameter estimates from
580 similar systems (the Great Lakes and Lake Simcoe). Our model results provide insights into the
581 functioning of the Lake Champlain food web and suggests an alternative and plausible system
582 response to alewife invasion contrary to the Great Lakes’ experience. The model results are
583 generally supported by the available empirical information and by what is known about some
584 key species relationships – for example, thiamine does not appear to be a detriment to lake trout
585 in Lake Champlain vs other lakes (Ladago et al., 2020), lack of evidence for free embryo
586 predation by alewife (Riley and Marsden, 2009), and general observations about the system since
587 alewife invaded. Overall, our simple representation of the Lake Champlain food web suggests
588 Lake Champlain was a different context for alewife invasion, and their entrance into the system
589 benefited lake trout in a drastically different way than in the Great Lakes.

590 **Conclusions**

591 Our model demonstrates that the context of Lake Champlain at the time of alewife invasion
592 may have buffered against their potential negative impacts as observed in the Great Lakes, and
593 surprisingly, boosted predator production. However, these results also demonstrate that the
594 invasion had the potential to alter energy flow throughout the lake’s food webs, changing the
595 degree to which communities rely on pelagic- vs. benthic-derived production. This likely
596 indicates an impact on the connectivity and energy movement among lake zones; predators now
597 have the potential to extract more energy via the local pelagic fish community, and in turn rely
598 less on production acquired outside of their preferred habitat. Our model can be applied to

599 predict the viability and potential impact of future management actions, such as stocking
600 responses to the recent addition of wild recruits to lake trout populations.

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830 **Tables**

831 **Table 1:** Input used to initialize Ecopath model of the Main Lake of Lake Champlain food web.
 832 Bold parameter values indicate model-derived; trophic level is calculated by the model.

#	Group name	Trophic Level	Biomass (t/km ²)	P/B or Z (/year)	Q/B (/year)	EE
1	Sea Lamprey	5.319	0.030	1.200	6.746	0.000
2	Lake Whitefish	3.890	0.161	0.510 ¹	6.100 ¹	0.200 ¹
3	Yellow Perch	4.114	0.069	1.300 ¹	11.500 ¹	0.400 ¹
4	Lake Trout	<i>Age 0</i>	0.004	0.010 ¹	14.760 ¹	0.000
5		<i>Age 1</i>	3.947	0.030	0.800	7.855
6		<i>Age 2+</i>	4.608	0.161	0.800	4.076
7	Atlantic Salmon	<i>Age 0</i>	0.009	0.010	15.000	0.000
8		<i>Age 1</i>	3.947	0.060	0.800	8.237
9		<i>Age 2+</i>	4.099	0.253	0.800	4.722
10	Burbot		4.200	0.083	0.630 ¹	3.400 ¹
11	Stocked Walleye	<i>Age 0-0.5</i>	0.0003	0.990	3.860 ¹	0.000
12		<i>Age 0.5+</i>	4.383	0.007	0.800	1.315
13	Wild Walleye	<i>Age 0-0.5</i>	3.632	0.0001	0.990	3.860 ¹
14		<i>Age 0.5+</i>	4.383	0.004	0.800	1.315
15	Rainbow Smelt		3.959	0.544	1.386 ³	7.861 ³
16	Alewife		3.386	0.974	1.300 ²	14.600 ²
17	Troutperch		3.873	0.121	1.200 ⁴	8.100 ⁴
18	Slimy Sculpin		3.882	0.101	1.300 ³	2.500 ³
19	Other Fish/Invert		2.866	9.555	2.500	10.000
20	Predatory Zooplankton		3.000	21.38	8.300 ¹	21.842 ¹
21	<i>Mysis</i>		3.105	14.400	2.800 ¹	22.400 ¹
22	Benthic Invertebrates		2.670	1.041	1.760 ¹	12.800 ¹
23	Herbivorous Zooplankton		2.000	32.08	21.000 ¹	52.500 ¹
24	Phytoplankton		1.000	5.951	365.000	0.800 ¹
25	Detritus		1.000	80.000		0.134

¹ Kao et. al 2016 (Lake Huron)² Kao et. al 2018 (Lake Michigan)³ Goto et. al 2020 (Lake Simcoe)⁴ Kao et al. 2014 (Lake Huron, Saginaw Bay)

835 **Table 2:** Estimates of diet used for the Lake Champlain Ecopath model. Values represent proportional prey contributions to predator
 836 diet; prey and predator numbers refer to Table 1.

<i>Prey #</i>	Predator #																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>1</i>																	
<i>2</i>	0.100																
<i>3</i>						0.050						0.200		0.200			
<i>4</i>																	
<i>5</i>									0.020								
<i>6</i>	0.444																
<i>7</i>																	
<i>8</i>						0.020											
<i>9</i>	0.333																
<i>10</i>	0.111									0.010							
<i>11</i>																	
<i>12</i>	0.006																
<i>13</i>																	
<i>14</i>	0.006																
<i>15</i>			0.150		0.062	0.350		0.062	0.100	0.130		0.100		0.100			
<i>16</i>			0.200		0.083	0.490		0.083	0.200	0.270		0.210		0.210			
<i>17</i>						0.010				0.030		0.030		0.030			
<i>18</i>					0.036	0.010		0.036		0.040		0.030		0.030			
<i>19</i>		0.900	0.550		0.167	0.050		0.167	0.630	0.200		0.370		0.370			0.100
<i>20</i>					0.070			0.070					0.300		0.337	0.325	0.100
<i>21</i>		0.100			0.274	0.010		0.274	0.020	0.070			0.300		0.563	0.100	0.500
<i>22</i>			0.100		0.189	0.010		0.189	0.030	0.250		0.060		0.060			0.200
<i>23</i>					0.120			0.120					0.400		0.100	0.525	0.100
<i>24</i>																0.050	
<i>25</i>																	

837

Import

1

1

1

<i>Prey #</i>	Predator #					
	18	19	20	21	22	23
1						
2						
3						
4						
5						
6						
7						
8						
9						
10						
11						
12						
13						
14						
15		0.001				
16		0.001				
17		0.001				
18						
19		0.200				
20	0.150	0.150		0.450	0.200	
21	0.450	0.040		0.050		
22	0.350				0.030	
23	0.050	0.100		1	0.100	0.220
24		0.200		0.100	0.150	1
25		0.307		0.300	0.400	

839 **Figure Captions**

840 **Figure 1:** Map of Lake Champlain, USA. The dark line outlines the Main Lake. Stars mark
841 Rouses Point, NY (44°59'56.5"N, 73°21'25.1"W) and Crown Point, NY (43°57'57.0"N
842 73°25'34.5"W), the northern and southern limits of the Main Lake basin. Inset: Position of Lake
843 Champlain within the northeast region of the United States and southern Quebec.

844 **Figure 2:** Fish prey species model output. The grey column indicates the period of alewife
845 invasion, 2003-2007. (A) Biomass (t/km²) of Lake Champlain prey fish species over the modeled
846 period (1995-2020). Lines represent EwE predictions for rainbow smelt (█), troutperch (█),
847 slimy sculpin (█), and alewife (█); points represent rainbow smelt trawling survey data.
848 (B) Trophic level (calculated from EwE output) over the modeled period for pelagic (rainbow
849 smelt and alewife, black) and benthic (troutperch and slimy sculpin, grey) prey fish communities.
850 (C) Biomass (t/km²) of Lake Champlain *Mysis* over the modeled period (1995-2020). Solid lines
851 represent EwE prediction; points represent *Mysis* biomass data (Ball et al., 2015).

852 **Figure 3:** Adult (age 2+) lake trout model output. For all panels, grey box outlined with dotted
853 lines indicates the period (2003-2007) over which alewife entered the system. (A) Biomass
854 (t/km²) of age 2+ lake trout over the modeled period (1995-2020). Solid lines represent EwE
855 predictions; points represent population modeling biomass estimates (RSME=0.02). (B)
856 Proportional contributions of rainbow smelt (█), alewife (█), *Mysis* (█), all benthic prey
857 (including troutperch, slimy sculpin, and benthic invertebrates, █), and other prey (█) to
858 age 2+ lake trout diet over the modeled period. (C) EwE calculated age 2+ lake trout mortality
859 (/yr) over the modeled period. Grey lines represent pre- and post-alewife invasion averages (D)
860 Pathway-specific trophic level for lake trout via pelagic (black) and benthic (grey) fish prey, and
861 energy intake (relative to primary production) by lake trout via pelagic (black, dotted) and
862 benthic (grey, dotted) fish prey.

863 **Figure 4:** Yellow perch model output. For all panels, grey box outlined with dotted lines
864 indicates the period (2003-2007) over which alewife entered the system. (A) EwE predicted
865 biomass (t/km²) of yellow perch over the modeled period (1995-2020). (B) Proportional
866 contributions of rainbow smelt (█), alewife (█), benthic invertebrates (█), and other
867 prey (█) to yellow perch diet over the modeled period. (C) Pathway-specific trophic level for
868 yellow perch via “coldwater” fish prey and energy intake (relative to primary production) by
869 yellow perch via “coldwater” fish prey.

870 **Figure 5:** Burbot model output. For all panels, grey box outlined with dotted lines indicates the
871 period (2003-2007) over which alewife entered the system. (A) EwE predicted biomass (t/km²)
872 of burbot over the modeled period (1995-2020). (B) Proportional contributions of rainbow smelt
873 (█), alewife (█), all benthic prey (including troutperch, slimy sculpin, and benthic
874 invertebrates, █), *Mysis* (█) and other prey (█) to age 2+ lake trout diet over the
875 modeled period. (C) Pathway-specific trophic level for burbot via pelagic (black) and benthic
876 (grey) fish prey, and energy intake (relative to primary production) by burbot via pelagic (black,
877 dotted) and benthic (grey, dotted) fish prey.

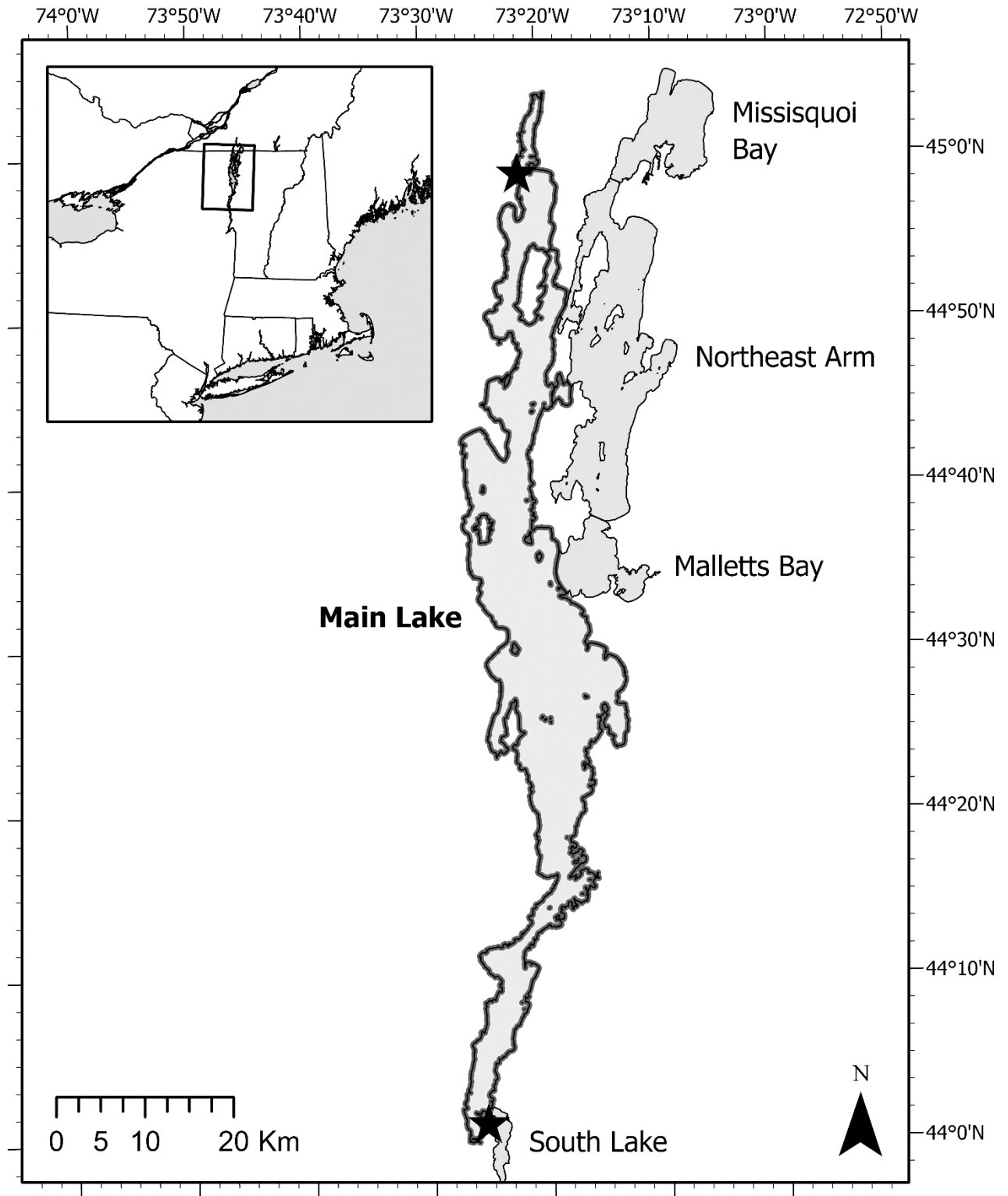
878 **Figure 6:** Total (stocked + wild) walleye model output. For all panels, grey box outlined with
879 dotted lines indicates the period (2003-2007) over which alewife entered the system. (A) EwE
880 predicted biomass (t/km²) of walleye over the modeled period (1995-2020). (B) Proportional
881 contributions of rainbow smelt (█), alewife (█), all benthic prey (including troutperch,

882 slimy sculpin, and benthic invertebrates, (——), *Mysis* (—■—), yellow perch (—■■■), and other
883 prey (■—) to walleye diet over the modeled period. (C) Pathway-specific trophic level for
884 walleye via pelagic (black) and benthic (grey) fish prey, and energy intake (relative to primary
885 production) by walleye via pelagic (black, dotted) and benthic (grey, dotted) fish prey.

886

887 **Figures**

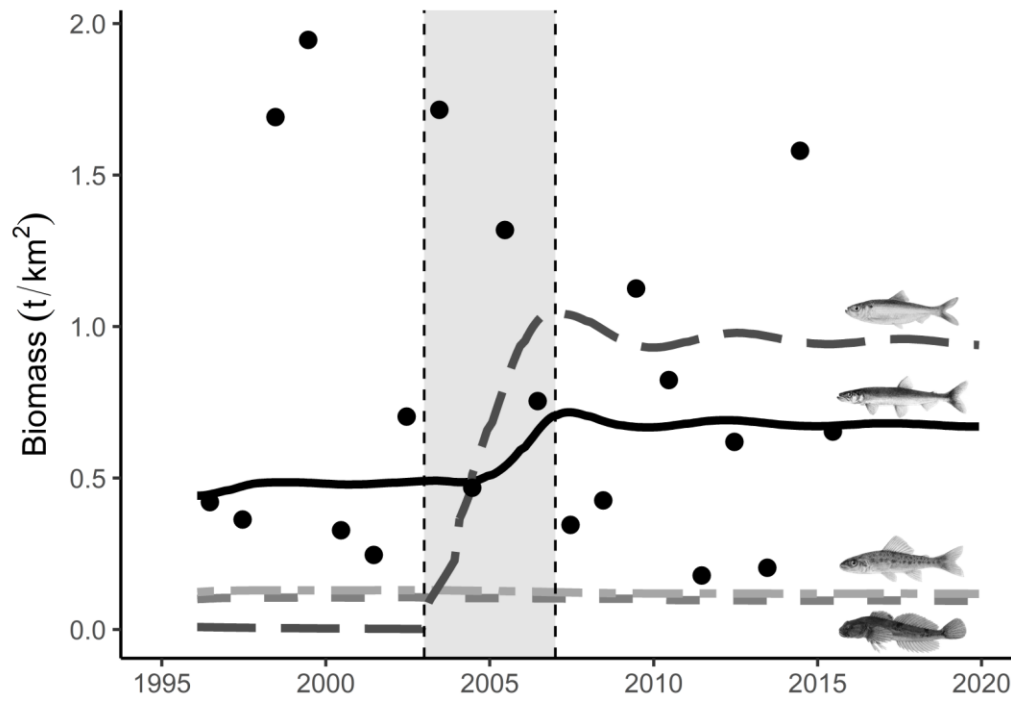
888 **Figure 1**



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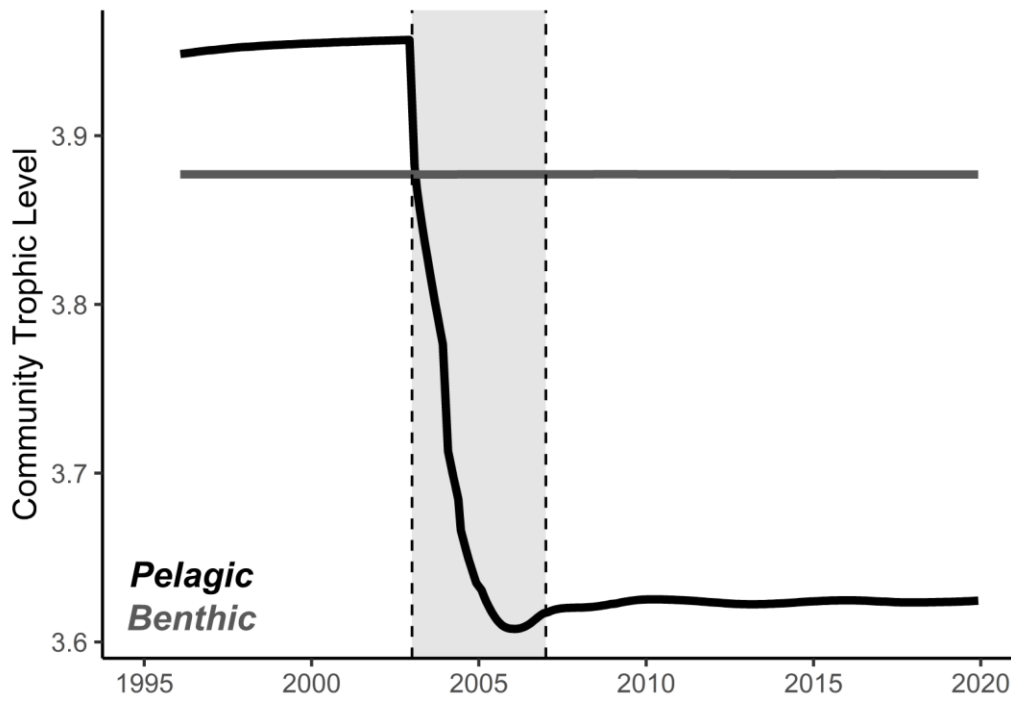
890 **Figure 2**

891 **A)**



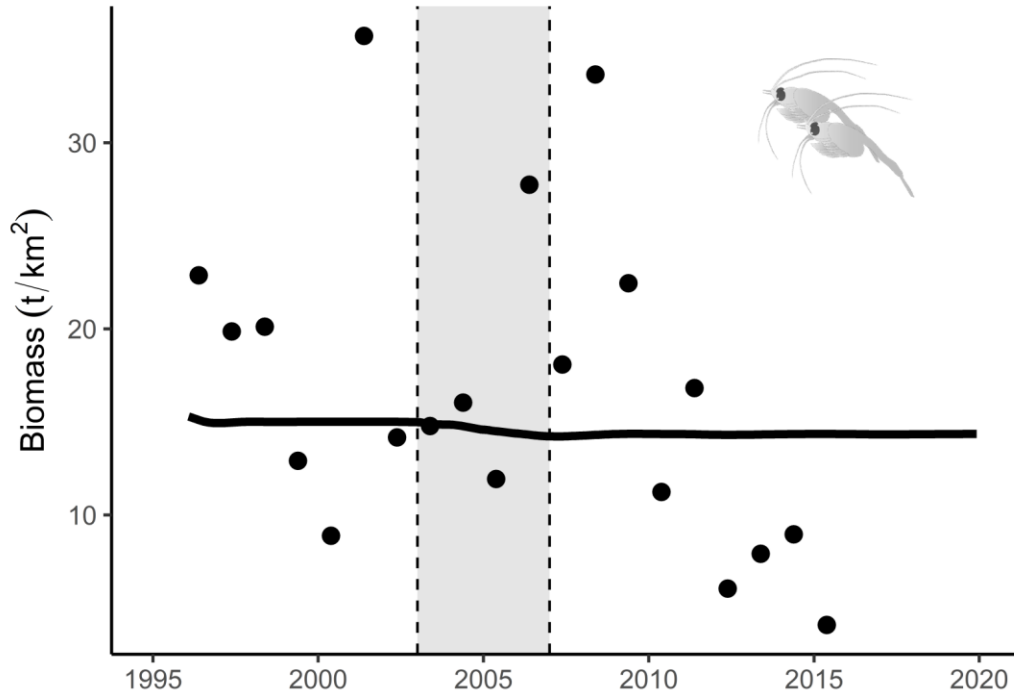
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893 **B)**



894

895 C)

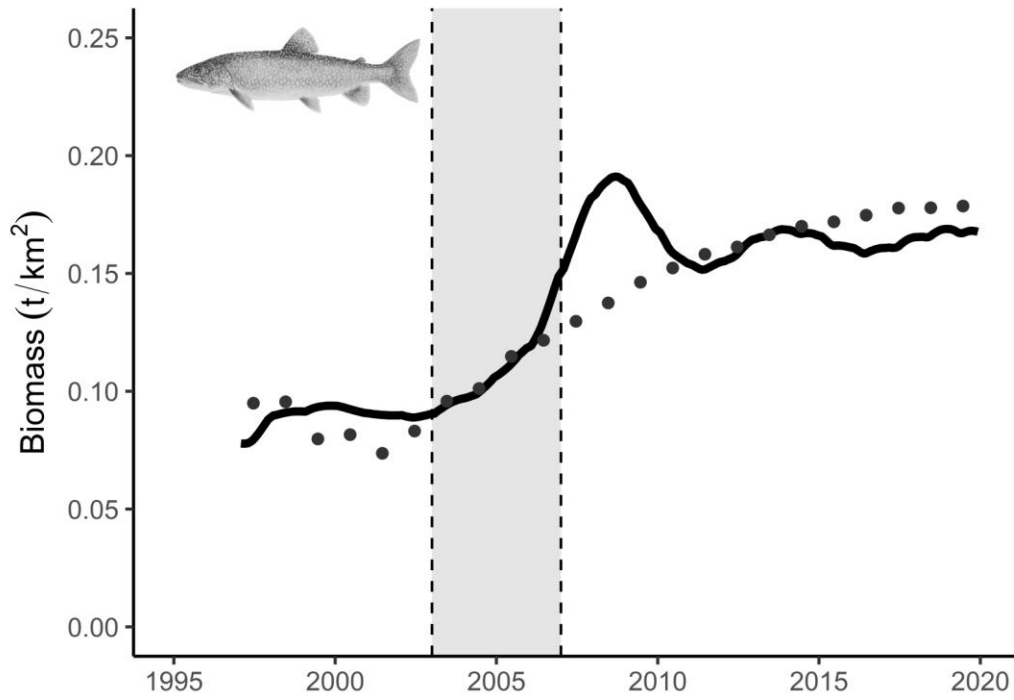


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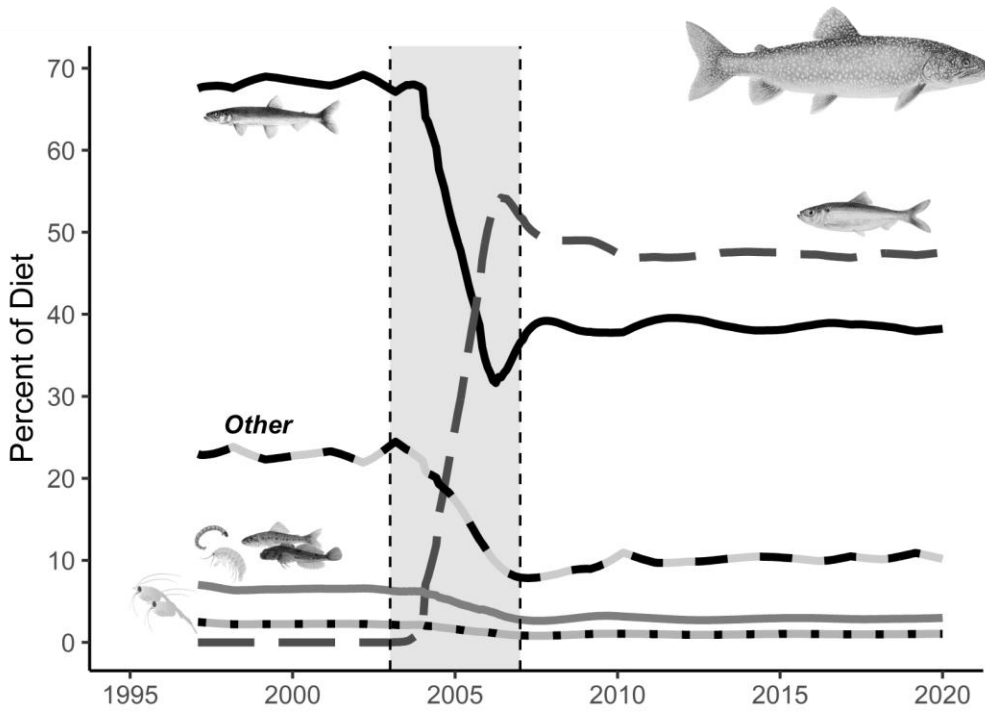
898 **Figure 3**

899 **A)**



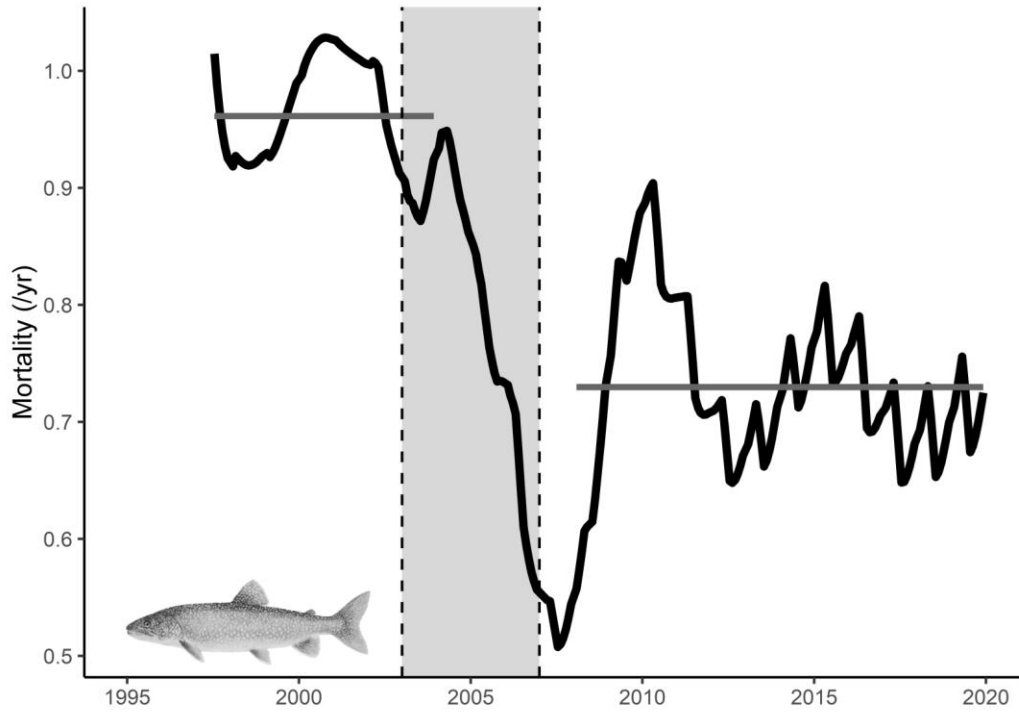
900

901 **B)**



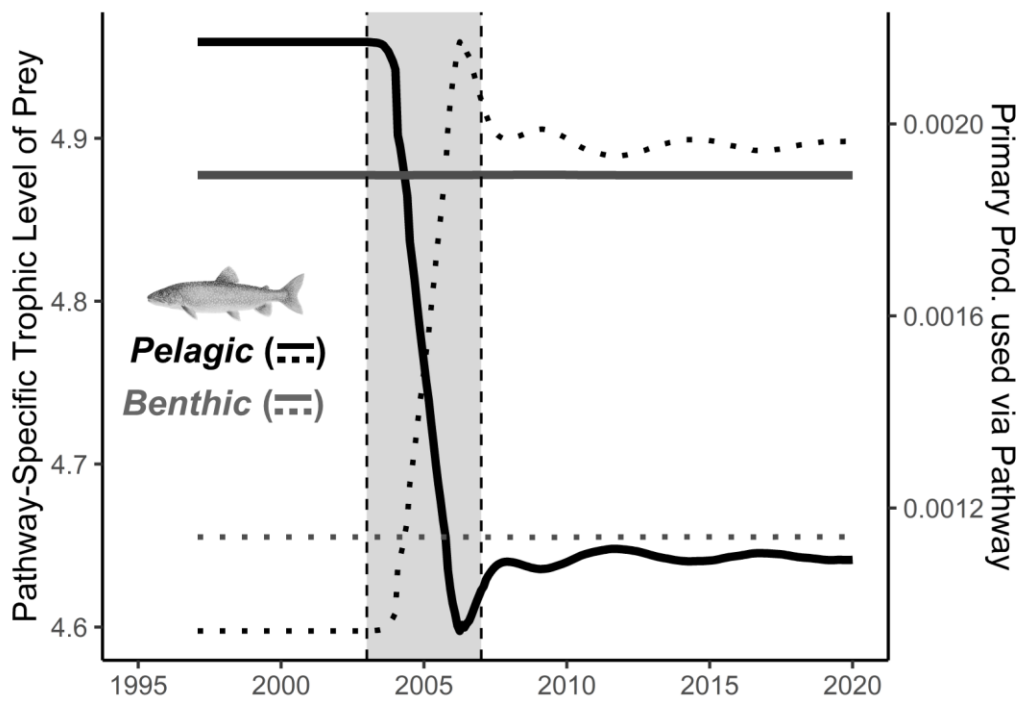
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903 C)



904

905 D)

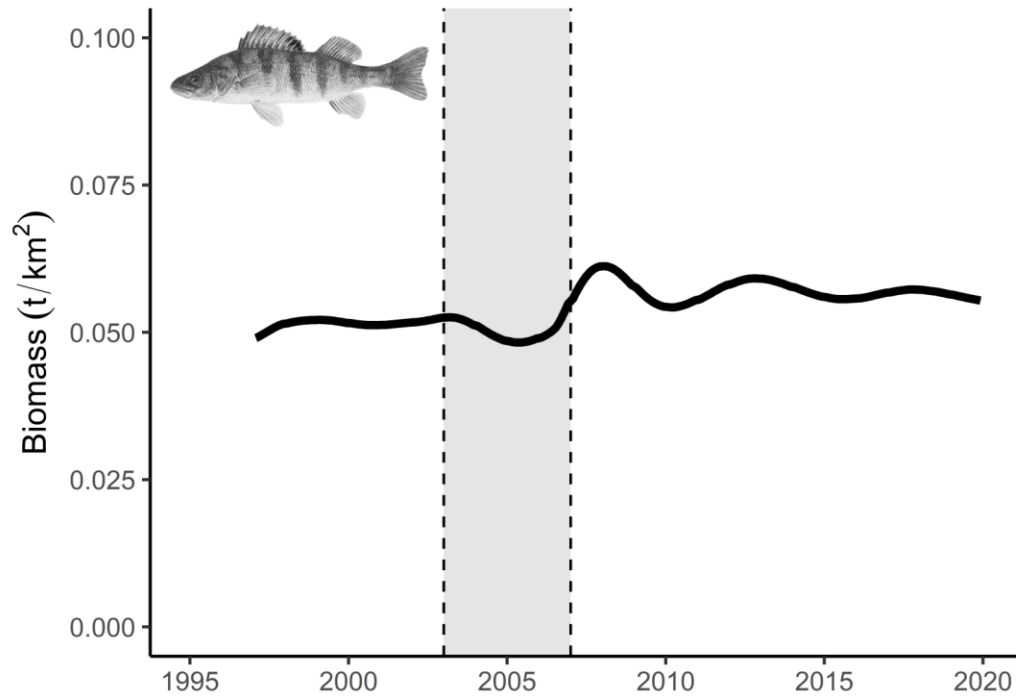


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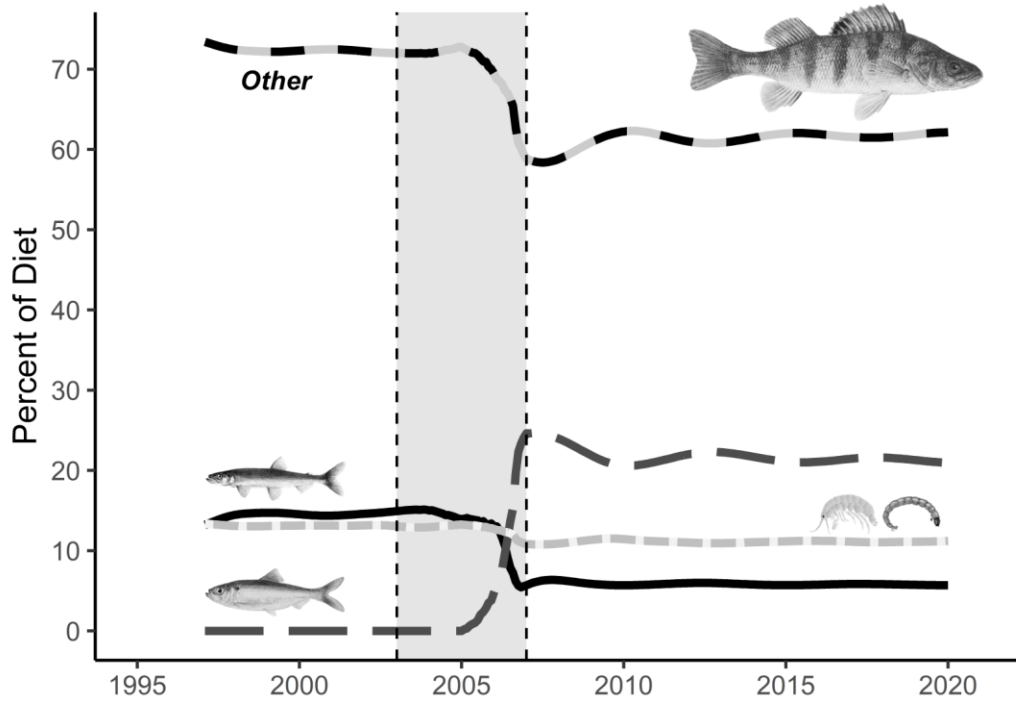
908 **Figure 4**

909 **A)**



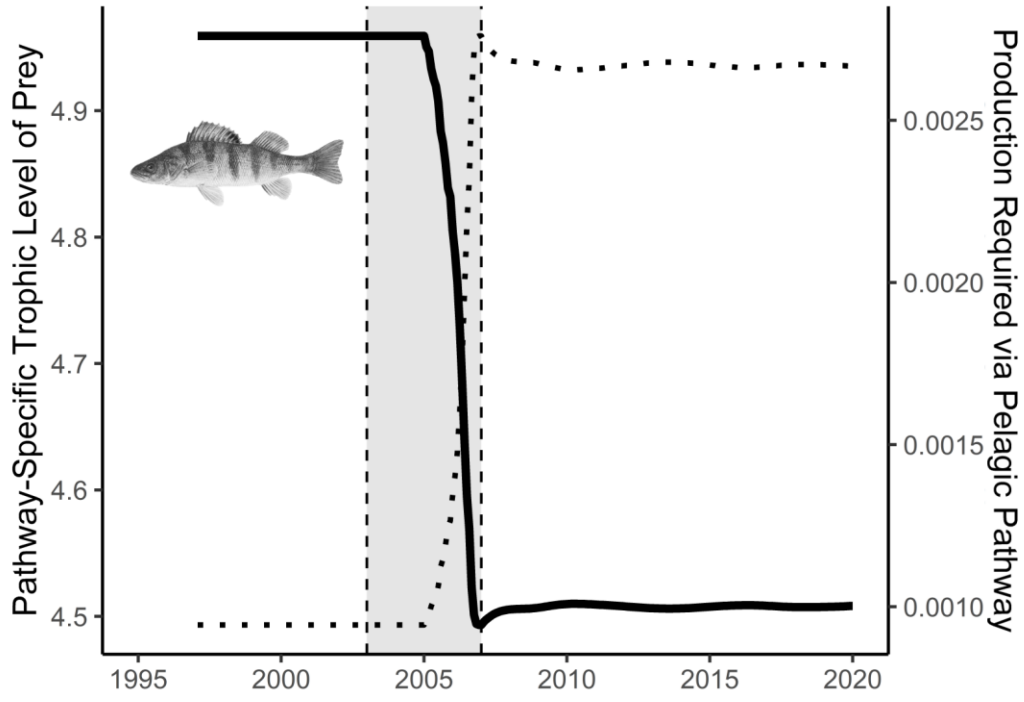
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911 **B)**



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913 C)

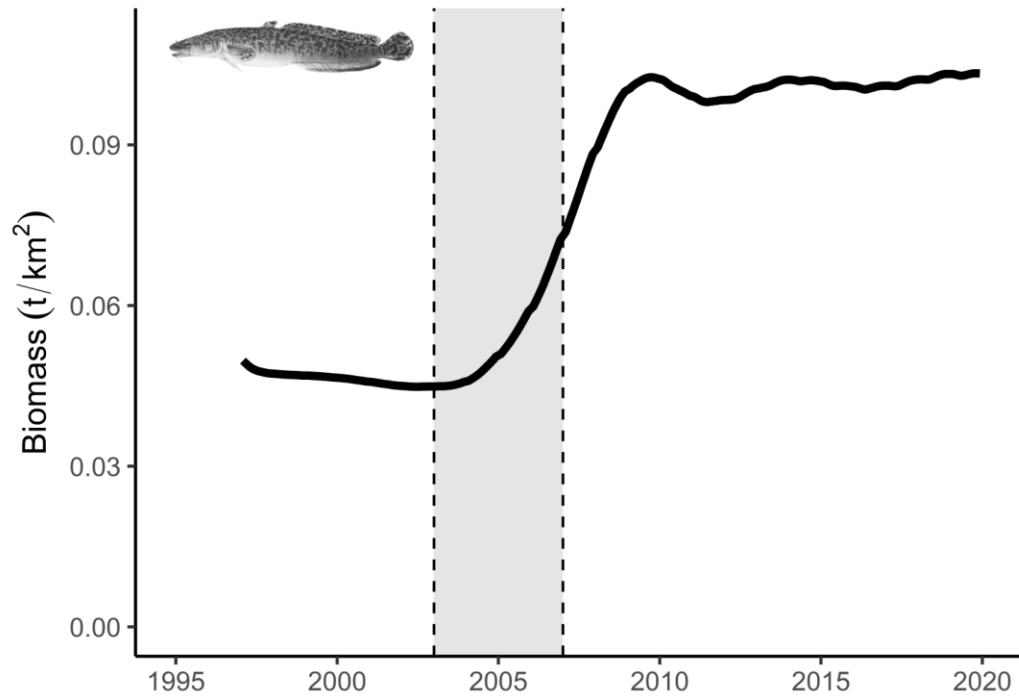


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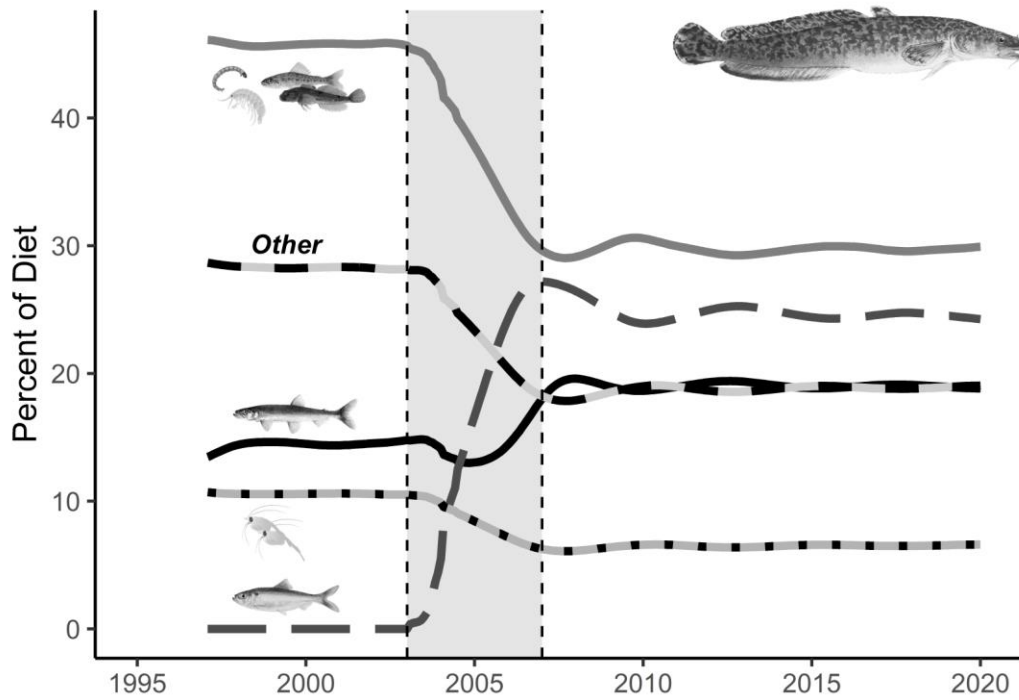
916 **Figure 5**

917 **A)**



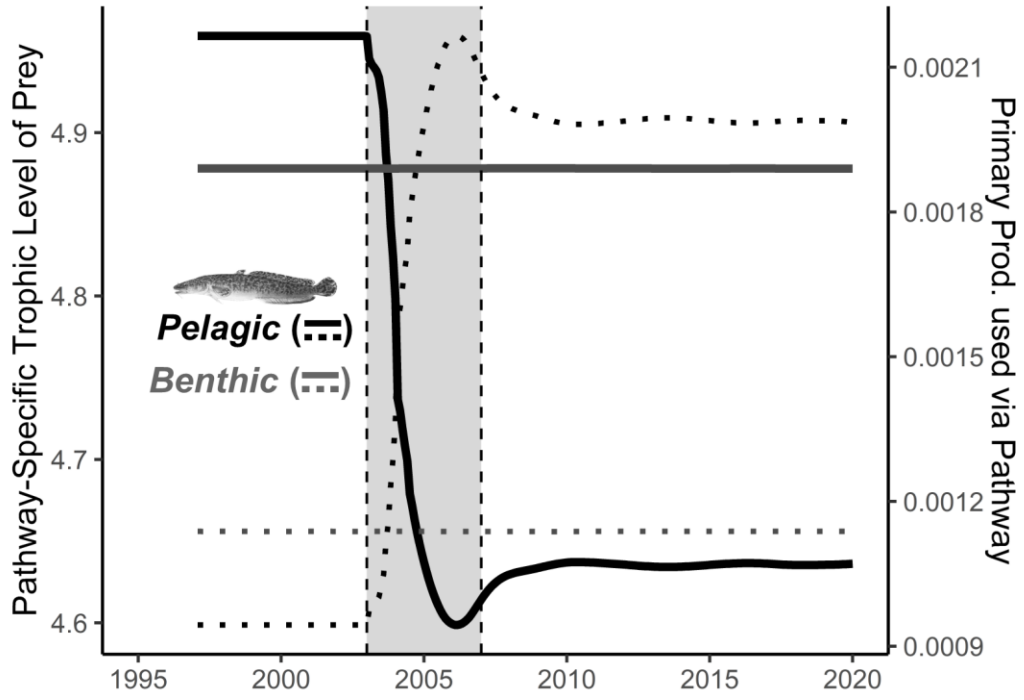
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919 **B)**



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921 C)

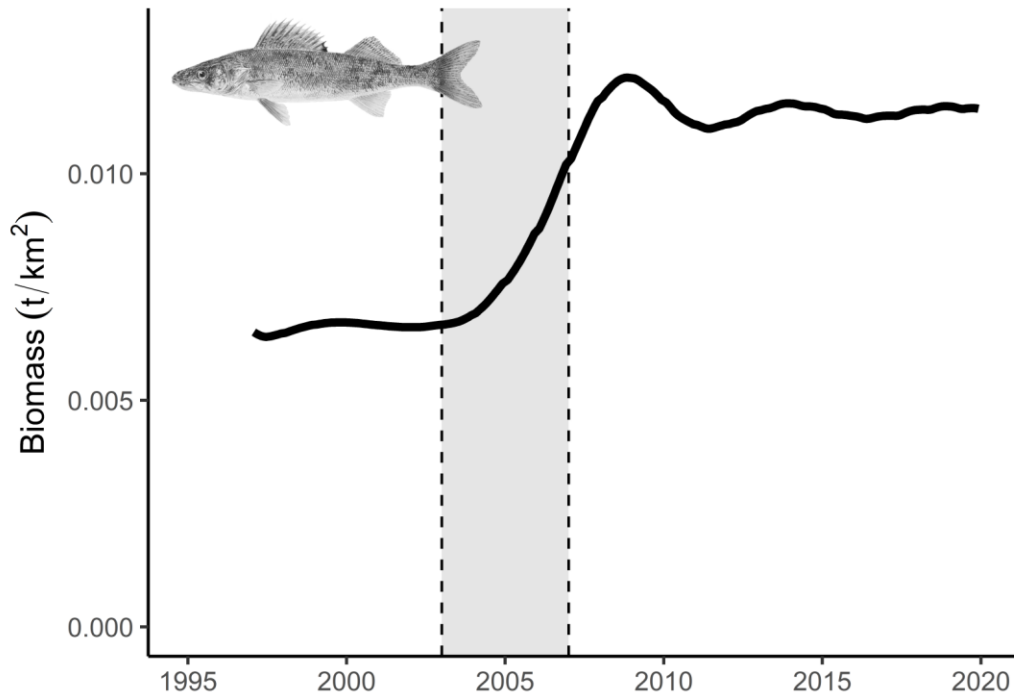


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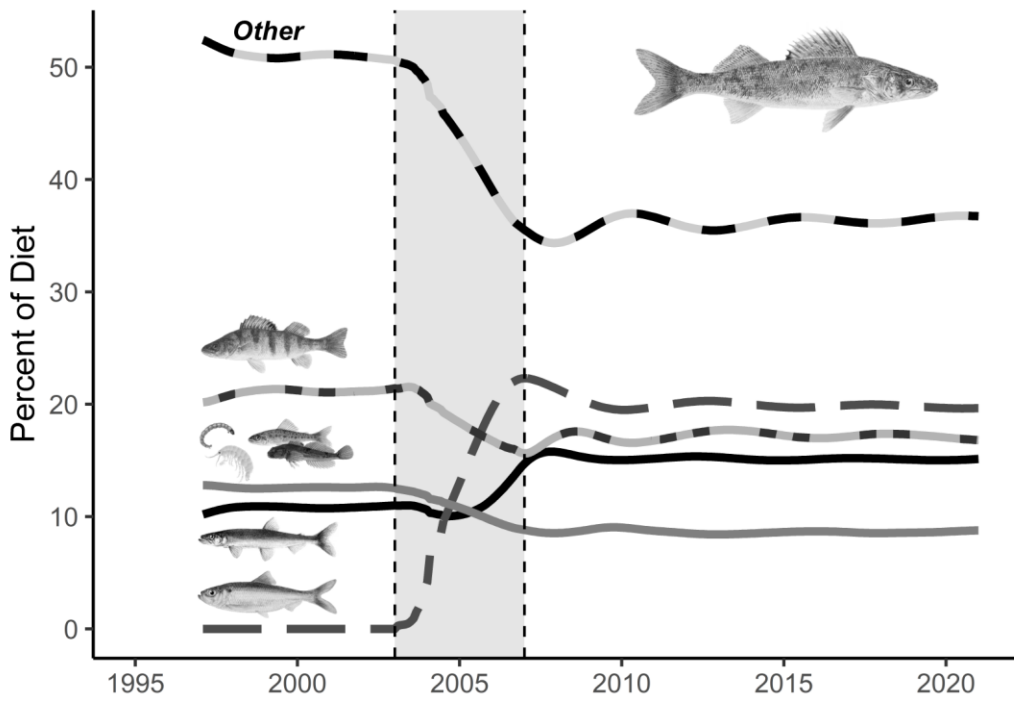
924 **Figure 6**

925 **A)**



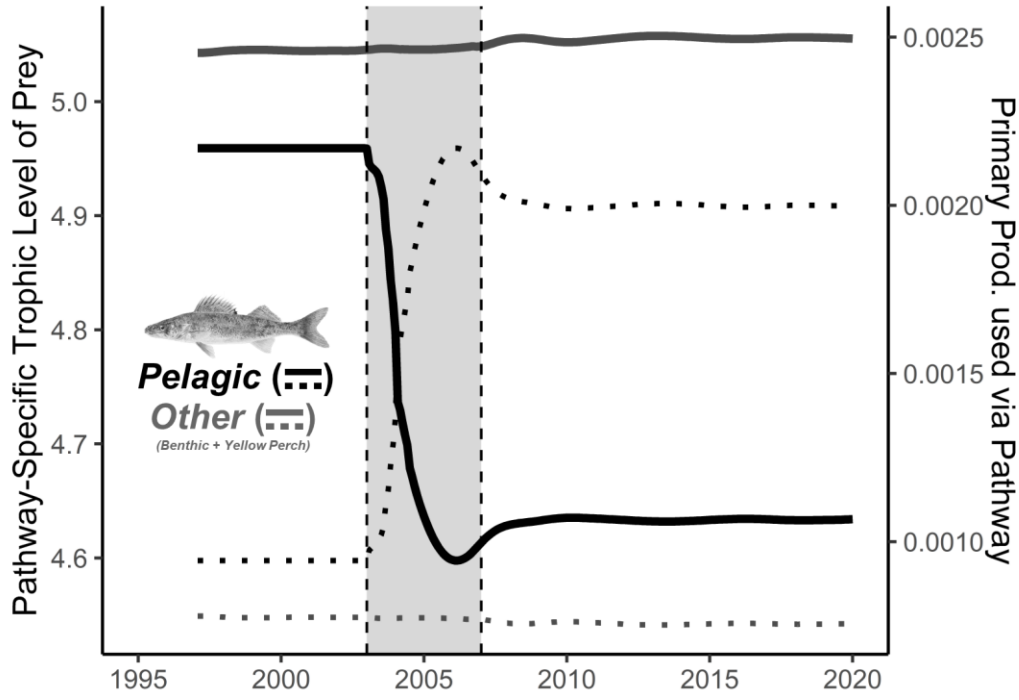
926

927 **B)**

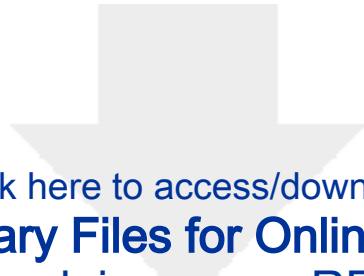


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929 C)



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Supplementary Files for Online Publication

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