Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)



NRC Research Press

ARTICLE



# Effects of urbanization of coastal watersheds on growth and condition of juvenile alewives in New England

Rita Monteiro Pierce, Karin E. Limburg, Daniella Hanacek, and Ivan Valiela

**Abstract:** *Alosa pseudoharengus* (alewife) has declined throughout New England. A factor that may be responsible for such stock reductions is urbanization of watersheds discharging into alewife nursery ponds. We found that young-of-the-year (YOY) alewife length, weight, condition factor, and growth rate decreased in relation to increased urban land cover on watersheds of nine Massachusetts and Maine ponds. The watersheds ranged from 3% to 60% urbanized land cover. YOY $\delta^{15}N$ increased significantly in proportion to urbanized land cover on watersheds, suggesting a concrete link between watershed land cover and YOY alewife metrics, which is in agreement with previous knowledge that N discharges from more urbanized watersheds bear higher $\delta^{15}N$. The New England results confirmed results across a wide latitudinal gradient that suggested that the size of YOY alewife decreased as urban land cover on watersheds increased. The dominant influence of urban land cover in the YOY is highlighted by the fact that YOY alewife from ponds with the highest percentage of urban cover reached $\delta^{15}N$ as high as that of adult spawners migrating from the ocean, who feed at higher trophic levels.

**Résumé :** Les gaspareaux (*Alosa pseudoharengus*) sont en déclin partout en Nouvelle-Angleterre, et un facteur qui pourrait être responsable de telles réductions des stocks est l'urbanisation des bassins versants des étangs d'alevinage des gaspareaux. Nous avons constaté que les diminutions de la longueur, de la masse, de l'embonpoint et du taux de croissance des jeunes gaspareaux de l'année sont reliées à une augmentation de la couverture urbaine dans les bassins versants de neuf étangs du Massachusetts et du Maine. La proportion de la couverture urbanisée des bassins versants va de 3 % à 60 %. Les valeurs de $\delta^{15}N$ des jeunes de l'année montrent une augmentation significative proportionnellement à la couverture urbanisée des bassins versants, indiquant un lien concret entre la couverture des bassins versants et des paramètres associés aux gaspareaux de l'année, ce qui concorde avec le fait déjà établi que les apports de N provenant de bassins versants plus urbanisés ont des $\delta^{15}N$ plus élevés. Ces résultats pour la Nouvelle-Angleterre corroborent des résultats obtenus le long d'un large gradient latitudinal qui donnaient à penser que la taille des gaspareaux de l'année diminue parallèlement à l'augmentation de la couverture urbaine dans les bassins versants. L'influence dominante qu'exerce cette dernière sur les jeunes de l'année est toutefois mise en relief par le fait que les gaspareaux de l'année issus d'étangs dont les bassins versants ont les plus hauts pourcentages de couverture urbaine ont des $\delta^{15}N$ aussi élevés que ceux de géniteurs adultes migrant de l'océan qui s'alimentent à des niveaux trophiques plus élevés. [Traduit par la Rédaction]

## Introduction

The alewife (*Alosa pseudoharengus*) once ranked among the most abundant species along the North American east coast, with individual populations estimated in the tens to hundreds of millions (Hall et al. 2012). Coastal alewife populations have been in decline since the 1960s, and dramatically so in the 2000s (Limburg and Waldman 2009; ASMFC 2012). By 2005 the commercial landings of river herring (alewife and its congener the blueback herring (*Alosa aestivalis*)) were only 1% of the 1958 catch (Fig. 1), prompting increased public concern about these stocks of cultural and historical commercial importance. In 2006 the state of Massachusetts approved a 3-year moratorium on river herring, which was extended until further notice. Other states (Connecticut, Rhode Island, New Jersey, and North Carolina) have also closed their fisheries for river herring. The US National Marine Fisheries Service has listed both species of river herring as Species of Concern and is currently considering listing both as Threatened under the Endangered Species Act.

Alewife populations range from the Gulf of St. Lawrence and northern Nova Scotia to North Carolina (Collette and Klein-MacPhee 2002). Anadromous adults run into coastal rivers, estuaries, and ponds in spring (mid-March to mid-May) to spawn, returning to sea shortly thereafter. Eggs hatch within days; juveniles grow throughout the summer in headwater ponds and river sections, and then migrate from rivers and estuaries out to sea, depending on food availability, stream discharge, and water temperature (Richkus 1975; Kosa and Mather 2001). The anadromous life history of alewife exposes the populations to changes in ocean, river, and watershed conditions, and allows the species to play a variety of roles in the environments it uses during its life history. For example, adults migrating in from the sea can provide nutrient subsidies to the streams and ponds where they spawn and often die (Durbin et al. 1979; Walters et al. 2009; Twining et al. 2013). *Alosa* spp. are well known to alter the size structure of zooplankton in lakes and ponds due to size-selective feeding (Brooks and Dodson 1965). These species are also important forage fishes, the

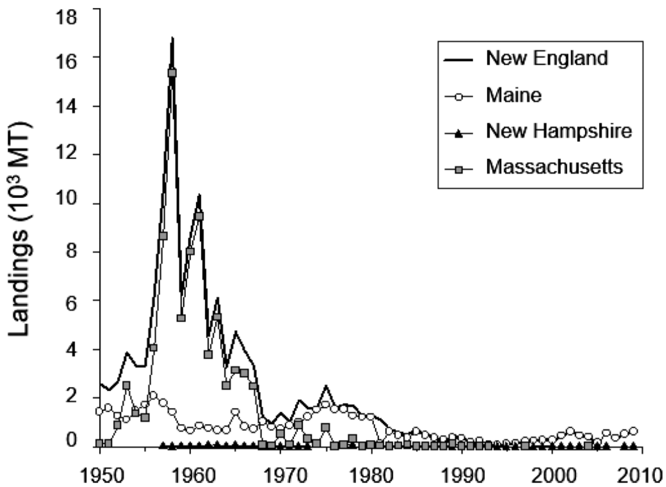
Received 3 November 2018. Accepted 18 September 2019.

**R. Monteiro Pierce* and K.E. Limburg.** College of Environmental Science and Forestry, State University of New York, 1 Forestry Drive, Syracuse, NY 13210, USA.
**D. Hanacek and I. Valiela.** The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA.
**Corresponding authors:** Karin E. Limburg (emails: klimburg@esf.edu) and R. Monteiro Pierce (ritasomonteiro@gmail.com).
*Present address: 106 North Street, Portland, ME 04101, USA.



 Published at www.nrcresearchpress.com/cjfas on 22 September 2019.

**Fig. 1.** Commercial landings of river herring (*Alosa pseudoharengus* and *A. aestivalis* combined) in the northeastern United States (data: ASMFC 2012; NOAA Fisheries, Fisheries Statistics Division 2018).




losses of which have disrupted coastal marine food webs (Limburg and Waldman 2009; Hall et al. 2012; Ames and Lichter 2013).

A number of causes have been suggested for the large reductions in alewife populations (Moring 2005), including lower water levels in streams (Yako et al. 2002), predation, the loss, fragmentation, and degradation of habitat, overfishing, and bycatch (Deegan and Buchsbaum 2005). One other factor that could impair alewife success is reduced water quality associated with increasing urbanization of watersheds discharging into the nursery habitats (Limburg and Schmidt 1990; Fitzgerald et al. 1999; Oczkowski and Nixon 2008; Turner and Limburg 2016). Studies of fish responses to urban gradients have found decreases in diversity and morphometric variables with increasing impervious surface cover or other urban land indicators (Wang et al. 1997; Yoder et al. 1999; Daniels et al. 2002; Utz et al. 2010). Conversion from forested to developed land increases nutrient loads from watersheds into streams and estuaries, lowers water quality (Valiela et al. 1992, 1997; Smith et al. 2003), and reduces anadromous fish habitat (Alberti et al. 2007; Lohse et al. 2008; Coles et al. 2010). Limburg and Schmidt (1990) found inverse correlations between urbanization and alewife egg and larval production in 16 Hudson River tributary watersheds. These results, on aggregate, suggest that the degree of urban development on watersheds discharging into waters adversely affects alewife and seems likely to affect the early stages of young-of-the-year (YOY) fish in particular.

In this paper, we examined how the degree of urbanization of New England coastal watersheds that discharge into nursery ponds affects YOY alewife there. The choice of life stage (near end of first growing season) integrates the factors of production and growth up to the time of emigration from pond to sea, and individuals that are larger and in better condition at egress should have greater chances of survival and hence fitness (Limburg 1996; Sogard 1997).

First, we identified nine coastal ponds receiving discharges from watersheds with a degree of urbanization spanning a wide range (3%–60% of the area of the watersheds). Second, we assessed length, weight, growth rate, and condition factor in populations of YOY alewife within the nine ponds and then compared these morphometric variables to the degree of urbanization on the contributing watersheds. These data test the hypothesis that juvenile alewife exhibit signs of poorer condition in waters receiving discharges from watersheds with a greater degree of urbanized land covers. Third, to more unambiguously link the possible impairment of YOY performance to variables directly associated with urbanized land uses, we measured nitrogen stable isotope ratios ($\delta^{15}N$) in YOY alewife collected from each of the nursery ponds. Assessments of $\delta^{15}N$ have been used for multiple purposes (Peterson and Fry 1987; Fry 2006), one of which is to establish position within trophic webs, and a second is to reveal contributions from different sources of N discharged into water bodies. Wastewater-derived N $\delta^{15}N$ values range from +10‰ to +20‰, fertilizer used in agricultural land from −3‰ to +3‰, and atmospheric deposition within +2‰ to +8‰ (McClelland et al. 1997; McClelland and Valiela 1998; Cole et al. 2006). Heavier $\delta^{15}N$ values follow increasing urbanization, largely owing to the influence of elevated $\delta^{15}N$ signatures in wastewater, in Cape Cod (McClelland et al. 1997; Griffin and Valiela 2001; Cole et al. 2006; Martinetto et al. 2006) and elsewhere (Limburg et al. 2005; Ulseth and Hershey 2005; Vander Zanden et al. 2005; Reynolds-Vargas et al. 2006; Dillon and Chanton 2008). Therefore, $\delta^{15}N$ is a useful tool to demonstrate concretely the link between juvenile alewife in water bodies and the mix of specific N sources associated with urbanization that are discharged from contributing watersheds. Our primary focus was to use alewife $\delta^{15}N$ as an index of urbanization impact, but we also examined carbon isotopic ratios as a potential secondary tracer (Oczkowski et al. 2014).

## Methods

### Site description and land use on watersheds

This study was conducted at nine areas used by alewives as nursery habitats along the coast of New England (Fig. 2). Six sites in Cape Cod, Massachusetts, received spawner adults entering from Cape Cod Bay (Herring River, Herring Brook, Stony Brook) or Vineyard Sound (Oyster Pond, Coonamessett Pond, Johns Pond). Three other watersheds were within the Androscoggin River basin (Marshall Pond, Taylor Pond, Sabattus Pond) in southern Maine. These sites were selected because land cover on the contributing watersheds showed different degrees of urbanization, and the range of land use was representative of the Northwest Atlantic coastal region of North America (Table 1). Watershed area ranged from 1.3 to 81.1 km², of which urbanized area varied between 3.1% to 60.4%. Area of the ponds ranged between 0.28 and 7.98 km².

To quantify the degree of urbanization in each watershed, Monteiro (2011) delineated the watershed for each site using water table contours from the US Geological Survey (Cape Cod sites, Savoie 1995), with boundaries previously determined using 1:24 000 scale contours (http://megis.maine.gov/catalog/, Maine study sites). Monteiro (2011) used the 2001 National Land Cover Data set (NLCD2001 version 2), developed by the Multi-Resolution Land Characteristics Consortium (http://www.mrlc.gov), with 30 m resolution considering 16 categories, based on satellite imagery acquired in 2001. Urbanized area in each watershed (Table 1) was estimated by adding areas of open space, barren land, and low, medium, and high intensity residential land use, using geographic information system (GIS) software (ArcGIS 10.1, ESRI, Redlands, California).

### YOY alewife

Juvenile alewives departing to the sea were sampled in all study sites between August and October 2008 (Table 2). The staggered dates were due to differences in weather conditions that caused the fish to emigrate, and time of sampling was advised by local fish wardens. We used a variety of gear, including dip nets 0.5 m wide, 1 cm mesh, a small (1 m) scap net, and a 5 m × 1.3 m straight seine (1 cm mesh), deployed at the outlet of each pond, collecting until at least 20 individuals were obtained. Between 20 and 100 fish from each site were caught and frozen immediately.

To assess condition of YOY alewives, we recorded, for each fish collected in each of the nine sites, total length (TL) to the nearest millimetre and wet weight (WW) to the nearest 0.1 g. Fulton condition factor, $K = 10^5 \times WW \times TL^{-3}$, was calculated as a measurement of physical condition (Le Cren 1951; Pope and Kruse 2007). Fish with higher $K$ are heavier at a given length than those with lower $K$.

**Fig. 2.** Location of the nine study sites on Cape Cod and southern Maine: 1, Oyster Pond; 2, Coonamessett Pond; 3, Johns Pond; 4, Stony Brook; 5, Herring Brook; 6, Herring River; 7, Marshall Pond; 8, Taylor Pond; and 9, Sabattus Pond. Map shows developed and undeveloped areas on Cape Cod and historical river herring runs (data: www.mass.gov/mgis; ASMFC 2012). [Colour online.]

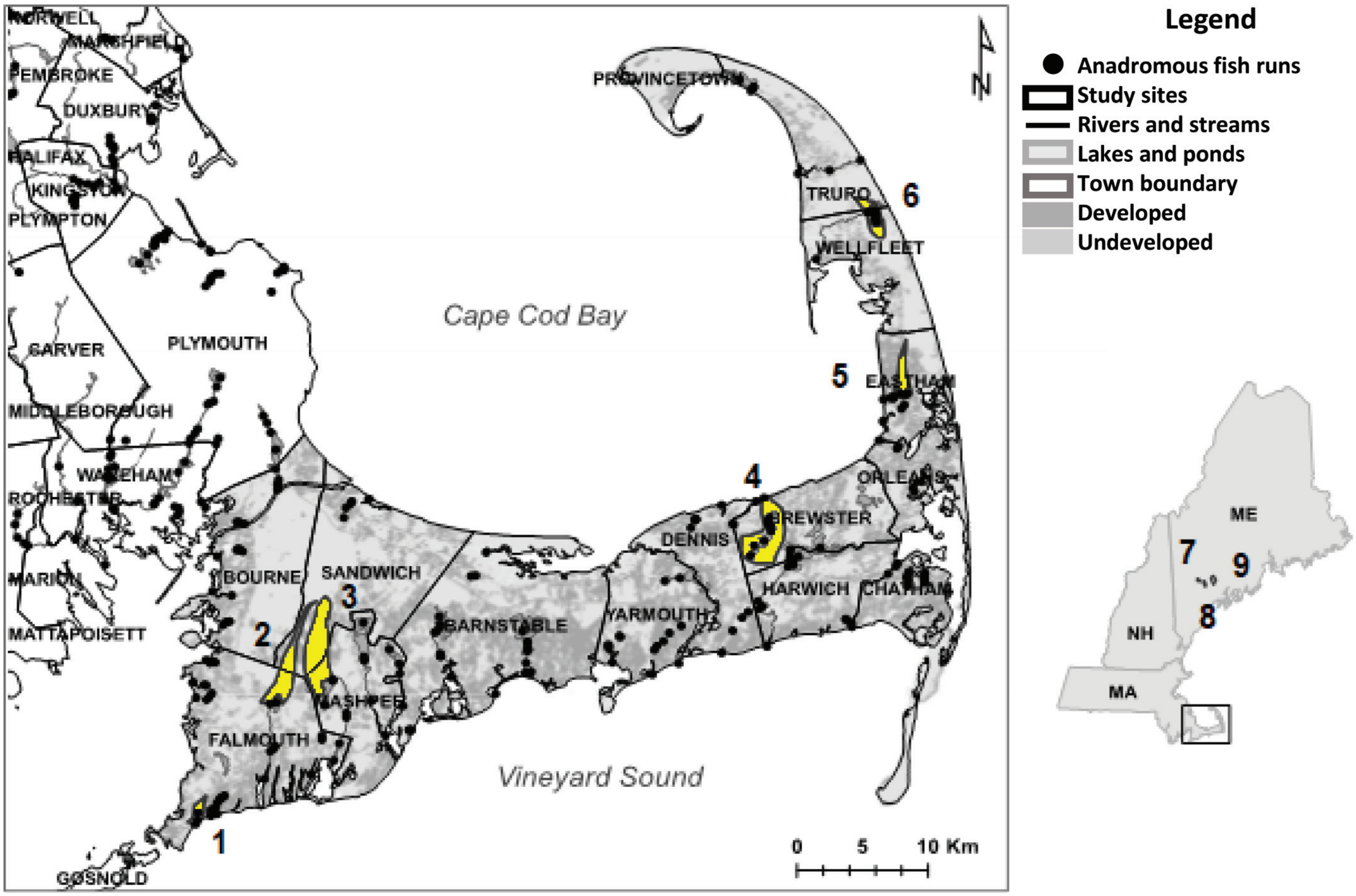



**Table 1.** Characteristics of the study sites used as nursery areas by alewives.

| Site | % Urbanized area | Pond volume ($10^3$ $m^3$) | Pond area ($km^2$) | Pond perimeter (km) | Watershed area ($km^2$) | Mean depth (m) | Max. depth (m) |
|---|---|---|---|---|---|---|---|
| **Maine** | | | | | | | |
| Marshall Pond | 3.1 | 2 176 | 0.64 | 11.27 | 22.6 | 3.4 | 12.2 |
| Taylor Pond | 6.8 | 13 728 | 2.64 | 8.69 | 37.7 | 5.2 | 13.4 |
| Sabattus Pond | 10.2 | 34 314 | 7.98 | 22.85 | 81.1 | 4.3 | 5.8 |
| **Massachusetts** | | | | | | | |
| Oyster Pond | 34.7 | 840 | 0.28 | — | 1.3 | 3 | 6.2 |
| Coonamessett Pond | 45.2 | 3 762 | 0.66 | 4.82 | 6.3 | 5.7 | 10.4 |
| Johns Pond | 60.4 | 10 823 | 1.37 | 7.61 | 10.1 | 7.9 | 19.8 |
| Stony Brook | 14.6 | 4 980 | 1.66 | — | 10.4 | 3 | 9.1 |
| Herring Brook | 59.9 | 2 156 | 0.44 | 3.33 | 2.3 | 4.9* | 11 |
| Herring River | 7.1 | 4 852 | 0.67 | — | 2.4 | 9.5 | 18.9 |

*Mean depth of Herring River site was not available, was assumed to be half of maximum depth.

To measure age of YOY, pairs of sagittal otoliths were dissected from the fish, cleaned of any debris or connective tissue, triple-rinsed in ultrapure Milli-Q water, air dried, and stored in plastic bags. Each otolith was then mounted on a petrographic slide with cyanoacrylate glue and ground to expose the core and all the daily growth increments (DGIs), and polished to 3 μm with lapping film at the Woods Hole Oceanographic Institution (Woods Hole, Massachusetts). Age was determined as the mean value of two countings of otolith DGIs at × 400 magnification (validated by KL on known-age YOY *Alosa* (Limburg 1994)). Ages were further verified by random samples in which previously aged otoliths were photographed and daily increments counted "blind" (i.e., without knowing the previously determined age). If age readings for an individual otolith were more than 10% apart, it was re-counted, and final age was determined as the average of three or more readings.

To estimate growth rates of YOY, we determined the age of each individual by counting otolith DGIs. Daily growth rate was computed by subtracting the estimated length at hatch (3.7 mm, the mean of a range of 2.5 to 5.0 mm; Jones et al. 1978) from total length and dividing by age.

**Table 2.** Dates of observations in 2008 of spawning adult alewives and emigrating young of the year (YOY) in each of the nine study sites, total length, wet mass, and age of YOY samples.

| Site | Date when spawning adults were observed | Date when migrating YOY were collected | YOY total length* (mm) | YOY weight* (g) | Mean age* (days) |
|---|---|---|---|---|---|
| **Maine** | | | | | |
| Marshall Pond | 15 May | 15 Aug. | 74.5 (4.9) | 3.3 (0.8) | 73 (4.9) |
| Taylor Pond | 15 May | 30 Sep. | 122.3 (7.9) | 15.6 (3.0) | 96 (6.7) |
| Sabattus Pond | 15 May | 23 Sep. | 105 (19.5) | 10.4 (4.8) | 99 (10.6) |
| **Massachusetts** | | | | | |
| Oyster Pond | 3 Mar. | 27 Sep. | 80.7 (9.1) | 4.4 (1.5) | 114 (11.7) |
| Coonamessett Pond | 18 Apr. | 28 Oct. | 67.9 (6.9) | 2.3 (0.7) | 120 (7.7) |
| Johns Pond | 2 Apr. | 29 Sep. | 56.1 (3.2) | 1.1 (0.3) | 104 (6.5) |
| Stony Brook | 10 Apr. | 27 Sep. | 84.4 (5.1) | 4.7 (0.9) | 103 (5.1) |
| Herring Brook | 10 Apr. | 2 Sep. | 64.6 (6.8) | 2.1 (0.7) | 98 (7.0) |
| Herring River | 23 Apr. | 27 Sep. | 97.8 (7.1) | 7.8 (2.0) | 115 (7.4) |

*YOY metrics are means (± standard deviation). Adults were collected in a separate study (Monteiro 2011).

### Stable isotope analyses

We measured $\delta^{15}N$ and $\delta^{13}C$ on dorsal white muscle tissue of 20 alewives per site. For each site, five fish were analyzed individually, and 15 fish were grouped into three pooled samples with no repetition, resulting in a total of eight muscle tissue samples per study site. (Due to budget limitations, we could not analyze all fish individually.) Tissue samples were dried at 60 °C for 48 h to a constant weight, and then homogenized into a fine powder using a mortar and pestle, weighed, and loaded into tin capsules for combustion and further stable isotope analysis. Stable isotope analyses were conducted using a Europa ANCA-SL elemental analyzer – gas chromatograph preparation system attached to a continuous-flow Europa 20–20 gas source stable isotope ratio mass spectrometer, at the Stable Isotope Laboratory at the Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts. The isotope ratios were expressed as $\delta X$ (‰) = $[(R_{sample} / R_{standard}) - 1] \times 10^3$, where $X$ is $^{15}N$ or $^{13}C$, and $R$ is the ratio of $^{15}N/^{14}N$ or of $^{13}C/^{12}C$, where standard references are atmospheric $N_2$ and carbon in PeeDee limestone (Peterson and Fry 1987).

In a separate related study, adult alewife entering these watersheds from the Atlantic Ocean in March–May to spawn were also collected and analyzed for stable isotope ratios of C and N (details in Monteiro 2011). Of these, 12 adults per site were included here to compare with the YOY, testing the hypothesis that marine-origin $\delta^{15}N$ in adult spawners did not relate to within-watershed urbanization.

### Statistical analyses

Analyses were conducted in Excel (Microsoft Corp.), Statistica (TIBCO Software, Inc.), and the R programming language (R Core Team 2019). To determine whether isotopic signature, fish metrics, condition factor $K$, and growth rates of juvenile alewives were related to percentage of urbanized land use on watersheds, we performed linear regression analyses using the mean value of each study site (type I). $p$ values less than 0.05 were accepted as significant. We also further explored the data sets with linear mixed models using the R packages lme4 (Bates et al. 2019) and lmerTest (Kuznetsova et al. 2019) to test for random effects of pond and sampling date, since the former differed geographically and the latter ranged over 2 months. This allowed us to use all the data and to test the relative influences of age, urbanization, and possible interactions.

For the isotopic signature of juvenile fish, means and variance between individual ($N$ = 5/site) and pooled samples ($N$ = 3/site) were compared for each watershed. In the cases where means of individual and pooled samples were significantly different ($p > 0.05$), only the five individual data points were used. Otherwise, all data points were treated as replicates in determining the mean value per site, which were then used in the regression analysis for stable isotope data.

Means of total lengths, weights, condition factor $K$, and growth rates (mm·day$^{-1}$) within each site were regressed on percent watershed urban cover. Growth rates were also regressed on mean YOY $\delta^{15}N$ per site, testing whether the heavier isotopic ratios (from more urban dietary sources) were correlated with decreased growth rates. Finally, YOY lengths were compared with mean lengths at first egress to ocean reported by Turner and Limburg (2016) as a function of percent watershed urban cover, and similarly, YOY $\delta^{15}N$ was compared with adult $\delta^{15}N$ as a function of percent watershed urban cover.

## Results

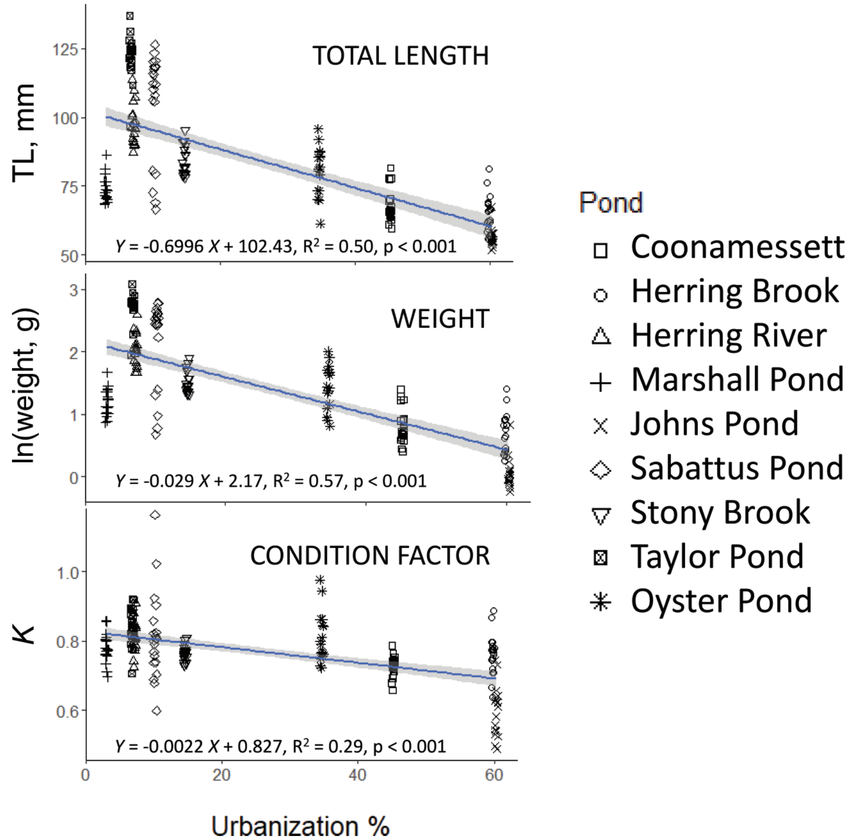
### Effects of degree of watershed urbanization on morphometry of YOY alewife

Measurements of size and weight of YOY alewife differed widely among ponds (Table 2) and made it feasible to test whether there were relationships between measures of YOY length, wet weight, and condition factor (Fig. 3) and the degree of urbanized land cover on watersheds. Increased watershed urbanization was associated with significant decreases in total length, wet weight, and condition factor (Fig. 3). Values for total length and wet weight (but not $K$) measured in fish in Maine tended to be more variable than in fish measured in Massachusetts water bodies (Fig. 3). The large variability in the Maine data could be related to larger geomorphic differences among the Massachusetts and Maine sites (Table 1). Linear mixed model analysis identified significant effects of fish age, percent watershed urbanization, and their interaction on total length and fish growth rate, but with only additive effects of age and percent urbanization influencing ln(weight) and Fulton condition factor $K$ ($p < 0.001$). Best models (evaluated by Bayesian Information Criteria) included both pond (i.e., location) and sampling date (i.e., time in the season).

### Effect of degree of watershed urban land cover on YOY growth rates

Growth rates of YOY alewife, calculated from length (Fig. 3, top) and age (Table 2), decreased nonlinearly in ponds receiving discharges from watersheds with more urbanized land covers (Fig. 4, top). Growth rates of consumers often decrease with age or size (Valiela 2015), so differences in age of YOY alewife sampled (Table 2) could be partially responsible for changes such as those shown in Fig. 4. To determine whether the decreased YOY growth (Fig. 4) could be related to differences in YOY size or age, Monteiro (2011) ran regressions on Cape Cod sites and found no relationship between growth rate and YOY alewife age ($F$ = 2.5, $p$ = 0.15) or of $K$ ($F$ = 0.13, $p$ = 0.73) and YOY alewife age. Similarly, there was no apparent relationship between mean age and mean total length (Table 2), and inspection of age:length plots within individual watersheds showed great scatter (not shown). Nevertheless, linear

**Fig. 3.** Total length (top panel), wet weight (middle panel), and Fulton condition factor *K* (bottom panel) of young-of-the-year alewife plotted versus percent urbanized watershed cover. See text for discussion of mixed effects model results.




mixed modeling, where individuals within ponds are considered, found significant relationships of age, percent urbanization, and their interaction term on growth rates when ponds and sampling date were treated as random factors (*p* of all terms <10⁴, with Pond accounting for 12% and Date for 13.5% of variance).

### Link of stable isotope signatures and urbanization of watersheds

The δ$^{15}$N values measured in alewife muscle tissue were significantly higher in ponds whose watersheds had greater urban land cover (Fig. 5, top). The robust relationship of δ$^{15}$N and degree of watershed urbanization emerged in spite of the large differences in characteristics of watersheds and water bodies sampled (Table 1). Geomorphic pond characteristics and isotopic signatures in the YOY alewife were not significantly related (Monteiro 2011). In contrast, δ$^{13}$C did not provide much information as a tracer of urbanization or landscape effects, because there was no significant link between δ$^{13}$C and degree of urban cover on contributing watersheds (Fig. 5, bottom) or to pond morphometry (data not shown).

YOY alewife size, growth, and condition all decreased in ponds whose watersheds were more urbanized (Fig. 3). The implied strong linkage between watershed urbanization and the YOY alewife population is further emphasized by the significant decrease in growth rate of YOY alewife in relation to δ$^{15}$N values measured in the alewife YOY (Fig. 4, bottom).

## Discussion

The clearly significant link of decreased growth rates and condition factor of YOY alewife to increased urban land coverage and δ$^{15}$N is likely to result, at least in part, from differences in N inputs from contributing watersheds, with associated deleterious effects on water quality. Watershed discharges with heavier δ$^{15}$N values are associated with eutrophication that may impair water quality in receiving waters (McClelland et al. 1997; McClelland and Valiela 1998; Griffin and Valiela 2001; Cole et al. 2006; Martinetto et al. 2006; Valiela 2015). The significant relationship of fish δ$^{15}$N and degree of urbanization in our study watersheds (Fig. 5, top) resulting from a land-use effect (i.e., heavier allochthonous δ$^{15}$N signatures in organisms consumed by the young fish) appears to bear this out. The results presented here demonstrate that dominant and deleterious effects associated with discharges from urbanizing watersheds can affect populations of consumers — in our case, juvenile alewives — that are important members of aquatic food webs (Cole et al. 2006) and are consequential as fishery stock and finfish food supplies.

Alternatively, the heavier δ$^{15}$N signatures could result from trophic effects (larger fish feeding higher in food webs (Peterson and Fry 1987; Fry 2006)). For example, differences among ponds could lead to differences in growth, and larger YOY alewife fed higher up in the aquatic food web. The increase in δ$^{15}$N in YOY alewife (Fig. 5, top) with increasing percent watershed urban land cover was about 5‰–6‰, values that would be interpreted as a shift of nearly two trophic steps up the food web (Peterson and Fry 1987; Fry 2006). More carnivorous diets might lead to faster growth (Griffin and Valiela 2001), but instead we found significantly lower growth rates (Fig. 4). However, there was no demonstrable link of age and length in the YOY alewife. In this case, δ$^{15}$N did not behave as a reliable indicator of trophic position, as it has in other aquatic systems (Peterson and Fry 1987), but instead reflected the contrasting isotopic inputs from watersheds with different degrees of urbanization.

Eutrophication (over-fertilization) typically stimulates algal blooms, which then die and decay, consuming dissolved oxygen

**Fig. 4.** Growth rate of young-of-the-year alewife versus $\delta^{15}$N of muscle tissue (bottom). Growth rate of young-of-the-year alewife versus percentage of the watershed with urban cover (top). OP, Oyster Pond; CP, Coonamessett Pond; JP, Johns Pond; SB, Stony Brook; HB, Herring Brook; HR, Herring River; MP, Marshall Pond; TP, Taylor Pond; SP, Sabattus Pond. Error bars are standard deviation.

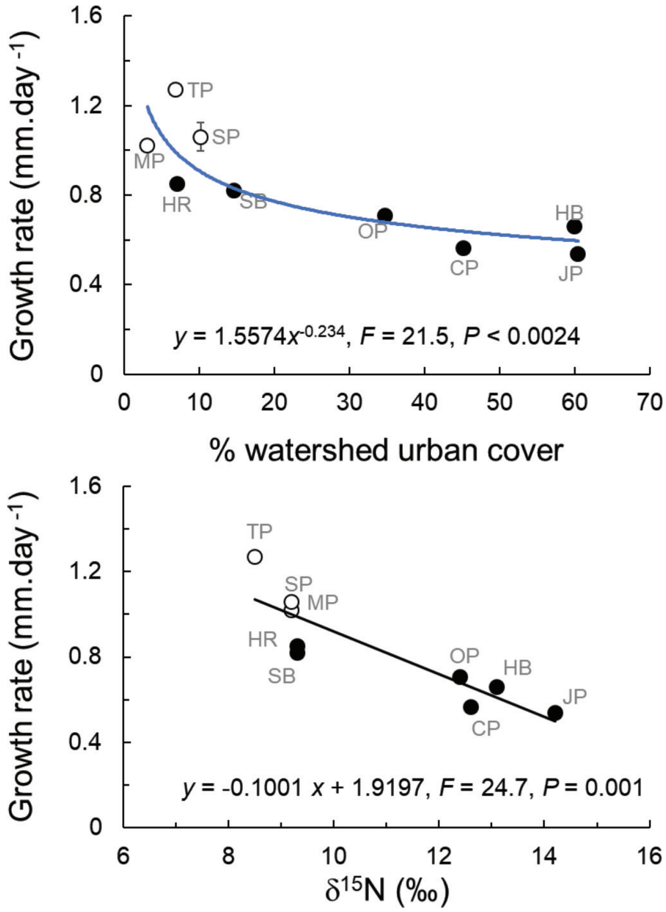
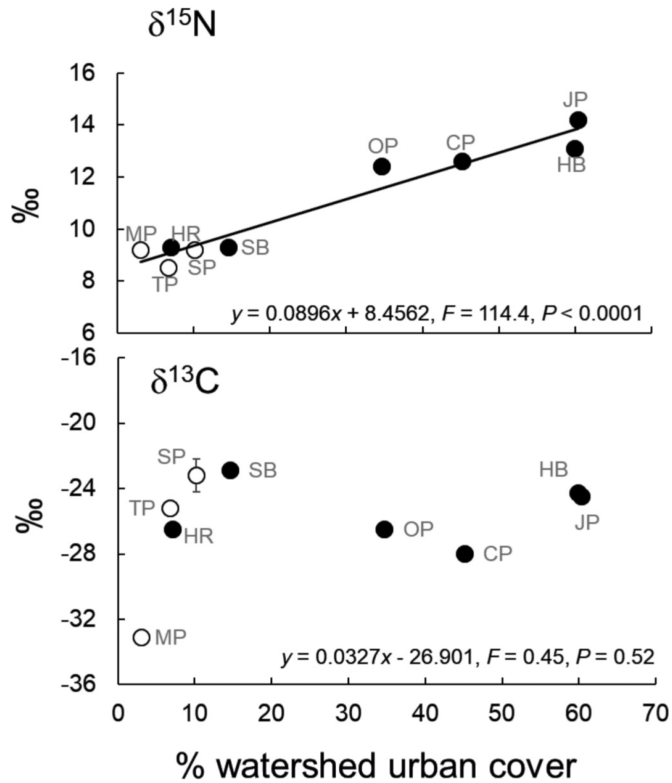



**Fig. 5.** $\delta^{15}$N (top) and $\delta^{13}$C (bottom) ($\bar{x} \pm$ se) in muscle tissue of young-of-the-year alewife collected in 2008 versus percent of the watershed containing urban land covers: Massachusetts sites (black circles), Maine sites (white circles). OP, Oyster Pond; CP, Coonamessett Pond; JP, Johns Pond; SB, Stony Brook; HB, Herring Brook; HR, Herring River; MP, Marshall Pond; TP, Taylor Pond; SP, Sabattus Pond. Standard errors were smaller than symbols in some sites.



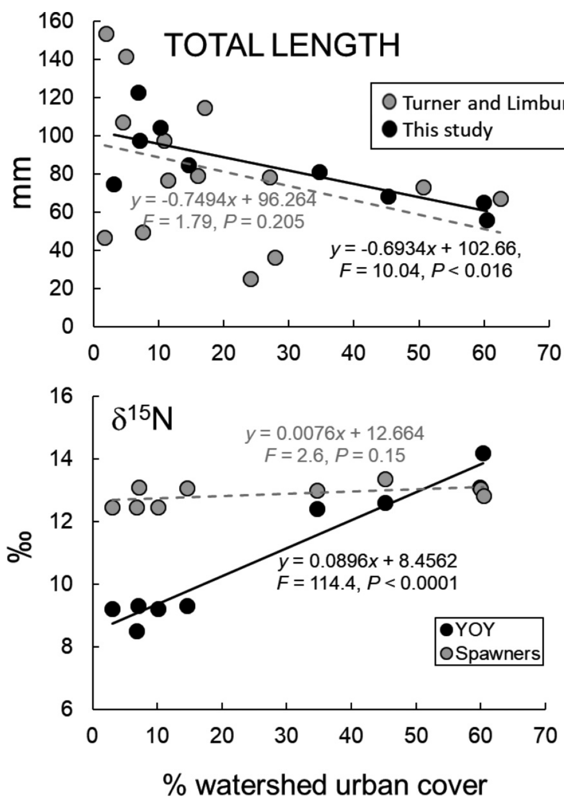

(DO) from the water column. Hypoxia is generally defined as DO concentrations falling below 2 mg·L$^{-1}$, a level that adversely affects many higher aquatic organisms (Diaz and Rosenberg 2008). Some of the Cape Cod ponds in our study, notably those in the Oyster Pond (34.7% urban cover), Coonamessett Pond (45.2%), Herring Brook (59.9%), and Johns Pond (60.4%) catchments, were identified in the study year as having water quality issues, specifically elevated nutrients (MADWM 2008) and low summertime DO (Eichner 2009). Interestingly, the otoliths of YOY alewife from Herring Brook and Oyster Pond displayed distinctive periods of very slow mid-summer growth, in which the daily growth increments became very thin and translucent (a hallmark of stress; Rice et al. 1985). Otolith chemistry analyzed for one of the Herring Brook YOY showed elevated levels of manganese, a chemical proxy for hypoxia exposure (Limburg et al. 2015). These lines of evidence suggest that those YOY alewife were likely exposed to low DO conditions and experienced a "growth squeeze" during extended hypoxic episodes, and likely could not exit the ponds until autumn rains raised water levels at the outlet.

In this work, we report measurements of length of YOY alewife for sites in Massachusetts and Maine; we can extend the geographic reach of these results by comparison with similar measurements done across alewife nursery sites from Florida to Maine (Fig. 6, top), as reported by Turner and Limburg (2016). First, the Massachusetts and Maine results fit well within the larger scatter of the broader geographic survey, and best-fit slopes were similar. It seems reasonable to conclude that the finding of decreased size achieved by YOY alewife in ponds affected by inputs from more urban watersheds is applicable across a wide geographic range. Second, both data sets reveal much larger variation in less developed settings; there, other factors are likely to affect alewife YOY performance, and their effects can be large and variable. Both data sets also reveal that urban development on watersheds can become a dominant effect, overcoming other controls: as urbanization increases, alewife YOY performance — in this example portrayed by length — converges on lower values, overwhelming the role of other factors.

We note that other factors can affect fish size at age, including conspecific density and (or) co-occurrence with similar species. In the ponds we studied, densities were unknown, but Oyster Pond, Herring Brook, and Herring River contain only alewife, whereas Coonamessett Pond, Johns Pond, and Stony Brook also support blueback herring (MADMF 2016). These span a range of volumes and areas (Table 1), and no distinctive patterns were apparent. Although we cannot rule out these other factors, nevertheless the evidence suggests that habitat characteristics (oxygen, temperature, conductivity, turbidity, etc.) related to percent urban cover played a dominant role in the patterns of fish production we observed.

Twining et al. (2013) noted the diverse importance of incoming spawners in the case of anadromous fish, including alewife, in nursery ecosystems. To ascertain whether populations of adult alewife retained legacy effects from their nursery areas, Monteiro (2011) sampled stable nitrogen isotopic signatures of spawner ale-

**Fig. 6.** Total length (top) of young-of-the-year (YOY) fish against percent watershed urban cover for alewife from this work (black circles) and similar data from Turner and Limburg (2016) (grey circles). $\delta^{15}N$ (bottom) in muscle tissue of juvenile (black circles) and adult spawning (grey circles) alewife collected in ponds in Massachusetts and Maine.




wife that were entering the study ponds (Fig. 6, bottom). Two points emerge from this comparison. First, there was no significant relation between $\delta^{15}N$ and percent watershed urban cover in adults entering spawning sites, suggesting that the signatures that clearly reflected pond of origin for YOY fish (Fig. 3, top) were effectively lost in the 3 or more years that the spawners spend at sea (where typical $\delta^{15}N$ values are about 13‰; Sherwood and Rose 2005). Adult signatures, therefore, show no legacy effects, at least in the case of $\delta^{15}N$. Second, the $\delta^{15}N$ of adult alewife are about two trophic steps higher than those of YOY fish from non-urban sites (Fig. 3). This is reasonable, because the adults were much larger (mean 265 mm, range 220–290 mm) than the YOY alewife and feed farther up the trophic web at sea (Collette and Klein-MacPhee 2002). For adult alewife that differ sufficiently in size compared with YOY, $\delta^{15}N$ does reflect trophic level position, unlike the case of the much smaller YOY.

The stable isotope and morphometric results presented here suggest that discharges from watersheds with increased urban land uses led to reduced size, condition, and growth of juvenile alewife and that these effects occurred across sites with a large variety of geomorphic settings and conditions. The joint application of morphometric, age and (or) growth, and stable isotope evidence makes clear that the effects are significant. The data also provide an example of the use of isotopic data for basic understanding of ecological effects, as a reliable indicator useful to assess landscape-level effects on important species, and as a relatively practical means to inform managers of possible stock impairment.

The implications of these findings could have important consequences for alewives (in this case study) and for anadromous fishes in general. Because smaller fish are more vulnerable to predation (Sogard 1997) and more likely to have poorer wintertime condition and hence lower survival (Dutil and Lambert 2000), these factors can contribute to reduced fitness of emigrating individuals (Limburg 1996). Even if surviving, if smaller size at egress is not compensated for by higher growth at sea, smaller females would, *ceteris paribus*, have smaller roe sacs and thus lower fecundity. Populations would therefore be adversely affected both in terms of lowered abundances and fecundity. Turner and Limburg (2016), surveying river herring from Florida to Maine, found that river herring total length at egress was positively correlated with watershed size, estuary area, and length of accessible river, and negatively correlated with urban land cover and with latitude. Their findings place the present study in a broader context, and together, both studies point to the need for multiple watershed protections that include reducing the impact of urbanization and improving access to spawning and nursery habitats.

## Acknowledgements

We thank the many people who provided help for this project in the laboratory and the field, especially, M. Brown of the Maine Department of Marine Resources; M. Armstrong, B. Chase, J. Hughes, and C. Martinsen of the Massachusetts Division of Marine Fisheries (MADMF), for critical administrative and field support. S. Turner (MADMF) provided critical information on fishes and passage improvements in the Cape Cod watersheds. We thank S. Thorrold for the use of facilities for otolith analyses at his Fish Ecology Laboratory at the Woods Hole Oceanographic Institution (Woods Hole, Massachusetts). We also thank B.J. Peterson, The Ecosystems Center, MBL; P. Martinetto, Universidad Nacional de Mar del Plata, Argentina; three anonymous reviewers; and the Associate Editor for improving the manuscript with helpful advice. A portion of this research was supported by an award from the Estuarine Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanic and Atmospheric Administration.

## References

Alberti, M., Booth, D., Hill, K., Coburn, B., Avolio, C., Coe, S., and Spirandelli, D. 2007. The impact of urban patterns on aquatic ecosystems: an empirical analysis in Puget lowland sub-basins. Landsc. Urban Plan. **80**: 345–361. doi:10.1016/j.landurbplan.2006.08.001.

Ames, T.P., and Lichter, J. 2013. Gadids and alewives: structure within complexity in the Gulf of Maine. Fish. Res. **141**: 70–78. doi:10.1016/j.fishres.2012.09.011.

ASMFC. 2012. River herring benchmark stock assessment. Stock assessment report No. 12-02 of the Atlantic States Marine Fisheries Commission, Arlington, Va., USA.

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2019. lme4: linear mixed models using 'Eigen' and S4, version 1.1-21. Available from https://github.com/lme4/lme4/.

Brooks, J.L., and Dodson, S.I. 1965. Predation, body size, and composition of plankton. Science, **150**(3692): 28–35. doi:10.1126/science.150.3692.28. PMID: 17829740.

Cole, M.L., Kroeger, K.D., McClelland, J.W., and Valiela, I. 2006. Effects of watershed land use on nitrogen concentrations and $\delta^{15}N$ nitrogen in groundwater. Biogeochemistry, **77**: 199–215. doi:10.1007/s10533-005-1036-2.

Coles, J.F., Cuffney, T.F., McMahon, G., and Rosiu, C.J. 2010. Judging a brook by its cover: the relation between ecological condition of a stream and urban land cover in New England. Northeast. Nat. **17**: 29–48. doi:10.1656/045.017.0103.

Collette, B.B., and Klein-MacPhee, G. 2002. Bigelow and Schroeder's fishes of the Gulf of Maine. 3rd ed. Smithsonian Institution Press, Washington, D.C., USA.

Daniels, R.A., Riva-Murray, K., Halliwell, D.B., Vana-Miller, D.L., and Bilger, M.D. 2002. An index of biological integrity for northern Mid-Atlantic Slope drainages. Trans. Am. Fish. Soc. **131**: 1044–1060. doi:10.1577/1548-8659(2002)131<1044:AIOBIF>2.0.CO;2.

Deegan, L.A., and Buchsbaum, R. 2005. The effect of habitat loss and degradation on fisheries. *In* The decline of fisheries resources in New England: evaluating the impact of overfishing, contamination, and habitat degradation. *Edited by* R. Buchsbaum, J. Pederson, and W.E. Robinson. MIT Sea Grant College Program Publication, Cambridge, Mass., USA. pp. 67–96.

Diaz, R.J., and Rosenberg, R. 2008. Spreading dead zones and consequences for marine ecosystems. Science, **321**(5891): 926–929. doi:10.1126/science.1156401. PMID:18703733.

Dillon, K.S., and Chanton, J.P. 2008. Nitrogen stable isotopes of macrophytes assess stormwater nitrogen inputs to an urbanized estuary. Estuar. Coasts, **31**: 360–370. doi:10.1007/s12237-007-9028-1.

Durbin, A.G., Nixon, S.W., and Oviatt, C.A. 1979. Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. Ecology, **60**: 8–17. doi:10.2307/1936461.

Dutil, J.-D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **57**(4): 826–836. doi:10.1139/f00-023.

Eichner, E. 2009. Eastham freshwater ponds: water quality status and recommendations for future activities. Final Report to Town of Eastham, MA. Coastal Systems Group, University of Massachusetts School of Marine Science and Technology, New Bedford, Mass., USA.

Fitzgerald, D.G., Lanno, R.P., and Dixon, D.G. 1999. A comparison of a sentinel species evaluation using creek chub (*Semotilus atromaculatus* Mitchill) to a fish community evaluation for the initial identification of environmental stressors in small streams. Ecotoxicology, **8**: 33–48. doi:10.1023/A:1008853413528.

Fry, B. 2006. Stable isotope ecology. Springer Science+Business Media LLC, New York, USA.

Griffin, M.P.A., and Valiela, I. 2001. $\delta^{15}N$ isotope studies of life history and trophic position of *Fundulus heteroclitus* and *Menidia menidia*. Mar. Ecol. Prog. Ser. **214**: 299–305. doi:10.3354/meps214299.

Hall, C.J., Jordaan, A., and Frisk, M.G. 2012. Centuries of anadromous forage fish loss: consequences for ecosystem connectivity and productivity. BioScience, **62**: 723–731. doi:10.1525/bio.2012.62.8.5.

Jones, P.W., Martin, F.D., and Hardy, J.D., Jr. 1978. Acipenseridae through Ictaluridae. Vol. 1. *In* Development of fishes of the Mid-Atlantic Bight: an atlas of egg, larval and juvenile stages. U.S. Fish and Wildlife Service, Biological Services Program. FWS/OBS-78/12.

Kosa, J.T., and Mather, M.E. 2001. Processes contributing to variability in regional patterns of juvenile river herring abundance across small coastal systems. Trans. Am. Fish. Soc. **130**: 600–619. doi:10.1577/1548-8659(2001)130<0600:PCTVIR>2.0.CO;2.

Kuznetsova, A., Brockhoff, P., and Christensen, R. 2019. lmerTest: tests in linear mixed effects models, version 3.1-0. Available from https://github.com/runehaubo/lmerTestR.

Le Cren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. **20**: 201–219. doi:10.2307/1540.

Limburg, K.E. 1994. Ecological constraints on growth and movement of young-of year American shad, *Alosa sapidissima* (Wilson) in the Hudson River, New York. Ph.D. dissertation, Cornell University, Ithaca, New York, USA.

Limburg, K.E. 1996. Growth and migration of 0-year American shad (*Alosa sapidissima*) in the Hudson River estuary: otolith microstructural analysis. Can. J. Fish. Aquat. Sci. **53**(1): 220–238. doi:10.1139/f95-160.

Limburg, K.E., and Schmidt, R.E. 1990. Patterns of fish spawning in Hudson River tributaries: response to an urban gradient? Ecology, **71**: 1238–1245. doi:10.2307/1938260.

Limburg, K.E., and Waldman, J.R. 2009. Dramatic declines in North Atlantic diadromous fishes. BioScience, **59**: 955–965. doi:10.1525/bio.2009.59.11.7.

Limburg, K.E., Stainbrook, K.M., Erickson, J.D., and Gowdy, J.M. 2005. Urbanization consequences: case studies in the Hudson Valley. *In* The effects of urbanization on stream ecosystems. *Edited by* L.R. Brown, R.H. Gray, R.M. Hughes, and M. Meador. Am. Fish. Soc. Symp. 47. pp. 23–37.

Limburg, K.E., Walther, B.D., Lu, Z., Jackman, G., Mohan, J., Walther, Y., et al. 2015. In search of the dead zone: use of otoliths for tracking fish exposure to hypoxia. J. Mar. Syst. **141**: 167–178. doi:10.1016/j.jmarsys.2014.02.014.

Lohse, K.A., Newburn, D.A., Opperman, J.J., and Merenlender, A.M. 2008. Forecasting relative impacts of land use on anadromous fish habitat to guide conservation planning. Ecol. Appl. **18**: 467–482. doi:10.1890/07-0354.1. PMID:18488609.

MADMF. 2016. Cape Cod watersheds. Massachusetts Division of Marine Fisheries. Available from https://www.mass.gov/files/documents/2016/08/no/tr16-anad-p2-cape-cod.pdf [accessed 23 May 2019].

MADWM. 2008. Final Massachusetts Year 2008 Integrated List of Waters. Final Listing of the Condition of Massachusetts' Waters Pursuant to Sections 303(d) and 305(b) of the Clean Water Act. Massachusetts Division of Watershed Management, Watershed Planning Program, Worcester, Mass., USA.

Martinetto, P., Teichberg, M., and Valiela, I. 2006. Coupling of estuarine benthic and pelagic food webs to land-derived nitrogen sources in Waquoit Bay, Massachusetts, USA. Mar. Ecol. Progr. Ser. **307**: 37–48. doi:10.3354/meps307037.

McClelland, J.W., and Valiela, I. 1998. Linking nitrogen in estuarine producers to land-derived sources. Limnol. Oceanogr. **43**: 577–585. doi:10.4319/lo.1998.43.4.0577.

McClelland, J.W., Valiela, I., and Michener, R.H. 1997. Nitrogen-stable isotope signatures in food webs: a record of increasing urbanization in coastal watersheds. Limnol. Oceanogr. **42**: 930–937. doi:10.4319/lo.1997.42.5.0930.

Monteiro, R.M. 2011. Land use effects on anadromous alewife in the Gulf of Maine: Beyond conventional fisheries considerations. Ph.D. thesis, College of Environmental Science and Forestry, State University of New York, Syracuse, New York, USA.

Moring, J. 2005. Recent trends in anadromous fishes. *In* The decline of fisheries resources in New England: evaluating the impact of overfishing, contamination, and habitat degradation. *Edited by* R. Buchsbaum, J. Pederson, and W.E. Robinson. MIT Sea Grant College Program Publication, Cambridge, Mass., USA. pp. 25–42.

NOAA Fisheries, Fisheries Statistics Division. 2018. Annual commercial landings statistics. Available from https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index [accessed 11 October 2018].

Oczkowski, A., and Nixon, S. 2008. Increasing nutrient concentrations and the rise and fall of a coastal fishery: a review of data from the Nile Delta, Egypt. Estuar. Coast. Shelf Sci. **77**: 309–319. doi:10.1016/j.ecss.2007.11.028.

Oczkowski, A., Markham, E., Hanson, A., and Wigand, C. 2014. Carbon stable isotopes as indicators of coastal eutrophication. Ecol. Appl. **24**: 457–466. doi:10.1890/13-0365.1. PMID:24834733.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320. doi:10.1146/annurev.es.18.110187.001453.

Pope, K.L., and Kruse, C.G. 2007. Condition. *In* Analysis and interpretation of freshwater fisheries data. *Edited by* C.S. Guy and M.L. Brown. American Fisheries Society, Bethesda, Md., USA. pp. 423–471.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Reynolds-Vargas, J., Fraile-Merino, J., and Hirata, R. 2006. Trends in nitrate concentrations and determination of its origin using stable isotopes ($^{18}O$ and $^{15}N$) in groundwater of the western Central Valley, Costa Rica. Ambio, **35**: 229–236. doi:10.1579/05-R-046R1.1. PMID:16989507.

Rice, J.A., Crowder, L.B., and Binkowski, F.P. 1985. Evaluating otolith analysis for bloater *Coregonus hoyi*: Do otoliths ring true? Trans. Am. Fish. Soc. **114**: 532–539. doi:10.1577/1548-8659(1985)114<532:EOAFBC>2.0.CO;2.

Richkus, W.A. 1975. Migratory behavior and growth of juvenile anadromous alewives, *Alosa pseudoharengus*, in a Rhode Island drainage. Trans. Am. Fish. Soc. **104**: 483–493. doi:10.1577/1548-8659(1975)104<483:MBAGOJ>2.0.CO;2.

Savoie, J. 1995. Altitude and configuration of the water table, western Cape Cod aquifer, Massachusetts, March 1993. U.S. Geological Survey Open-File Report 94-462.

Sherwood, G.D., and Rose, G.A. 2005. Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. Estuar. Coast. Shelf Sci. **63**: 537–549. doi:10.1016/j.ecss.2004.12.010.

Smith, S.V., Swaney, D.P., Talaue-McManus, L., Bartley, J.D., Sandhei, P.T., McLaughlin, C.J., et al. 2003. Humans, hydrology, and the distribution of inorganic nutrient loading to the ocean. BioScience, **53**: 235–245. doi:10.1641/0006-3568(2003)053[0235:HHATDO]2.0.CO;2.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. **60**: 1129–1157.

Turner, S.M., and Limburg, K.E. 2016. Juvenile river herring habitat use and marine emigration trends: comparing populations. Oecologia, **180**: 77–89. doi:10.1007/s00442-015-3443-y. PMID:26369780.

Twining, C.W., West, D.C., and Post, D.M. 2013. Historical changes in nutrient inputs from humans and anadromous fishes in New England's coastal watersheds. Limnol. Oceanogr. **58**: 1286–1300. doi:10.4319/lo.2013.58.4.1286.

Ulseth, A.J., and Hershey, A.E. 2005. Natural abundances of stable isotopes trace anthropogenic N and C in an urban stream. J. N. Am. Benthol. Soc. **24**: 270–289. doi:10.1899/03-080.1.

Utz, R.M., Hilderbrand, R.H., and Raesly, R.L. 2010. Regional differences in patterns of fish species loss with changing land use. Biol. Conserv. **143**: 688–699. doi:10.1016/j.biocon.2009.12.006.

Valiela, I. 2015. Marine ecological processes. 3rd ed. Springer-Verlag, New York, USA.

Valiela, I., Foreman, K., LaMontagne, M., Hersh, D., Costa, J., Peckol, P., et al. 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries, **15**: 443–457. doi:10.2307/1352389.

Valiela, I., Collins, G., Kremer, J., Lajtha, K., Geist, M., Seely, B., et al. 1997. Nutrient loading from coastal watersheds to receiving estuaries: new method and application. Ecol. Appl. **7**: 358–380. doi:10.1890/1051-0761(1997)007[0358:NLFCWT]2.0.CO;2.

Vander Zanden, M.J., Vadeboncoeur, Y., Diebel, M.W., and Jeppesen, E. 2005. Primary consumer stable nitrogen isotopes as indicators of nutrient source. Environ. Sci. Technol. **39**: 7509–7515. doi:10.1021/es050606t. PMID:16245822.

Walters, A.W., Barnes, R.T., and Post, D.M. 2009. Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. Can. J. Fish. Aquat. Sci. **66**(3): 439–448. doi:10.1139/F09-008.

Wang, L., Lyons, J., Kanehl, P., and Gatti, R. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries, **22**: 6–12. doi:10.1577/1548-8446(1997)022<0006:IOWLUO>2.0.CO;2.

Yako, L.A., Mather, M.E., and Juanes, F. 2002. Mechanisms for migration of anadromous herring: An ecological basis for effective conservation. Ecol. Appl. **12**: 521–534. doi:10.1890/1051-0761(2002)012[0521:MFMOAH]2.0.CO;2.

Yoder, C.O., Miltner, R.J., and White, D. 1999. Assessing the status of aquatic life designated uses in urban and suburban watersheds. *In* Retrofit opportunities for water resource protection in urban environments: a national conference, Chicago, Ill., USA. pp. 16–28. EPA/625/R-99/002.