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Feeling the Squeeze: Adult Run Size and Habitat Availability Limit Juvenile River Herring Densities in Lakes

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Abstract

Maximum densities of juvenile river herring (Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*) vary among freshwater lakes, likely due to densities of adult spawners. Differences in habitat availability and lake water quality may also contribute to variation in juvenile river herring productivity between populations, yet these relationships have not been tested across a large geographic scope. In this study we investigated relationships between juvenile river herring densities and (1) spawning adult river herring densities, (2) lake habitat availability, and (3) lake water quality in 29 freshwater lakes in the northeastern USA. Purse seines were used at night to sample juvenile river herring monthly in June–August 2014 and 2015, with concurrent collection of lake-specific physical (e.g., lake surface area, mean depth, depth to thermocline), chemical (e.g., nitrogen, phosphorus, dissolved organic carbon [DOC]), and biological (chlorophyll *a*, adult spawning density) data. Spawning adult density (number of adults per surface area of lake) explained 66.6% of the variation in juvenile densities using a generalized additive model. Juvenile densities increased with increasing adult density, peaking at roughly 1,000 adults/ha, and then declined at higher adult densities, suggesting a limit to carrying capacity in juvenile production. Linear mixed-effects models revealed that differences in water quality and habitat across lakes explained additional variation in juvenile densities. Specifically, DOC was negatively related to juvenile densities,

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suggesting that DOC limits the amount of suitable, well-oxygenated epilimnion habitat available to juvenile river herring in late summer. Our results can be used to help understand expected juvenile production based on adult density within a lake, to inform expectations about juvenile growth and survival, and to understand the mechanisms for how changes in habitat availability and water quality affect river herring populations.

Fisheries scientists and managers aim to quantify juvenile fish densities and factors limiting densities to predict future stock abundances (Ney 1999). Spawning adult abundance is often assumed to be the most important factor regulating recruitment. In its simplest form, fish abundance at one life stage is a function of abundance at a previous stage (Paulik 1973; Rothschild 1986). This link between life stages underpins the foundation of stock–recruitment modeling frequently used to guide management (Needle 2001; Subbey et al. 2014); however, the function of the predictive relationships between adult fish densities and juvenile densities are poor or undeveloped for many species. Moreover, the number of juveniles that reach adulthood is a function of mortality and emigration, which are influenced by environmental factors such as habitat availability. The combined effects of high variability and variation in habitat availability make predicting adult–juvenile relationships a challenge, and for many species the available information is insufficient for use in management.

Anadromous river herring (collectively Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*) are ecologically similar species that likely act as a single population when occupying the same habitat as juveniles. Adults migrate from coastal waters in the northwestern Atlantic Ocean into inland freshwater environments to spawn each spring (Bigelow and Schroeder 1953; Loesch 1987). Juvenile recruits occupy freshwater lakes and rivers during early growth and development before emigrating into estuarine and then coastal environments, which typically occurs mid-June through October (Bigelow and Schroeder 1953; Richkus 1975). As a result of these large migrations across ecosystem boundaries, river herring have been impacted by bycatch in marine fisheries, historic commercial overfishing at sea, degraded freshwater habitat quality, and migration barriers in streams (Limburg and Waldman 2009; Hall et al. 2011; ASMFC 2012; Hall et al. 2012; Cournane et al. 2013), all of which have contributed to sharp population declines.

Quantifying the number of juveniles produced can complement ongoing adult monitoring and is critical for understanding links between recruitment and adult run size and for assigning sources of mortality. Currently, adult river herring counts during spawning migrations are used to monitor population trends, determine stock status, and evaluate management decisions (Crecco and Gibson 1990; ASMFC 2012). However, adult counts are limited in their precision and ability to inform stock assessments because they do not capture key demographic and habitat-related processes occurring across critical life history periods that include adult spawning behavior, juvenile growth in freshwater ecosystems, juvenile migration to the ocean, and juvenile marine movements. Thus, it is not possible to use adult counts to identify causes of declines and partition mortality across life stages, which is problematic given that river herring productivity is likely limited by both biotic and abiotic factors that act on several ontogenetic stages. Without knowing the life stage(s) where bottlenecks to recovery occur, management is unlikely to be successful.

Previous studies have suggested a weak relationship or no relationship between spawning adult river herring abundance and the number of juveniles produced (Havey 1973; Walton 1987; Jessop 1990a) and demonstrated high spatial and temporal variability of adult counts and resulting reproduction. Some of these studies are limited in geographic scope, often using data from only a single river over many years (e.g., 11 years in Havey 1973; 16 years in Jessop 1990a, 1990b) or that include multiple water bodies in close proximity in a single year (e.g., 11 rivers in Kosa and Mather 2001; 20 rivers in Rosset et al. 2017). Moreover, the type of data used to inform juvenile production estimates may be based on a variety of methods ranging from back-calculation from adult numbers assuming proportions of first time spawners (Gibson and Myers 2003) to enumerating juvenile emigrants (e.g., Havey 1973; Kosa and Mather 2001; Gahagan et al. 2010). Recent work refined sampling methods for juvenile river herring and highlighted the high variability in juvenile densities in 16 coastal northeastern U.S. lakes (0.03–0.87 river herring/ m^3; Devine et al. 2018), providing data to assess the adult–juvenile relationship from a variety of systems across the northeastern United States. Refined information about the adult–juvenile relationship can inform regional assessments of monitored populations and decipher the influence of adult abundance and habitat.

Restoration and management plans for anadromous species generally treat all available or potential spawning and nursery habitats as if they are equal in quality. Thus, the spawning and nursery habitat quantity for anadromous species is typically defined as the length of river or surface area of inland lakes (ASMFC 2012; PFMC 2016). For a pelagic species like river herring, freshwater spawning and nursery habitat quantity in lakes

is typically measured by surface area, depth, and volume, of which lake volume has been shown to explain some variability in juvenile river herring abundance (Kosa and Mather 2001). These measures are simple to collect and have allowed researchers to construct estimates of habitat loss (Hall et al. 2011; Mattocks et al. 2017). Unfortunately, the assumption that all available habitat is suitable and of equal quality omits key information about within-river and within-lake habitat requirements that will impact decision making regarding best management approaches. Evidence from landlocked populations in the Laurentian Great Lakes of North America suggests that juvenile Alewives often select for subhabitats within a lake relative to prey availability and feeding behavior (Janssen and Luebke 2004), upwelling events (Heufelder et al. 1982), and surface temperature regimes (Nash and Geffen 1991; Dufour et al. 2008). It is likely that anadromous juveniles exhibit similar heterogeneity in their spatial distribution within lakes, and lakes with limited high-quality habitat may have earlier emigration or reduced survival, thus reducing juvenile densities.

Water quality is also a critical aspect for characterizing habitat and thus has potential to explain variation in juvenile river herring densities among lakes. Water quality in lakes is largely driven by sources of nutrients, such as total phosphorous (TP), total nitrogen (TN), and dissolved organic carbon (DOC), but there is limited information about how variability in these parameters affects juvenile river herring production. Durbin et al. (1979) proposed that pulses of TN and TP from anadromous adult river herring would provide a net benefit to the production of higher trophic levels by increasing food availability through activity at the microbial level. In contrast, recent work has suggested that elevated TN levels as a result of increased urbanization may limit juvenile river herring growth (Monteiro Pierce et al. 2019). Thus, more work is needed to understand how the type and source of nutrients (natural or anthropogenic) potentially influence juvenile production. Thermal and dissolved oxygen (DO) regimes are also closely tied to nutrient levels (Dillon and Rigler 1974). For example, reduced light and heat penetration as a result of increases in DOC have been repeatedly shown to reduce fish productivity by restricting primary production (Karlsson et al. 2009; Finstad et al. 2014; Craig et al. 2017) and limiting available habitat for many forms of aquatic life (Morris et al. 1995; Finstad et al. 2014). Similar responses may occur for river herring in lakes, but these relationships have not been tested directly. Previous work has primarily examined the effect of environmental conditions on juvenile river herring in the context of triggers to juvenile migration from lakes (e.g., Kosa and Mather 2001; Iafrate and Oliveira 2008; Gahagan et al. 2010) and does not provide information about habitat and environmental factors that may affect larval survival and limits to their production.

In this study, we used a recently developed and tested juvenile sampling method (Devine et al. 2018) to estimate juvenile river herring densities across 29 freshwater lakes in the northeastern USA. Specifically, we investigated the effects of (1) spawning adult river herring densities, (2) within-lake habitat availability, and (3) lake water quality on juvenile river herring densities. The results provide insights into the factors that may influence anadromous river herring productivity during their residence in freshwater ecosystems, which may help assign causes of decline and guide prescriptions for recovery.

METHODS

Study Sites

Study lakes were located in coastal northeastern USA from Greenwich, Connecticut, to Damariscotta, Maine (Figure 1; Table 1). Lake selection was nonrandom and intended to represent a wide range of morphometric, physical, and biological characteristics commonly exhibited throughout the region (Table 2). The 29 study lakes were 8–1,861 ha in surface area, had mean depths of 1.5–15.2 m, and had summer surface temperatures of 17.6–28.7°C. Each site has established estimates of spawning adult river herring through monitoring at natural runs or where adult spawner abundance existed from stocking events.

Data Collection

Fish and water quality were sampled at 29 lakes over 2 years. In 2014, 20 lakes were sampled monthly between June and August (3 months). In 2015, 11 lakes were sampled monthly between June and August (3 months) and two lakes (Snipatuit and Mianus lakes) were sampled in July only. Four lakes (Pentucket, Upper Mystic, Whitmans, and Snipatuit) were sampled in both years. Adult river herring abundances were estimated from counts during their upstream migration by state and federal fisheries management agencies and volunteer citizen groups. Methods included visual counts conducted by volunteers, electronic counts collected using Smith-Root (model 1101 or 1601) electronic resistivity counters, and video counts using underwater cameras and motion detection software suites (i.e., Salmonsoft, iSpy). In five lakes, river herring were introduced via stocking (i.e., capturing adults from below a dam and depositing them upstream into the lake) and adults were individually counted.

We used a 30.5-m × 4.3-m purse seine (485 m^3 volume encircled when deployed to full depth) with 2.22-mm delta mesh to sample juvenile river herring after sunset (2000–0200 hours) following methods described by Devine et al. (2018). The seine was deployed, pursed, and immediately retrieved (hereafter, referred to as a haul) at a minimum of three locations (range = 3–18) within each lake during
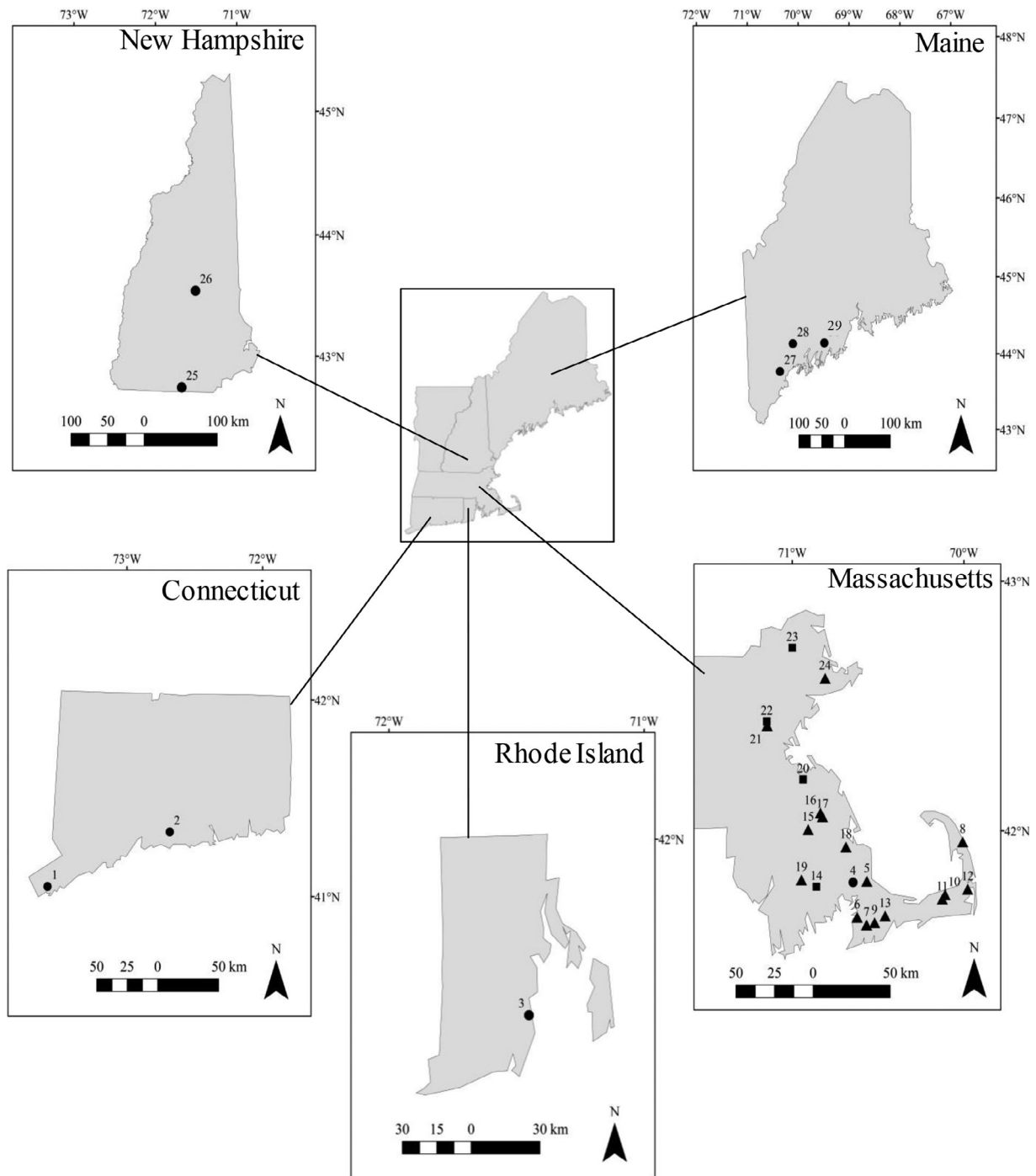
FIGURE 1. Study locations ($n = 29$; numbers above study locations correspond to lake information presented in Table 1) and years sampled (triangles = 2014, circles = 2015, squares = 2014 and 2015) within the five coastal states in the northeastern United States.

each sampling event. Purse-seine sampling locations were randomly generated using ArcGIS following methods described by Rosset et al. (2017). River herring were captured from the purse-seine pocket using dip nets, enumerated, and returned immediately to open water. Sampling coordinates, time of day, processing time, lake depth at the sample site, wind speed, and substrate (when observed from net encountering lake bottom) were recorded for each haul. If water depth was <4.3 m (depth of seine), the volume was adjusted accordingly.

TABLE 1. Geographic information for the 29 coastal northeastern USA lakes sampled in this study. Lake numbers refer to the mapped locations in Figure 1.

Lake number	Lake name	City, state	Latitude	Longitude
1	Mianus	Greenwich, Connecticut	41°02'50"N	73°35'14"W
2	Guilford	Guilford, Connecticut	41°19'55"N	72°41'02"W
3	Gilbert Stuart	North Kingstown, Rhode Island	41°31'25"N	71°27'04"W
4	Glen Charlie	Wareham, Massachusetts	41°47'29"N	70°38'50"W
5	Great Herring	Bourne, Massachusetts	41°47'49"N	70°33'52"W
6	Cedar	North Falmouth, Massachusetts	41°38'58"N	70°37'20"W
7	Coonamessett	Falmouth, Massachusetts	41°37'08"N	70°33'59"W
8	Gull	Wellfleet, Massachusetts	41°57'22"N	70°00'30"W
9	Johns	Mashpee, Massachusetts	41°37'40"N	70°31'14"W
10	Lower Mill	Brewster, Massachusetts	41°44'26"N	70°06'33"W
11	Upper Mill	Brewster, Massachusetts	41°43'50"N	70°06'58"W
12	Pilgrim	Orleans, Massachusetts	41°45'52"N	69°58'45"W
13	Santuit	Mashpee, Massachusetts	41°39'15"N	70°27'31"W
14	Snipatuit	Rochester, Massachusetts	41°46'25"N	70°51'42"W
15	Robbins	East Bridgewater, Massachusetts	42°00'17"N	70°54'25"W
16	Oldham	Pembroke, Massachusetts	42°04'00"N	70°50'09"W
17	Furnace	Pembroke, Massachusetts	42°03'20"N	70°49'35"W
18	Billington	Plymouth, Massachusetts	41°56'03"N	70°41'01"W
19	Long	Lakeville, Massachusetts	41°47'47"N	70°56'50"W
20	Whitmans	Weymouth, Massachusetts	42°12'21"N	70°56'09"W
21	Lower Mystic	Medford, Massachusetts	42°25'36"N	71°08'51"W
22	Upper Mystic	Medford, Massachusetts	42°26'07"N	71°08'51"W
23	Pentucket	Georgetown, Massachusetts	42°43'59"N	70°59'39"W
24	Chebacco	Essex, Massachusetts	42°36'44"N	70°48'32"W
25	Potanipo	Brookline, New Hampshire	42°44'26"N	71°40'36"W
26	Winnisquam	Laconia, New Hampshire	43°32'28"N	71°30'25"W
27	Highland	Westbrook, Maine	43°46'22"N	70°21'21"W
28	Sabattus	Sabattus, Maine	44°08'48"N	70°06'07"W
29	Damariscotta	Damariscotta, Maine	44°10'33"N	69°29'03"W

Water quality was sampled during dusk, preceding fish sampling, at the deepest point in each lake. Water temperature, conductivity, pH, and DO were measured using a multiparameter YSI-650MDS (YSI, Yellow Springs, Ohio) at 0.5 m off the bottom, the middle of the water column, and 0.5 m below the surface in 2014 and at 1-m intervals from surface to bottom in 2015. The average of two Secchi depth measurements was used to characterize turbidity. Surface water samples for TN and TP were collected just below the lake surface in an acid-washed 60-mL bottle. Samples of DOC and chlorophyll *a* were collected by filtering surface water through a pre-ashed, 42-mm Whatman glass fiber filter. All samples were placed on ice and frozen completely within 10 h.

Several physical habitat variables were calculated to serve as measures of available suitable habitat. Surface area and shoreline distance data were extracted using the trace tool in ArcGIS. The maximum and mean depth were determined from bathymetry maps produced by state agencies. Depth to thermocline was estimated monthly for each lake sampled in 2015 using temperature profile data and the "rLakeAnalyzer" package in Program R (Read et al 2011). For the four lakes sampled in 2014 and 2015, we assumed thermocline depths to be similar across years. We estimated thermocline depth for six additional lakes in 2014 using temperature data collected by watershed associations that monitor water quality throughout the summer.

Statistical Analysis

Different models were used for each study objective. We used a generalized additive model in objective 1 to evaluate the adult–juvenile density relationship and inspect possible inflection points. Multiple linear regression was used in objective 2 to examine the additive effect of several physical habitat variables on juvenile densities. Finally, we applied a series of linear mixed-models in

TABLE 2. Mean, range (minimum and maximum), and abbreviation for physical habitat and water quality characteristics across months sampled for the 29 coastal northeastern USA lakes in this study.

Characteristics	Abbreviation	Minimum	Maximum	Mean
Physical habitat				
Area (ha)[a]	Area	8.01	1,861.00	243.89
Mean depth (m)[a]	MeanD	1.50	15.21	4.91
Maximum depth (m)	MaxD	1.82	25.92	11.30
Shoreline length (km)	Shore	1.38	64.69	10.58
Elevation (m)	Elev	−0.54	146.66	20.64
Depth to thermocline (m)[a]	Thermo	0.75	8.34	4.44
Water quality				
Surface temperature (°C)[a]	Temp	17.66	28.74	24.16
Dissolved organic carbon (mg/L)[a]	DOC	1.49	11.10	4.64
Secchi depth (m)[a]	Secchi	0.20	5.80	1.86
Total phosphorous (μg/L)[a]	TP	0.61	71.50	26.44
Total nitrogen (mg/L)[a]	TN	0.12	1.86	0.51
Chlorophyll a (μg/L)	Chla	−0.33	90.57	13.27

[a]Variables tested in models.

objective 3 to investigate the effects of water quality variables and their interaction with time using a single variance structure.

Effects of adult density on juvenile density (objective 1).— We used additive modeling (Hastie and Tibshirani 1990; Zuur et al. 2007) to investigate the relationship between adult river herring densities and juvenile densities. This smoothing method was applied because preliminary analyses indicated nonlinearities in the relationship, a common aspect of stock–recruit models where density-dependent effects decrease survivorship of young at large stock sizes (Beverton and Holt 1957; Ricker 1975; Shepherd 1982). Thus, we hypothesized that our river herring data set would exhibit similar attributes, but we did not want to constrain the relationship within a stock–recruitment framework.

We fit nonparametric data (generalized additive model) and used $\log_e$ transformed densities for juvenile and adult life stages as the dependent and independent variables in the model, respectively. Adult density (number/ha) was calculated as the number of adults per hectare of accessible lake surface area upstream of a counting station. Juvenile river herring densities (number/m^3) were derived from purse-seine sampling and averaged across purse-seine hauls in each lake for each month to estimate monthly density. We used the mean of only June and July because these months generally yield the highest catch rates with the greatest precision (Devine et al. 2018) and thus better reflect peak densities and reduce uncertainty in results. A single density estimate rather than a mean was used for two lakes (Snipatuit and Mianus) sampled only once in July. We used a Gaussian distribution with cubic B-splines (s) to estimate the smoother (Hastie and Tibshirani 1990). Deviance explained was used as a measure of goodness of fit, and the

normality assumption was tested by plotting a histogram of residuals and by applying a Shapiro–Wilk test. The generalized additive model was fit using the "mgcv" package in Program R (Wood 2006).

Effects of physical habitat on juvenile density (objective 2).— Multiple linear regression was used to investigate the effect of adult density and several physical habitat variables (e.g., lake surface area, mean depth, and thermocline depth) on juvenile density. We used mean juvenile density from June and July for each lake as the response variable. Prior to analysis, juvenile density was $\log_e$ transformed and adult density and all physical habitat variables were normalized with a z-score transformation, inspected for outliers using Cleveland dot plots (Cleveland 1993), and checked for collinearity using variance inflation factors. We excluded predictor variables with variance inflation factor values >2 in a stepwise fashion (Zurr et al. 2007). All combinations of additive models were fit, and we used Akaike information criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002) to evaluate support for the most parsimonious of 16 candidate models.

Effects of water quality on juvenile density (objective 3).— We fit and compared a series of linear mixed-effects regression models to examine the effects of water quality (surface water temperature, TP, TN, secchi depth, chlorophyll a, and DOC) on monthly juvenile river herring densities ($\log_e$ transformed). Mixed models were appropriate for our hierarchical data—1 month of data for 2 lakes, 3 months of data for 27 lakes, and 6 months (over 2 years) of data for 4 lakes—by incorporating a hyperparameter that uses a single variance structure for all levels in a group (Snijders and Boskers 1999; Raudenbush and Bryk 2002). Prior to analysis, all water quality variables were

normalized with a z-score transformation and outliers and collinear variables were removed.

To avoid a very large number of fitted models, we used a series of steps to select models (Zuur et al., 2009). In step 1, we evaluated support for an interaction term between Julian date and each variable because we suspected the relationships between juvenile density and water quality to change with time. We fit five models that incorporated water quality variables as fixed effects and the categorical variable "lake" was used as a random effect. The interaction between DOC and Julian date was the only interaction term supported, and we included this term in subsequent models to account for temporal variability in DOC. We did not find support for a random slope term in any of these initial models (χ^2 test: $P = 0.38$) and thus proceeded with only a random intercept variance structure for all remaining models. In step 2, we fit a set of 80 candidate models containing the top model(s) from step 1 (i.e., with ΔAIC_c values <2; Burnham and Anderson 2002). The remaining models included all combinations of additive effects between surface temperature, TN, TP, secchi depth, and DOC, and we report the results for the final set of 80 candidate models. In step 3, we refit the top-performing models using restricted maximum likelihood to obtain standardized coefficient estimates, standard errors, and P-values. Lastly, we examined residuals of the top model to verify normality and homogeneity assumptions and inspect for autocorrelation patterns. A Shapiro–Wilk normality test was applied on model residuals, and residuals were plotted against fitted values and against quantiles of the standard normal distribution. The final model with and without a first-order autocorrelation function was compared using AIC_c. Mixed models were fit using the "lme4" package in R (Bates et al. 2015).

To evaluate variable importance for objectives 2 and 3, we determined the proportion of variance explained independently and jointly by each variable in the data sets using hierarchical partitioning of negative log-likelihoods (Chevan and Sutherland 1991). This approach was used to minimize any influence of multicollinearity among variables in the data sets and to assess the independent effect of each variable on juvenile river herring density. Negative joint effects can occur when variables act to obscure the explained variance of another variable. Partitioning analyses were implemented using the "hier.part" package in R (Walsh and Mac Nally 2013), and analyses on all data sets were performed in R version 3.2.2 (R Core Team 2015).

RESULTS

Effects of Adult Density on Juvenile Density (Objective 1)

Juvenile densities ranged from 0.03 (Robbins Lake) to 24.86 (Pilgrim Lake) river herring/m³, and the number of total purse-seine hauls at each lake ranged from 3 (Mianus Lake) to 63 (Upper Mystic Lake) (Figure 2). Juvenile densities were greatest in June for all lakes except for Damariscotta, Highland, and Upper Mystic (2014 and 2015), which were greater in July. Adult densities from fishway counts and stocking events ranged from 5 (Robbins Lake) to 7,466 (Upper Mystic Lake) herring/ha (adult abundances ranged from 271 to 689,669 fish [mean = 143,335]). There was a significant nonlinear relationship between adult density and juvenile density ($F = 10.41$, $P < 0.001$; Figure 3), and adult density explained 66.6% of the deviance in juvenile density. The relationship was linear at low to moderate adult densities, peaked at roughly 1,000 fish/ha (back-transformed from log_e scale), and declined at higher adult densities. The model showed a reasonably good fit but generally underestimated values as adult density increased (Figure 3).

Effects of Physical Habitat on Juvenile Density (Objective 2)

Lake surface area ranged from 8.01 ha (Cedar Lake) to 1,861 ha (Damariscotta Lake), with a majority (66%) of lakes less than 100 ha (Table 2). Study lakes varied widely in depth, with mean depths ranging from 1.51 m (Cedar Lake) to 15.21 m (Upper Mystic Lake). Shoreline length ranged from 1.38 km (Cedar Lake) to 64.69 km (Damariscotta Lake), with most lakes (88%) having less than 10 km of shoreline. Depth to thermocline ranged from 0.75 m (Robbins Lake) to 8.34 m (Damariscotta Lake), and a majority of lakes (65%) experienced thermocline depths less than 5 m (Table 2). Due to strong collinearity between lake area and shoreline length ($R^2 = 0.95$, $P < 0.001$; Table 3) and mean depth and maximum depth ($R^2 = 0.96$, $P < 0.001$; Table 3), we excluded shoreline length and maximum depth as predictors in the model.

The best-performing regression model describing variation in juvenile density included adult density as the single predictor variable and had almost twice as much support as the second-ranked model (Table 4). Adult density was positively related to juvenile density (adjusted $R^2 = 0.48$, $P = 0.001$), and the model explained 48% of the variation in juvenile density. The second-ranked model was similar to the top model but included thermocline depth as a second predictor. The third model included thermocline depth and surface area, and the fourth model included surface area in addition to adult density. Mean depth was not supported in the top models (i.e., $\Delta AIC_c < 2$; Table 4). Although goodness of fit increased incrementally with the addition of habitat variables, these models had lower AIC_c weights due to the greater number of parameters.

Results from hierarchical partitioning supported the multiple regression findings. Across our study lakes, adult density and thermocline depth were the most important contributors to explained variation in juvenile density (Figure 4A). Adult density had the largest independent contribution to explained variance ($I = 33.7\%$), while
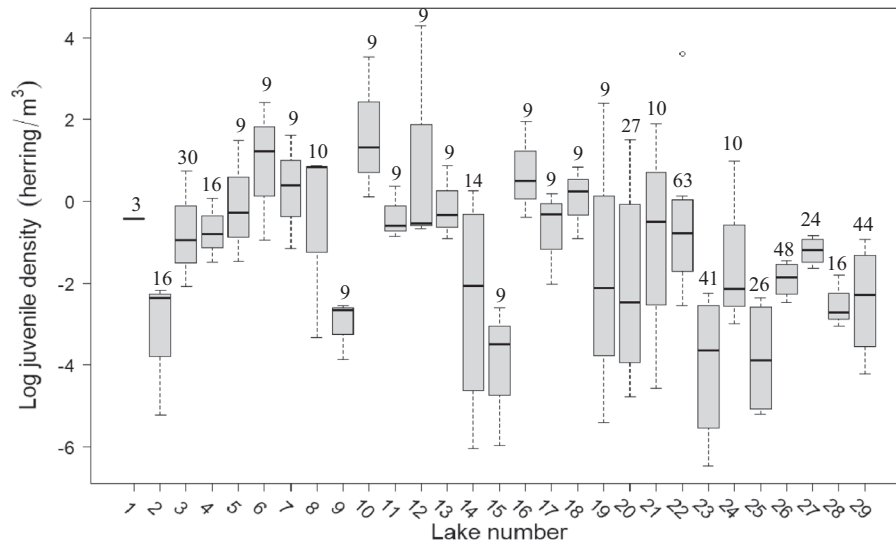
FIGURE 2. Density (log$_e$ scale) of juvenile river herring sampled from 29 lakes using a purse seine, with the number of purse-seine hauls reported above each box. Box plots show the median (center dark line), the lower and upper bounds for 50% confidence intervals (box dimensions), and the maximum and minimum value (whiskers). Sites 14, 20, 22, and 23 were sampled in 2014 and 2015.
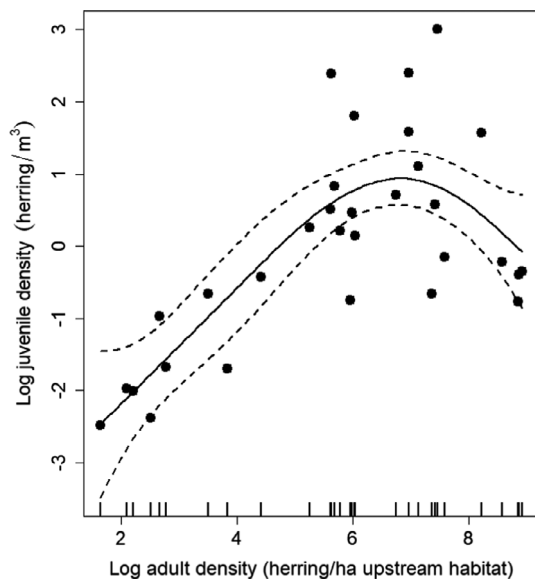

FIGURE 3. The relationship between adult and juvenile river herring density (both on log$_e$ scale) fit by a generalized additive model that used a Gaussian error distribution with cubic B-splines. The tick marks on the x-axis represent observations of adult density. The solid line represents the mean, and the dashed line defines the 95% confidence intervals.

thermocline depth ($I = 14.7\%$), surface area ($I = 7.6\%$), and mean depth ($I = 3.8\%$) had smaller contributions (Figure 4A). Some variance in the data could not be ascribed separately to any one predictor, and thus joint contributions with other variables were important for adult density ($J = 13.9\%$) and thermocline depth ($J = 6.2\%$). There was a negative joint contribution for surface area ($J = 2.6\%$),

which suggests that when included in models with other variables, surface area will suppress any shared variance explained (Chevan and Sutherland 1991). In our model selection framework, thermocline depth was positively related to juvenile density ($\beta = 0.875$, $P = 0.035$), but its effect became less pronounced when including surface area in the model ($\beta = 0.530$, $P = 0.078$; Table 5).

Effects of Water Quality on Juvenile Density (Objective 3)

There was wide variance in water quality variables among the 29 lakes and across the 3 months (Table 2). For example, surface water temperature ranged from 17.66°C (Gull Lake) to 28.74°C (Pentucket Lake), TP ranged from 0.61 µg/L (Upper Mystic Lake) to 71.50 µg/L (Robbins Lake), and DOC values ranged from 1.49 mg/L (Glen Charlie Lake) to 11.10 mg/L (Robbins Lake) (Table 2). Surface temperature increased in all lakes from June through August, while the temporal trends in TP, TN, DOC, and chlorophyll a were more site-specific, with some lakes having highest levels in late summer and other lakes highest in June. Several water quality variables were significantly correlated, including Secchi depth and chlorophyll a ($R^2 = -0.57$; $P < 0.001$), DOC and Secchi depth ($R^2 = -0.41$; $P < 0.05$), chlorophyll a and surface temperature ($R^2 = -0.34$; $P < 0.05$), and TN and TP ($R^2 = 0.32$; $P < 0.001$) (Table 3). We excluded chlorophyll a as a predictor variable for subsequent analyses due to collinearity with multiple variables and incomplete observations across both years.

The top water quality model explaining variation in juvenile density included DOC, Julian date, an interaction between DOC and Julian date, and surface temperature (Table 4). In the model, the relationship between

TABLE 3. Correlation coefficients (lower diagonal) and P-values (upper diagonal) of physical habitat and water quality variables used in analyses. Significant correlations ($P < 0.05$) are highlighted in bold italics, and ns = not significant. Variables were $\log_e$ transformed. Refer to Table 2 for explanation of variables.

Variable	Area	MeanD	MaxD	Shore	Thermo	Temp	DOC	Secchi	TP	TN	Chla
Area	1	0.043	0.001	0.001	0.005	ns	0.004	0.004	ns	0.010	ns
MeanD	*0.20*	1	0.001	0.001	0.001	ns	0.001	0.001	0.001	ns	ns
MaxD	*0.34*	*0.96*	1	0.001	0.001	ns	0.001	0.001	0.001	ns	ns
Shore	*0.95*	*0.26*	*0.41*	1	0.001	ns	0.004	0.003	ns	0.019	ns
Thermo	*0.40*	*0.66*	*0.72*	*0.49*	1	ns	0.005	ns	0.018	ns	ns
Temp	−0.05	−0.16	−0.17	−0.07	−0.28	1	ns	ns	ns	ns	0.002
DOC	*−0.35*	*−0.47*	*−0.50*	*−0.43*	*−0.51*	0.18	1	0.001	ns	ns	ns
Secchi	*0.28*	*0.52*	*0.58*	*0.29*	0.25	−0.14	*−0.41*	1	0.003	0.001	0.001
TP	−0.07	*−0.40*	*−0.44*	−0.11	*−0.34*	0.07	0.18	*−0.28*	1	0.001	ns
TN	*−0.25*	0.01	−0.10	*−0.23*	−0.13	0.01	0.16	*−0.40*	*0.32*	1	ns
Chla	0.10	0.16	0.15	0.09	0.16	*0.34*	−0.13	*−0.57*	−0.20	0.01	1

temperature and juvenile density was the only fixed effect not significant ($P = 0.065$), and the interaction term between DOC and Julian date indicates that the relationship between DOC and juvenile density changes with time (Table 6). This model had strong Akaike weight of evidence ($w_i = 0.41$) relative to other candidate models and fit the data reasonably well (adjusted $R^2 = 0.48$). All subsequent model combinations did not improve the goodness of fit, had very little weight of evidence relative to the top model, and had ΔAIC_c values >2 and thus were not supported (Table 4). We did not find support for an autocorrelation term in any model (likelihood ratio test: $L = 0.105$, $df = 1$, $P = 0.741$), suggesting that the variability observed due to environmental effects was properly modelled.

Hierarchical partitioning results for water quality variables were consistent with conclusions from mixed models. Most of the variance explained by each variable was related to its independent effects (Figure 4B). Julian date ($I = 15.9\%$) and DOC ($I = 10.2\%$) had the largest independent contributions to explained variance (Figure 4B) and thus remained in all top models regardless of combinations with other predictor variables (Tables 4 and 6). The variables TN ($I = 5.5\%$), temperature ($I = 3.1\%$), Secchi depth ($I = 2.4\%$), and TP ($I = 0.9\%$) were less descriptive of juvenile densities and had smaller independent contributions to explained variance (Figure 4B). The ratio of joint to independent contribution was greatest for temperature, and the joint contribution to explained variance was negative for all water quality variables tested in models, suggesting that each variable suppresses the explained variance of other variables used in modeling.

DISCUSSION

This study offers new insights into the abiotic and biotic factors that influence juvenile river herring densities in lakes

and can be used to inform expectations about juvenile productivity across a range of adult densities. Adult spawning density explained substantial variation in juvenile river herring densities. Our findings also demonstrate that habitat availability and water quality additionally influence juvenile density and provide a mechanistic link between DOC and thermocline depth. These measures can be used to better judge habitat availability, moving away from simple measures of homogenous habitat quantity. These results can inform expectations about the optimal level of recruitment within lakes and the potential increase in productivity from management and restoration actions, providing important information to help restore these imperiled fish.

Adult Spawner Density Drives Juvenile Density

Adult river herring spawner density was the primary factor influencing production of juveniles in freshwater nurseries. At low to medium adult densities, juvenile density increased linearly, but gains in juvenile density leveled off and eventually declined as adult density increased above 1,000 fish/ha. The decline at the highest levels of adult density may be a result of mortality, emigration, or both. The observed threshold of juvenile densities is consistent with simulation modelling by Barber et al. (2018) and supports the theory that recruitment is shaped by density-dependent processes that act on fish in the first year of life (Shepherd and Cushing 1980). As such, principal biological processes, such as individual growth and mortality, are often modified by competition for food resources, available habitat, or a combination of both (Myers and Cadigan 1993).

The gradient in density dependence we observed can be used to better restore and manage river herring populations. Common restoration actions include stocking gravid adults into rivers with newly opened habitat, improving fish passage (e.g., a specific type or size of fish ladder), or removing dams. However, decisions supporting

TABLE 4. Model selection results from the top-ranked multiple regression and mixed-effects models explaining variations in juvenile river herring densities across 29 lakes as a function of physical habitat and water quality predictors. The top five models are reported for 16 possible multiple regression models using physical habitat predictors and for 80 candidate linear mixed-effects models using water quality predictors and lake as a random effect. Parameter abbreviations are defined in Table 2; df = degrees of freedom; logLik = natural logarithm of the maximum likelihood; AIC_c = Akaike information criterion corrected for small sample size; ΔAIC_c = difference in AIC from top model; w_i = rounded model weights; AdjR^2 = adjusted model R-squared.

Model	df	logLik	AIC_c	ΔAIC_c	w_i	AdjR^2
Physical habitat top models						
Adult density	3	–40.84	89.00	0.00	0.32	0.48
Adult density + Thermo	4	–39.96	90.10	1.19	0.18	0.53
Adult density + Thermo + Area	5	–38.54	90.60	1.67	0.14	0.58
Adult density + Area	4	–40.24	90.70	1.75	0.13	0.51
Adult density + MeanD	4	–40.81	91.80	2.89	0.08	0.48
Water quality top models						
DOC × Julian date + Temp[a]	7	–92.94	202.00	0.00	0.41	0.48
DOC × Julian date + Temp + Secchi[a]	8	–92.64	204.47	2.15	0.14	0.49
DOC × Julian date + Temp + TN[a]	8	–92.82	204.83	2.51	0.12	0.48
DOC × Julian date + Temp + TP[a]	8	–92.89	204.98	2.65	0.11	0.48
DOC × Julian date + Temp + TP + Secchi[a]	9	–92.45	206.99	4.66	0.04	0.49

[a] Includes interaction term between DOC and Julian date.

prioritization of these actions have thus far not included objectives associated with habitat quality and density-dependent processes and instead may be based upon the best professional judgment of biologists or managers. Specifically, Havey (1973) and Walton (1987) both demonstrated a weak relationship between spawning stock and juvenile abundance at low stock levels through work in northern New England, and Jessop (1990a) found intermediate-stage stock–recruitment relationships (egg to juvenile and juvenile to adult) to be nonsignificant in the Saint Johns River, New Brunswick. However, when using spawning stock abundance to predict year-class at age 3 and adult returns 4–5 years later, Jessop (1990b) found a strong positive linear correlation. This suggests that year-class abundance is established by spawning stock abundance, and results from our study support this previous work. Prior studies were all based on studying single systems over multiple years, and the limited spatial scope and contradictory results restricts the ability of managers to incorporate this information into assessments and may not account for variability in habitat between systems. In contrast, our study is the first to adopt empirical juvenile density data collected from numerous lakes using a standardized sampling approach to explore adult–juvenile dynamics for anadromous river herring. While additional years of data with more adult densities greater than 1,000 adults/ha are needed to better describe the shape of the relationship in large runs, our results, based on a wide variety of systems throughout the northeastern USA, indicate that the model could be robust for predictions of juvenile densities based on adult densities, or vice versa, for most populations currently monitored.

Role of Habitat Availability for Juvenile River Herring

Defining available habitat for anadromous fish can help managers understand linkages between fish productivity and how a species' habitat uses are distributed. Surface area and maximum or mean depth of lakes have been widely applied as a proxy for the response to restoration actions (Summerfelt 1999). For river herring, some life history models and stock assessments currently rely on surface area as a proxy for habitat availability (ASMFC 2012; Nelson et al. 2020). In our study we found thermocline depth to be a better physical habitat predictor of juvenile river herring densities across lakes than surface area. The negative joint effect observed in hierarchical partitioning suggests that very large surface area may reduce the influence of thermocline depth. Our results suggest that using surface area as a proxy for habitat availability may omit key information about habitat suitability. Juvenile river herring likely experience a habitat "squeeze," whereby shallower thermocline depths create large regions with insufficient DO forcing fish and system production into a shrinking area of suitable epilimnion habitat that is likely to drive emigration or mortality. This phenomenon has been demonstrated in Striped Bass *Morone saxatilis* (Coutant 1985) and Brown Trout *Salmo trutta* (Finstad et al. 2014). Despite variability in maximum depth across study lakes, systems may experience relatively shallow thermoclines (<4 m) and may be characterized by a decreasing thermocline depth as summer progresses. Lower limits of DO for river herring (<4 mg/L; Klauda et al. 1991; Vanderploeg et al. 2009a) were recorded below most thermocline depths for the 29 lakes used in this study, potentially eliminating greater than
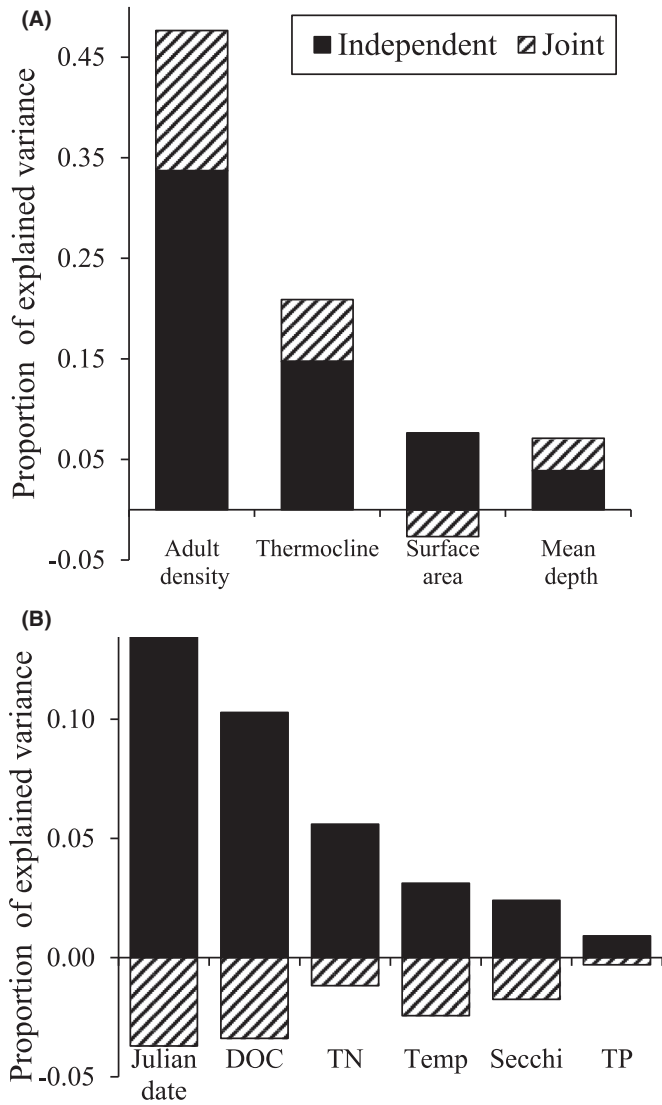
FIGURE 4. Proportions of variance in the densities of juvenile river herring explained independently and jointly by **(A)** the four physical habitat variables and **(B)** the six water quality variables (see Table 2 for variable definitions). Negative joint effects reflect that the variable acts as a suppressor of other variables towards shared variability in the full model.

northeastern USA (Devine et al. 2018) and decline throughout the summer due to a combination of pulses of emigration (Kosa and Mather 2001; Iafrate and Oliveira 2008; Gahagan et al. 2010) and natural mortality (Essig and Cole 1986; Havey 1973). These declines may be induced and amplified by high levels of DOC in many nursery systems. The major pathway for DOC to impact lakes is through terrestrial-derived inputs that get flushed in from the surrounding landscape and create a stained or dark-brown water color that reduces the depth of light and heat penetration and focuses energy absorption near the surface, which, in turn, produces a shallow thermocline and lower DO (Craig et al. 2015; Kelly et al. 2014). Dissolved organic carbon has been suggested to be the most important variable for predicting thermocline depth (Perez-Fuentetaja et al. 1999), and the negative relationship between DOC and thermocline depth in our study lakes corroborates the hypothesized link between these variables and provides a mechanism for the DOC–density relationship we observed.

The relationship between DOC and juvenile river herring is likely complex due to interactions with other water quality parameters and prey resources that exhibit seasonal variation. For example, modifications to thermal regimes during summer as a result of increased DOC may limit the quantity of suitable habitat for juvenile river herring and highlights the importance of accounting for time when making assessments. Evidence from landlocked Alewife populations in the Great Lakes system suggests that juveniles prefer warmer surface waters or shallow inshore areas (Dufour et al. 2008; Nash and Geffen 1991) and thus may avoid cooler, deeper regions of water established below the thermocline. The direct relationship between juvenile density and temperature was not significant in our modelling; however, the ratio of joint to independent contribution observed in variable partitioning was greatest for surface temperature and may have led to temperature being included in all top models. This suggests that temperature, mediated by DOC levels, likely plays a role in shaping available habitat, which is consistent with the squeeze hypothesis. Stratification regimes that are structured by DOC may also alter the availability of zooplankton, a critical food item for juvenile river herring growth and survival (Pardue 1983). Increases in DOC levels may offset the patchy aggregations and migration patterns of zooplankton (Downing 1991; Leech et al. 2005) and consequently allow key prey items, typically more tolerant of low DO than fish (Vanderploeg et al. 2009b), to reduce their predation risk to river herring by inhabiting hypoxic areas, a phenomenon observed in other pelagic fish communities (Larsson and Lampert 2011; Taylor and Rand 2003). It is unclear the extent to which spatial separation occurs between river herring and zooplankton as a result, but it is possible that river herring more often interact

50% of available habitat in most cases. Thus, lakes with deeper summer thermoclines may provide more suitable habitat for juvenile river herring. The positive relationship of thermocline depth to density presented in this study suggests that juveniles respond to stratification regimes and may predominantly use water depths at or above the thermocline.

Water Quality Modifies Available Habitat

We observed that water quality, most notably DOC, affected juvenile herring densities. Densities of juvenile river herring typically peak in June or July in the

TABLE 5. Standardized parameter estimates for the three top-ranked physical habitat candidate models explaining variation in juvenile river herring densities across 29 lakes. Parameter abbreviations are defined in Table 2.

| | Physical habitat models | | | | | | | | |
| | Adult density | | | Adult density + Thermo | | | Adult density + Thermo + Area | | |
Effect	β	SE	P	β	SE	P	β	SE	P
Intercept	−3.565	0.794	0.000	−3.746	0.810	0.000	−3.007	0.876	0.003
Adult density	0.584	0.131	0.000	0.515	0.145	0.002	0.461	0.151	0.006
Thermo				0.876	0.391	0.035	0.531	0.380	0.078
Area							−0.654	0.420	0.135

TABLE 6. Standardized parameter estimates for the three top-ranked water quality candidate models explaining variation in juvenile river herring densities across 29 lakes. Estimates of fixed effects and an interaction term (DOC × Julian date) are shown for the linear mixed-effects water quality models, with standard errors (SE) and P-values calculated using restricted maximum likelihood estimation. Parameter abbreviations are defined in Table 2.

| | Water quality models | | | | | | | | |
| | DOC × Julian date + Temp | | | DOC × Julian date + Temp + Secchi | | | DOC × Julian date + Temp + Secchi + TN | | |
Effect	β	SE	P	β	SE	P	β	SE	P
Intercept	7.826	1.554	<0.000	7.814	1.583	<0.000	8.151	1.658	<0.000
DOC	5.467	1.441	0.001	5.370	1.478	0.002	5.104	1.571	0.004
Julian date	−0.048	0.008	<0.000	−0.048	0.008	<0.000	−0.050	0.009	<0.000
Temp	0.387	0.199	0.065	0.371	0.207	0.089	0.410	0.208	0.064
Secchi				−0.139	0.283	0.629			
TN							0.134	0.185	0.479
DOC × Julian date[a]	−0.030	0.008	0.001	−0.030	0.008	0.002	−0.029	0.009	0.004

[a] Represents interaction term.

with and are dependent on prey resources that are produced within the epilimnion, and a paucity of available resources may promote emigration or increase mortality.

Implications for Managed Populations

The results presented in this study describe the densities of anadromous river herring that freshwater lakes can support and affirm the importance of restoration for increasing river herring population growth (Bowden 2014). Dam removal, fish passage structures, and stocking programs continue to grant river herring access to habitats that have been unavailable to them for centuries. However, the reduced juvenile densities at the highest adult densities in this study illustrates the importance of knowledge about carrying capacity of the target habitat in setting stocking levels or prioritizing management actions, such as dam removal or in-river harvest of adults. Expanding available habitat to make additional increases in system productivity once populations reach about 1,000 adults/ha and working to improve runoff into freshwater systems are

practical implications of this work. Additionally, our results may be helpful towards quantifying potential surplus adult production available for harvest without negatively impacting recruitment. A harvest strategy that maintains a minimum of 1,000 adults/ha is likely to provide near maximum juvenile densities. Given the conservation status of this species and the variability observed in many adult run counts, further investigation into these relationships is warranted prior to use for setting harvest recommendations. An experimental approach where adult densities are increased incrementally over time and juvenile densities are monitored for responses may be useful to gather experience about site-specific limits to productivity.

The spatial extent of suitable habitat for juvenile river herring may be squeezed vertically as a result of DOC shaping temperature and oxygen regimes, and we argue that suitable habitat quantity—as quantified by lake volume above the thermocline—is a valuable metric for evaluating restoration options. Measurements of habitat are important in fisheries management (Brown et al. 2018),

and we believe that our results can help move beyond designating available habitat as total surface area for river herring and instead point toward including DOC and thermocline depth to improve lake classification schemes (Summerfelt 1999) and fish–habitat relationships (Knudby et al. 2010). Identifying suitability of within-lake habitats can help identify water quality improvements that should improve system productivity when additional habitat is not available or cannot be accessed. For example, in Massachusetts, water quality assessments are typically used to determine river herring habitat potential and support selection of habitat restoration projects (Chase 2010). However, when such habitat management improvements are not feasible due to constrained resources or limited site-specific information, managing for a target adult run size may be a more practical option for achieving more immediate and predictable results. In terms of juvenile output from the system, for example, fishway modifications, experimentation of stocking densities, or managing in-river harvest may be more workable actions for reaching optimal productivity than extensive habitat restoration or other less proven approaches such as artificial destratification systems (Schladow and Fisher 1995), while watershed-scale improvements to water quality are undertaken.

By linking adult density and limnological features to juvenile density, this study contributes important information towards fully understanding river herring productivity. Because freshwater nursery lakes vary in their productive capacity, there will be limits to population increases from any single restoration activity, and balancing feasibility, cost, potential unintended consequences, and public acceptance with expected results will be required for addressing and prioritizing river herring management strategies. While suitable lake and pond nursery habitats are important, the relevance of riverine and estuarine habitats cannot be discounted. River herring have been shown to exhibit notable plasticity in their early life habitat use, and variability in watershed characteristics can be important for evaluating migration timing and strategies. For example, juveniles are able to exit lakes at an extremely small size and survive by utilizing alternative habitats, especially when nursery lakes are a substantial distance from the ocean (Turner and Limburg 2016). Continued and system-specific monitoring of juvenile density at sites with established natural runs and those with fish passage (e.g., dam removal and fishways) will help determine optimal adult run sizes that yield maximum juvenile densities and are needed to test the temporal validity of the stock–recruitment relationship presented here. More work is also needed to understand how juvenile densities influence individual growth during freshwater residence, as growth estimates, coupled with density estimates, can best identify density-dependent relationships, inform cues to emigration, and ultimately determine marine survival. To restore river herring moving forward, approaches to recovery could beneficially continue to monitor adult and juvenile densities in lakes, restore connectivity to previously uninhabited spawning grounds, and consider changes to habitat quantity and quality in decision making.

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